

NEMATODE MANAGEMENT IN COTTON

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Abstract. The five most important cotton-producing countries are China, United States, India, Pakistan, and Brazil. There are many other important cotton producing regions in Asia, Australia, Africa and the Americas. Cotton is grown entirely in tropical, subtropical, and warm-temperature climates, and the major nematodes of cotton are well adapted to warm environments. Globally, the most damaging nematodes of cotton are *Meloidogyne incognita* races 3 and 4 and *Rotylenchulus reniformis*. These nematodes are of concern in the United States, India, Pakistan, Egypt and Brazil. Additional nematodes of major importance in relatively restricted areas include *Hoplolaimus columbus* and *Belonolaimus longicaudatus* in the southeastern United States and *Pratylenchus brachyurus* in Brazil. *Meloidogyne incognita* frequently is involved in a cotton disease complex with Fusarium wilt that has far more impact on the crop than the nematode or the fungus alone. Until very recently, the primary strategies used for nematode management in cotton have been the application of fumigants and cholinesterase inhibitors, rotation with *Zea mays*, *Arachis hypogaea* or *Glycine max* and incorporation of soil amendments. The primary concern over *P. brachyurus* in Brazil is its potential to damage *Z. mays* or *G. max* grown in rotation with cotton. Promising seed treatments containing avermectin or harpin proteins have recently become available. Several cultivars resistant to *Meloidogyne incognita* races 3 and 4 have been released. Currently there is intense research toward the introgression of resistance to *R. reniformis* into upland cotton, *Gossypium hirsutum* from other *Gossypium* species. During the last two years DNA markers for major genes for resistance to *Meloidogyne incognita* and *Rotylenchulus reniformis* have been discovered in upland cotton and offer great potential in the development of resistant cultivars suitable for the wide range of growing conditions where cotton is produced.

1. INTRODUCTION

The most economically important nematode pathogens of cotton are *Meloidogyne incognita* (host races 3 and 4) and *Rotylenchulus reniformis*. Other species known to damage cotton include *Belonolaimus longicaudatus*, *Hoplolaimus columbus*, *Pratylenchus brachyurus* and *Meloidogyne acronea*. Additional nematodes associated with cotton include *Hoplolaimus aegypti*, *H. galeatus*, *H. indicus*, *H. seinhorsti*, *Longidorus* sp., *Paratrichodorus* sp., *Rotylenchulus parvus* (Louw, 1982), *Scutellonema* sp., and *Xiphinema* sp. Previous reviews of cotton nematodes include Blasingame (1994); Bridge (1992); Da Ponte, Jilho, Lordello, and Lordello (1998); Garber, DeVay, Goodel, and Roberts (1996); Heald and Orr (1984); Koenning et al. (2004); Lawrence and McLean (2001); Mueller and Lewis (2001); Overstreet and McGawley (2001); Robinson et al. (2001); Sasser (1972); Starr (1998); Starr and Page (1990); Thomas and Kirkpatrick (2001) and Veech (1984).

Starr's (1998) review provides an excellent, detailed comparison of the biology of the four major nematodes of cotton.

For those unfamiliar with nematodes, they comprise the animal phylum Nematoda and are commonly known as roundworms. They are unsegmented, multicellular animals with several hundred neurons and several simple organ systems (Maggenti, 1981). Most are microscopic. More than 10 000 species of nematodes occupy a diverse variety of terrestrial, marine, and parasitic niches. They are the most ubiquitous of all multicellular terrestrial animals. In cultivated fields, virtually every liter of soil will contain many nematodes, and usually several species. Most nematodes are vermiform (worm-like) throughout life, but parasitic stages of some species are swollen or even globose. Plant-parasitic nematodes have a stylet with which they perforate plant cells and ingest nutrients. Nematode stylets are minute, and most have a bore small enough to serve as a bacterial filter. Most plant parasitic nematodes are obligate plant parasites and can only feed on roots or foliage of vascular plants.

2. GEOGRAPHICAL DISTRIBUTION AND ECONOMIC IMPACT

Meloidogyne incognita (the southern root-knot nematode) and *Rotylenchulus reniformis* (the common reniform nematode) occur in tropical, subtropical, and warm temperate soils throughout most of the world, generally within 35° of the equator (Robinson et al., 2001; Taylor & Sasser, 1978). One or both species are present in most cotton-producing regions and are considered to be serious problems in cotton production wherever they occur.

In the United States, *M. incognita* is found on cotton in all cotton-producing states, and *R. reniformis* occurs only in states east of New Mexico (Heald & Robinson, 1990; Koenning et al., 2004; Lawrence & McLean, 1996; Robinson, 2007). There is current concern in the United States regarding recent increase in incidence and severity of *R. reniformis* infestations in the central cotton belt of the United States (Blasingame & Patel, 1987; Gazaway & McLean, 2003; Overstreet & McGawley, 2000; Robinson, 2007). The two remaining economically important cotton nematodes in the United States, *H. columbus* (the Columbia lance nematode) and *B. longicaudatus* (the sting nematode), both occur primarily in sandy soils in the Coastal Plain regions extending across North Carolina, South Carolina, and Georgia.

Meloidogyne incognita has been reported on cotton in numerous areas in Brazil, Africa, the Middle East, India, and China. A related root-knot nematode, *M. acronea*, is known to damage cotton in the Shire valley of Malawi (Africa) and in Cape Providence, South Africa (Starr & Page, 1990). A very high incidence (94%) of *Pratylenchus brachyurus* in cotton is of great concern in Mato Grosso do Sul, Brazil, due to its potential impact on corn and soybean grown in rotation with cotton (Da Silva et al., 2004). Of 184 samples collected from 15 'municípios' (roughly comparable to counties) in Mato Grosso do Sul State in Brazil, 28% and 17% were positive for *M. incognita* and *R. reniformis*, with 45% and 32% of those samples, respectively, above the damage threshold (Asmus, 2004).

Worldwide cotton yield losses due to nematodes were estimated to be 10.7% by Sasser and Freckman (1987), which was equivalent to 1.9 million metric tons of

cotton lint worth \$US 4 billion at 1987 prices. United States losses were estimated by the National Cotton Council of America (Blasingame, 2006) to be 1 178 000 bales (4.7%), valued at approximately \$US 550 million.

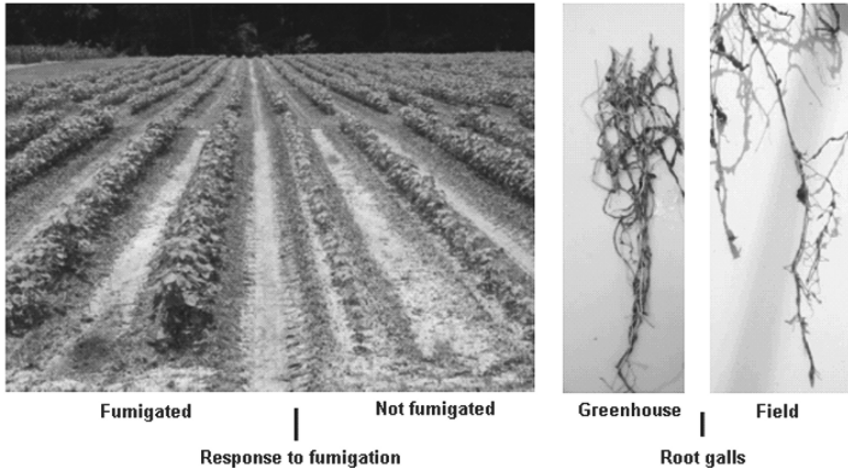


Figure 1. *Meloidogyne incognita* damage to cotton, Georgia, U.S.A. (courtesy of R. F. Davis).

3. SYMPTOMATOLOGY

3.1. *Meloidogyne* spp.

Distributions of *M. incognita* within fields usually are uneven and scattered (Blasingame, 1994; Thomas & Kirkpatrick, 2001). Infested areas (Fig. 1) are oblong in the direction of cultivation and are often 7–13 m long and 3–10 m wide. Infested areas within a field typically suffer 75–100% damage while other areas in the same field will show no symptoms. Earliest and greatest damage occurs on plants under water stress in the sandiest parts of a field. Severely infected plants often are half the height of normal plants, tend to appear nitrogen-deficient and wilt under drought stress, several days before symptoms appear in uninfected plants. Co-infection with *M. incognita* and the *Fusarium* wilt fungus, *Fusarium oxysporum* f. sp. *vasinfectum*, often kills plants; plants infected with only *M. incognita* rarely die. Symptoms of *M. incognita* are usually expressed first in sandier areas of the field.

The most obvious symptoms are galls on secondary roots (Blasingame, 1994; Shepherd & Huck, 1989; Thomas, 2001). Galls on cotton are typically smaller than on tomato and okra. Taproots and secondary roots often branch prematurely or abort, forming terminal galls (Fig. 1). Root systems are deficient in fibrous feeder roots and typically grow less than half as deep as root systems of healthy cotton plants. The galls mimic natural physiological sinks and compete with the rest of the plant for photosynthetic assimilates (Abrão & Mazzafera, 2001; Esau, 1977; Jones & Northcote, 1972).

Meloidogyne acronea, which has been reported only from Africa, has been studied less than *M. incognita*, but field symptoms and damage are generally similar to that observed for *M. incognita*. A notable difference is that the sedentary adult females of *M. acronea* protrude from the root surface, unlike the adult females of *M. incognita*, which generally are embedded in the root tissue (Page, 1985).

3.2. *Rotylenchulus reniformis*

Distributions and stunting symptoms within fields tend to be irregular in new infestations but uniform in old ones, so that the existence of a problem is less obvious (Blasingame, 1994; Heald & Heilman, 1971; Lawrence & McLean, 2001). In the United States, yield losses in infested fields commonly are less than 10% but may exceed 50% if the crop has been water-stressed. Under ideal growing conditions, it is possible for infected plants to exhibit no foliar symptoms at all. More often, however, plants stop rapid growth at the three or four leaf stage (Fig. 2), as if stunted hormonally, leaves take on a light or off green color, typical of potassium deficiency, and flowering and fruit set are delayed two nodes up the main stem.



Figure 2. Cotton fields infested with *Rotylenchulus reniformis* in Alabama (A) and Louisiana (B) (courtesy W. S. Gazaway and C. Overstreet).

Nematodes along roots can be detected with the unaided eye only by observing clumps of sand grains adhering to the gelatinous egg masses surrounding sedentary gravid females protruding from the root surface (Heald & Orr, 1984). Dirt particles remain after gently rinsing roots, making roots look dirty. Otherwise, nematode-infected root systems can appear more or less normal on casual inspection, perhaps with some loss of secondary roots, but without any galls, severely stunted taproots, or forked secondary roots characteristic of root-knot nematode infection on cotton. The primary symptoms, which are visible only with a microscope following special tissue preparation and staining, are extensive hypertrophy and dysfunction of the endodermal and pericyclic cell layers enclosing the vascular cylinder, and consequent blockage of water and nutrient uptake (Cohn, 1973).

3.3. *Hoplolaimus columbus*

This nematode occurs in sandy soils in the southeastern United States. Distributions within fields, like those of *M. incognita*, are uneven and scattered. Infested areas are usually oblong in the direction of cultivation, 7–17 m long and 3–10 m wide (Blasingame, 1994; Mueller & Lewis, 2001). In the United States, yield losses within infested fields are typically 10–25% but may exceed 50% in sandy fields under water stress. Severely infected plants may be stunted 50% or more and wilt under drought stress several days prior to uninfected plants. Leaves often exhibit nutrient deficiency symptoms – in particular, slight to moderate chlorosis characteristic of nitrogen deficiency. *Hoplolaimus columbus* typically feeds on the root tip of the radicle immediately following seed germination and on secondary roots as they develop, resulting in severely stunted root systems that penetrate only 7–10 cm deep, compared to 30 cm in healthy plants.

Other species of *Hoplolaimus* are not generally considered to be pathogenic to cotton but comparative studies are lacking. *Hoplolaimus galeatus* and *H. magnistylus* appear to be commonly encountered in cotton in the United States. Careful studies in Arkansas showed that *H. magnistylus* was not a serious pest of cotton (Robbins, McNeely, & Lorenz, 1998).

3.4. *Belonolaimus longicaudatus*

This nematode is limited primarily to soils containing more than 85% sand (Esser, 1976; Graham & Holdeman, 1953; Robbins & Barker, 1974). Heavy infestations in cotton fields cause stunted, chlorotic growth followed by premature wilting and senescence. Root systems are poorly developed and have dark, sunken lesions along the root axis that can spread laterally to girdle the root and cause it to break off. Although *B. longicaudatus* has a much more restricted geographical distribution than *M. incognita*, *R. reniformis* and *H. columbus*, it is a devastating parasite of cotton where it occurs in the United States, often killing all or most of the plants in large areas of infested fields (Sasser, 1972). It is particularly damaging in fields where *F. oxysporum* f. sp. *vasinfectum* is present.

4. BIOLOGY AND EPIDEMIOLOGY

4.1. *Meloidogyne incognita* and *M. acronea*

Important differences between root-knot nematodes of cotton are noted, as appropriate.

4.1.1. Life Cycle

Meloidogyne incognita and *M. acronea*, like other plant-parasitic nematodes, have four juvenile stages between the egg and the adult (Taylor & Sasser, 1978). Molting in *M. incognita* occurs between stages as the nematode increases in size. One molt occurs within the egg and three subsequently. The second-stage juvenile (J2) that

emerges from the egg is the motile, infective stage. It is vermiform, 0.30–0.4 mm. long, developmentally arrested, non-feeding and contains a large reserve of lipid stores within the cells of the intestine, which sustains it while in the soil.

After hatching from eggs, J2 move through soil and invade root tissue, usually near the root tip (Taylor & Sasser, 1978) or invade in the zone of elongation and migrate through the cortex toward the root tip (McClure & Robertson, 1973), where they stop and feed permanently on several contiguous protoxylem cells. In susceptible plants, feeding results in the transformation of these cells into greatly hypertrophied and globose nurse cells, referred to as giant cells. These cells are characterized by intense nuclear, ribosomal and mitochondrial proliferation indicative of accelerated metabolic activity, and they have been likened to the transfer cells involved in phloem loading and unloading in fruiting structures and other metabolic sinks in numerous plants (Bird, 1996; Esau, 1977; Jones & Northcote, 1972; Pate & Gunning, 1972). Each giant cell is multinucleate as a result of nuclear without cytoplasmic division.

During the next several weeks, the surrounding tissue differentiates and undergoes extensive hypertrophy and hyperplasia, forming a gall. The nematode molts three times, greatly enlarging during successive molts into a sausage-like shape and then a spheroid shape, about the size of a pin head. When this stage is reached, the female body of *M. incognita* remains almost completely embedded in root tissue, with only the posterior tip exposed, whereas much of the body of *M. acronea* protrudes from the root. Between 500 and 3 000 eggs (0.08×0.04 mm) are laid into a gelatinous matrix secreted at the root surface. The final molt in *M. incognita* occasionally produces a male, which is vermiform and many times larger than the J2 from which it grew. Adult males of *M. incognita* do not feed and are not required for reproduction. The eggs produced by females develop into embryos following mitotic parthenogenesis. At favorable temperatures ($\sim 30^{\circ}\text{C}$) the life cycle is complete in 21–30 days (Taylor & Sasser, 1978).

The life cycle of *M. acronea* is generally similar to that of *M. incognita*; however, *M. acronea* reproduces sexually. Males of *M. acronea* are common and protrusion of adult females from roots probably facilitates insemination (Jepson, 1987; Page, 1985).

4.1.2. Interactions

M. incognita aggravates fungal seedling diseases by providing portals of entry and delaying taproot growth (Heald & Orr, 1984; Walker et al., 1998, 1999). More importantly, *M. incognita* greatly increases the severity and incidence of Fusarium wilt by the fungus *F. oxysporum* f. sp. *vasinfectum* (Devay et al., 1997; Martin et al., 1956; Starr, Wheeler, & Walker, 2001). How predisposition to the fungus occurs is uncertain. However, galling causes extensive longitudinal cracking of the epidermis and cortex of cotton roots, which may facilitate fungal invasion (Shepherd & Huck, 1989). The *Fusarium* wilt/root-knot nematode disease complex frequently results in death of many plants in a field. In fields where only the nematode is present, plants are stunted but seldom killed (Blasingame, 1994). *Meloidogyne incognita*

also increases susceptibility to Verticillium wilt, but the effect is less pronounced than with Fusarium (Katsantonis, Hillocks, & Gowen, 2003).

4.1.3. Genetic Variability

The reproductive potentials of isolates of *M. incognita* vary differentially on different plant genotypes. Isolates differing in host specificity can come from widely separated localities or from the same field. Crop rotation practices in Atlantic coast states of the United States revealed isolates that could be assigned to one of four host races, depending on their ability to reproduce on cotton and the resistant tobacco (*Nicotiana tabacum*) cultivar NC-95 (Taylor & Sasser, 1978). Populations reproducing only on cotton were considered race 3 and those reproducing on both cotton and NC-95 were considered race 4. Most populations of *M. incognita* on cotton in the United States are race 3, whereas race 4 is commonly reported from South Africa and India (Jaskaran et al., 2000). There is evidence of variability among populations in California in ability to reproduce on resistant NemX (Ogallo et al., 1997, 1999). The reproductive rates of populations from Texas on cotton also differ (Zhou, Wheeler, & Starr, 2000).

4.2. *Rotylenchulus reniformis*

A second species of *Rotylenchulus*, *R. parvus*, has been reported on cotton from Africa. However, this discussion is restricted primarily to *R. reniformis*.

4.2.1. Life Cycle

Parasitic stages of the reniform nematode are similar in size to the J2 of *M. incognita*, and the reproductively mature females also are sedentary parasites of the stele (Gaur & Perry, 1991; Robinson, 2002, 2007; Robinson et al., 1997). However, there are important differences in their life cycles.

After hatching from the egg, the J2 remains vermiform and undergoes three additional molts before it can invade plant tissue and feed. Each molt yields a slightly smaller worm (Bird, 1983), and the final molt produces a vermiform, sexually differentiated adult. Populations of *R. reniformis* encountered on cotton are obligately amphimictic, and equal numbers of males and females are produced. Only females feed and they invade the cortex of roots that have already undergone primary differentiation, most commonly in the zone of elongation, although nematodes are found all along roots (Birchfield, 1962; Cohn, 1973; Heald, 1975; Rebois, Madden, & Eldridge, 1975; Robinson & Orr, 1980). The vermiform female does not migrate through cortical tissue along the length of the root like the J2 of *M. incognita*, but rather enters the cortex perpendicular to the root axis and comes to rest with the stoma pressed to the outer tangential wall of a single, usually endodermal, cell on which it feeds. This cell and a curved sheet of contiguous cells of the pericycle, undergo cell wall dissolution and slight hypertrophy without hyperplasia, producing a simple syncytium that nurses the developing female. In

contrast to the localized, globose giant cells induced by *M. incognita*, the *R. reniformis* syncytium often extends several root diameters along the root axis and a gall is not formed. Syncytial cells have enlarged nuclei and nucleoli, safraninophilic cytoplasm, and extensive proliferation of rough endoplasmic reticulum indicative of accelerated metabolism (Rebois et al., 1975).

Many cells, perhaps more than 100, can be involved in a single syncytium, so that when multiplied by the hundreds or thousands of females feeding on a single plant, the cumulative effect can be extensive. Within 6–14 days of root penetration, depending on temperature, the female becomes reproductively mature and, if inseminated, begins to deposit eggs into a gelatinous egg matrix (Rodríguez-Fuentes & Añorga-Morles, 1977; Sivakumar & Seshadri, 1971) similar to that of *M. incognita*. However, the neck elongates sufficiently that the swollen, kidney-shaped posterior two thirds of the body remains completely outside the root, exposed to the soil. The fully grown adult female is less than half the size of an *M. incognita* female, and the total number of eggs produced (60–200) is correspondingly smaller (Sivakumar & Seshadri, 1971). Paradoxically, *R. reniformis* usually occur in soil at population densities several times higher than *M. incognita*, which likely results from *R. reniformis* having a greater effective biotic potential due to a faster life cycle and greater number of potential feeding courts. There are more potential feeding sites for *R. reniformis* than for *M. incognita* on a cotton root system because *R. reniformis* interferes less with the development of fibrous roots, by initiating feeding sites within root zones that have already undergone primary differentiation.

Rotylenchulus reniformis is notorious for its ability to survive desiccation (Sehgal & Gaur, 1988, 1989; Womersley & Ching, 1989). The life cycle of *R. parvus* is similar to that of *R. reniformis* except that *R. parvus* reproduces parthenogenetically, and males are rare (Louw, 1982).

4.2.2. Interactions

Rotylenchulus reniformis can increase the incidence and severity of seedling diseases (Palmatee, Lawrence, VanSanten, & Morgan-Jones, 2004; Sanaralingham & McGawley, 1994) and may increase the incidence and severity of Fusarium wilt, although not to the extent of *M. incognita* (Brodie & Cooper, 1964; Khadr et al., 1972; Neal, 1954). It also has been reported to increase the incidence of Verticillium wilt, caused by the fungus *Verticillium dahliae* (Prasad & Padeganur, 1980). *Hoplotaimus columbus* appears to suppress *M. incognita* but not *R. reniformis* in sandy soils of the southeastern United States (Blasingame, 1994; Mueller & Lewis, 2001). *Rotylenchulus reniformis* may occur in sandy soils as well as finely textured soils but tends to occur at high populations in Texas only in soils with less than 40% sand (Robinson, Heald, Flanagan, Thames, & Amador, 1987; Starr, Heald, Robinson, Smith, & Krause, 1993). Pot studies confirm competition between *M. incognita* and *R. reniformis* (Diez, Lawrence, & Lawrence, 2003; Koenning, Walters, & Barker, 1996).

4.2.3. Genetic Variability

Less research has been done examining genetic variability in *R. reniformis* than in *M. incognita*. Some populations in India can and others cannot reproduce on both castor (*Ricinus communis*) and upland cotton, and these two groups of populations have been designated as races (Dasgupta & Seshadri, 1971a, 1971b). One population from India reproduces on sugarcane (Mehta & Sundara, 1989), a crop species immune to *R. reniformis* populations in Hawaii (Linford & Yap, 1940), Louisiana (Birchfield & Brister, 1962) and Puerto Rico (Ayala, 1962; Roman, 1964). Differences in reproduction and damage caused by 17 populations of *R. reniformis* from the United States on certain cultivars of cotton and soybean also have been observed (McGawley & Overstreet, 1995).

4.3. *Hoplolaimus columbus*

Hoplolaimus columbus is one of the largest nematodes in the genus *Hoplolaimus* (Mueller, 1993). It reproduces parthenogenetically, like *M. incognita*, and males are rare. However, it remains vermiform throughout life and feeds ectoparasitically as well as endoparasitically while migrating through roots. Root damage results from mechanical destruction of tissue, induction of necrosis and production of portals of entry for fungi and bacteria (Mueller, 1993; Mueller & Lewis, 2001).

4.4. *Belonolaimus longicaudatus*

Belonolaimus longicaudatus feeds ectoparasitically on root tips and cortical tissues and remains vermiform throughout life (Mueller & Sullivan, 1988). Although it does not invade tissue, adults are very large (1.6–2.6 mm) and have a large stylet that is more than half as long as the entire body of the J2 of *M. incognita* (Overstreet & McGawley, 2001; Robbins & Barker, 1974; Thorne, 1961). *Belonolaimus longicaudatus* is amphimictic.

5. MANAGEMENT

5.1. Sampling and Economic Thresholds

5.1.1. *Meloidogyne incognita*

Diagnostic soil and plant samples taken during midseason and fall are generally considered the best option for making management decisions (Starr, 1998). The presence of galling after midseason correlates highly with the distribution of *M. incognita* in a field, permitting areas that may require chemical treatment to be identified (Blasingame, 1994). Determining whether populations are sufficiently high to warrant treatment is more difficult. Both eggs and J2s contribute to over winter survival (Starr & Jeger, 1985). Eggs of *M. incognita* in the soil usually reach maximum numbers at harvest (Starr & Jeger, 1985) whereas J2 populations in soil continue to climb as eggs hatch during the fall, becoming more numerous than eggs, then decline faster than eggs during the winter so that eggs and J2 densities in the

soil are similarly low and often undetectable by spring. As a consequence, there are more eggs than J2 between May and October, and more J2 than eggs between November and April.

As a practical matter, a decision to apply nematicide or plant a resistant cultivar needs to be made well before planting time, and if the population in a field is not evaluated until near the end of the winter, both eggs and J2 will be at such low densities that a reliable measure of the density in the field may not be obtained. Field studies in California (Roberts & Matthews, 1984) and micro-plot studies in Texas (Starr, Jeger, Martyn, & Schilling, 1989) estimated spring time damage thresholds of 0.05–0.1 J2/cm³ soil. This is such a low density that some consultants consider detection of a single J2 in the spring sufficient basis for treatment. Because populations are so low in the spring, J2 population densities in the fall are often used as a predictor of damage resulting from the *M. incognita* eggs and J2 that will survive the winter. The recommended fall damage threshold for applying nematicides to control *M. incognita* in most cotton producing regions of the southeastern United States is 0.5–1 J2/cm³ soil. Populations this high at planting are quite damaging. Pot studies in soil naturally infested with *M. incognita* at 0.96 and 1.08 J2/g soil in India, for example, showed yield responses to carbofuran nematicide (2.0 kg a.i./ha) of 10% and 18%, respectively.

The University of California offers farmers and consultants a mathematical crop damage function relating J2 population density – at or soon after harvest – to percentage yield loss in the following spring. Losses predicted by this model for 0.15, 0.3 and 0.6 J2/g soil, respectively, are 5%, 11% and 22% (Garber et al., 1996; Goodell, McClure, Roberts, & Thomas, 1996). Alternatively, California farmers are offered a weighted gall rating technique whereby plants with 0%, 1–25%, 26–50%, 51–75% and 76–100% of their root systems galled are assigned ratings, respectively, of 0, 1, 2, 5, and 7. Numeric ratings for a collection of randomly selected root systems are averaged to obtain an index value that is used for recommending treatment (Garber et al., 1996; Goodell, et al., 1996).

Variable rate application of nematicides for *M. incognita* control in cotton is intriguing because damage is typically patchy within a field, but obtaining requisite nematode population data cost-effectively may be impossible (Wheeler, Baugh, Kaufman, Schuster, & Siders, 2000; Wrather, Stevens, Kirkpatrick, & Kitchen, 2002). Measurement of soil electrical conductivity, however, shows promise as a tool for rapidly and cheaply characterizing the distribution of projected damage from *M. incognita* across large fields (Wolcott et al., 2005). Recent technological innovations have led to increased use in cotton of yield mapping during harvesting, by means of harvester-mounted lint sensors integrated to a computer and global positioning sensors on board the farm tractor. In fields where nematode damage appears to occur in the same spots of the field every year, it is possible to fumigate test strips across a large field perpendicular to row direction before bedding and planting. Yield mapping of the crop produced can then be used to provide a database for site-specific nematicide application to the next year's crop.

5.1.2. *Rotylenchulus reniformis*

Several field and pot studies show that damage from *R. reniformis* to cotton can be expected when soil populations during seedling growth are between 1 and 10 nematodes/cm³ soil, equivalent to 0.8 and 8 nematodes per gram soil at 1.25 specific gravity (Elgawad, Ismail, & El-Metwally, 1997; Gilman, Jones, Williams, & Birchfield, 1978; Palanisamy & Balasubramanian, 1983; Patel, Patel, & Thakar, 2004; Sud, Varaprasad, Seshadri, & Kher, 1984; Thames & Heald, 1974). Because survival over winter is high, end-of-season samples are reliably used as the basis for nematode management decision in the next year's cotton crop. Treatment thresholds in use by consultants and farmers in the United States vary with growing conditions from about 8 to 16 nematodes/g soil collected at the end of the previous season (Koenning, 2002; Komar, Wiley, Kermerait, & Shurley, 2003; Overstreet, 2001; Sciumbato, Blessitt, & Blasingame, 2004). When spring samples are used, the treatment threshold employed is 20% 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. Diagnostic labs often are overwhelmed with samples in the fall; however, studies in Alabama (Lawrence et al., 2005a) have shown that a sample can be stored at 4°C for up to 180 days, and the original nematode density at the time when placed in storage can be calculated.

5.1.3. *Hoplolaimus columbus*

Soil populations of *H. columbus* in the restricted areas of the eastern United States where it occurs, typically do not decline until late winter (Blasingame, 1994; Mueller & Lewis, 2001). The economic threshold for undisturbed soil in the fall and early winter is one nematode/cm³ soil, and in the spring 0.3 nematode/cm³ soil. If the field has been disked or plowed, the threshold is 0.1 nematode/cm³ soil. *H. columbus* occurs in high numbers in roots but during much of the year sufficient numbers are present in soil to use extracted nematodes as an acceptable indicator of the total number present (Davis & Noe, 2000).

5.1.4. *Belonolaimus longicaudatus*

This nematode is very large and strong, and is devastating to a cotton crop at very low population densities. Thresholds in Florida field experiments ranged from 0.015–0.039 nematodes/cm³ soil, and a soil population of 0.8 nematodes/cm³ was sufficient to expect 100% yield loss (Crow, Weingartner, McSorley, & Dickson, 2000b). In controlled environmental chambers, 0.08 and 0.40 nematodes/cm³ soil reduced cotton fine roots by 39% and 70%, respectively (Crow, Dickson, Weingartner, McSorley, & Miller, 2000a).

5.2. Control

5.2.1. Natural Physical Factors

The temperature, texture, compaction and moisture of soil can profoundly influence the survival and population dynamics of nematodes parasitizing cotton. *M. incognita*

and *R. reniformis* generally occur at latitudes within 35° of the equator and have optimum temperatures for movement (Robinson, 1989, 1994; Robinson & Heald, 1989, 1991, 1993) and reproduction (Rebois, 1973; Taylor & Sasser, 1978) between 27°C and 32°C. However, survival in fallow soil is greatly prolonged at 10°C, while temperatures exceeding 45°C are lethal to hydrated eggs and juveniles (Heald & Robinson, 1987). In some regions soil texture is differentially correlated with the distributions of these two species. In Texas, high population densities of *M. incognita* were commonly found in soils with a wide range of sand content (10–90%) but were infrequently found in soils with more than 60% clay (Robinson et al., 1987; Starr et al., 1993) and high population densities tended to occur only in sandy soils. High population densities of *R. reniformis*, by comparison, tended to occur in soils with less than 50% sand.

In the United States, *B. longicaudatus* appears to be limited to the Coastal Plain of the Atlantic seaboard and occurs at damaging population densities almost exclusively in soils with greater than 85% sand (Esser, 1976). The vermiform stages of *R. reniformis* but not the J2 of *M. incognita* can survive for several years in soils dried below the permanent wilting point for plants (Birchfield & Martin, 1967; Heald & Inerra, 1988; Rodríguez-Fuentes, 1980; Tsai & Apt, 1979; Womersley & Ching, 1989). The ensheathed juveniles of *R. reniformis* may be better adapted for desiccation survival than the exsheathed vermiform females or the newly hatched vermiform J2.

5.2.2. Nematicides

The statement made by Sasser (1972) 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 gone. In the United States, the primary nematicides remaining available for use in cotton include the fumigants 1,3-dichloropropene and metam sodium and the cholinesterase inhibitors aldicarb and oxamyl (Gazaway et al., 2001; Koenning et al., 2004; Lawrence & McLean, 2000; Lawrence, McLean, Batson, Miller, & Borbon, 1990; Lawrence et al., 2005). Where it occurs naturally, cotton is a perennial with a fast-growing, deep taproot. Today as in 1972 (Sasser), the nematicide strategy for all nematodes in cotton is to save nematicide costs by focusing on protection of the young plant, and target the soil zone that the taproot will grow through during the first few weeks. This means fumigant placement 25–45 cm deep under the center of the bed, or granular nematicide either in the seed furrow or else band-incorporated over the top of the planting bed, with the option to also side-dress later.

5.2.2.1. Conventional Nematicides

Many nematicide efficacy tests have been conducted in cotton and the population suppression and yield responses obtainable with labeled rates have been well characterized, as have the economics (Gazaway et al., 2001; Kinloch & Rich, 2001; Lawrence et al., 1990; Overstreet & Erwin, 2003; Palanisamy & Balasubramanian, 1983; Thames and Heald, 1974; Zimet, Rich, LaColla, & Kinloch, 1999; Zimet, Smith, Kinloch, & Rich, 2002). The nematicide applications usually recommended

for managing nematodes in cotton in the United States are similar for *R. reniformis*, *M. incognita* and *H. columbus*. Nematicide application is recommended only when losses are expected to exceed 5%. Recommended rates of Nemacur (fenamifos) 15G and Temik 15G brand aldicarb are the same, 5.6–7.8 kg a.i./ha applied at-plant, often in-furrow. The rate usually recommended for 1,3-dichloropropene (Telone II) is 28 liters/ha applied 10–14 days pre-plant, preferably in the temperature range 16–25°C and usually followed by a low rate of Temik 15G at plant. Soil temperature and moisture optimal for planting are ideal for fumigation but a delay is required to avoid phytotoxicity (Heald & Orr, 1984). In California, a second application of 5.6–7.8 kg a.i./ha Temik 15G is sometimes side-dressed at first square (Garber et al., 1996; Goodell, et al., 1996). In Brazil, terbufos 150G (2.55 kg a.i./ha) has been found to be highly effective against *R. reniformis* and *P. brachyurus*, suppressing populations 93% and 97%, and increasing yields 38–49% (Gonçalves de Oliveira, Kubo, Siloto, & Raga, 1999). Foliar applications of oxamyl have also been used in cotton with good success in some regions (Lawrence & McLean, 2000).



Figure 3. Cotton yields in *R. reniformis* infested fumigated soils in Texas (A, C) and Louisiana (B, D) (plants on left in each photo were fumigated). B, D: courtesy C. Overstreet.

In the United States, granular in-furrow application of a sub-nematicidal rate of aldicarb is widely used prophylactically for early season insect control, and the cost of stepping up the rate (to 5.6–7.8 kg a.i./ha) for nematode control is low. Unfortunately the benefits typically are inferior to fumigation (Gazaway et al., 2001), consistent with the rule of thumb in cotton, that fumigants (Fig. 3) are more effective than granular nematicides (Orr & Brashears, 1977). Nonetheless, at

appropriate rates both aldicarb and 1,3-dichloropropene can be profitable, though economically risky, for management of *M. incognita* and *R. reniformis* (Zimet et al., 1999, 2002). A serious recent concern is the development of aldicarb-degrading microflora following long-term use as a prophylactic, demonstrated recently to be occurring in Alabama (McLean & Lawrence, 2003). It is unlikely that suppression of seedling disease-causing microflora by 1,3-dichloropropene and aldicarb is an important component of yield responses to fumigation observed in fields infested with nematodes, because careful studies have shown that the use of 1,3-dichloropropene and aldicarb in cotton fields does not significantly impact plant pathogenic fungi or saprophytic fungal populations (Baird, Carling, Watson, Scruggs, & Hightower, 2004). Site specific application of aldicarb for *M. incognita* management in cotton has been explored, but was found to be less cost-effective than uniform application (Wheeler et al., 1999; Wrather et al., 2002).

5.2.2.2. *Novel Nematicides*

Several recent tests explored the potential of strategic placement of anhydrous ammonia, a widely used nitrogen fertilizer formulation, for *R. reniformis* management in cotton. Significant yield improvements over the alternative nitrogen control were measured, but consistent suppression of nematode populations was not obtained (McLean, Lawrence, Overstreet, & Young, 2003). During the last 2 years, seed coat formulations of the anthelmithic avermectin-B1 have been extensively tested and are now commercially offered (Cochran, Long, Beckett, Payan, & Belles, 2006; Fasje & Starr, 2006; Kemerait et al., 2006; Schwarz, Graham, & Kleyla, 2006). Commercially available formulations of resistance-inducing harpin proteins as seed and foliar treatments also have recently been evaluated, and may find a place in nematode management in cotton (French et al., 2006).

5.2.2.3. *Yield Potential Recoverable with Nematicides*

Yield increases in recent years in fields infested with *R. reniformis* have often been only 5 or 10%, contrasted to the 40–60% yield suppressions measured in early studies examining the impact of *R. reniformis* on cotton (Birchfield & Jones, 1961; Jones, Newsom, & Finley, 1959), which were done with obsolete but highly effective fumigants. Studies in cotton fields infested with *R. reniformis* show that when conventional fumigation is used, most nematodes are killed 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 (Gazaway et al., 2001; Kinloch & Rich, 2001; Lawrence & McLean, 1996). This has been attributed to the high biotic potential of *R. reniformis*, and recolonization of the upper soil layer by nematodes deeper in the soil. In some fields, more than half of the *R. reniformis* inoculum in the field is deeper than 45 cm (Newman & Stebbins, 2002; Robinson, Cook, Westphal, & Bradford, 2005a; Robinson, Gutierrez, LaFoe, McCarty, & Jenkins, 2005b).

Occurrence of *R. reniformis* deep in the soil raises the question of nematicide efficacy relative to other possible nematode management options, such as crop rotation, biological control and host-plant resistance. If roots are deep and deep roots are important, then less than 100% of the total yield potential should be recovered by nematicide treatment, because nematicides treat only the upper portion of the soil profile. Analyses by Zimet et al. (1999, 2002) indicated that a substantial fraction of the yield potential could be tapped by fumigating shallow sandy soils in the Florida panhandle, which are relatively easy to penetrate due to the large pore space, low diffusive resistance and shallow roots. In comparison, tests in deep soils in Texas where cotton root growth may exceed 2 meters indicated deep placement of fumigant was needed to obtain maximum yield (Cook et al., 2003; Robinson et al., 2005; Westphal, Robinson, Scott, & Santini, 2004). Placing fumigant 81–100 cm below the surface in these fields, suppressed populations 90 cm deep in the soil throughout the season, strongly promoted deep root growth and increased yield by 100%, contrasted to 57% increase obtained by only fumigating 43 cm deep. The additional yield boost obtained by fumigating deeply is very important because it is part of the yield potential that might be tapped by planting a *R. reniformis*-resistant cultivar, should one become available.

5.2.3. Biological Control

Biological control has not yet been adopted as a standard practice for managing nematode problems in cotton production systems. However, *M. incognita* has been the subject of many studies examining the possible use of natural enemies of nematode in crops other than cotton.

Organisms investigated include the parasitic fungus *Hirsutella rhossiliensis*, nematodes trapping fungi (*Monacrosporium cionopagum* and *M. elliposporum*) (Robinson & Jaffee, 1996), mycorrhizal fungi (Sikora, 1979), egg parasitizing fungi, such as *Paecilomyces lilacinus*, the obligately parasitic bacterium *Pasteuria penetrans*, strains of *Gluconacetobacter diazotrophicus* (Bansal, Dahaya, Narula, & Jain, 2005) and predaceous nematodes (Stirling, 1991; Robinson & Jaffee, 1996).

In addition, several unidentified and known 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% (Wang, Riggs, & Crippen, 2004). 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% (Wang, Riggs, & Crippen, 2005). Isolates of *Paecilomyces lilacinus* also have been tested against *R. reniformis* in pots (Jayakuma, Ramakrishnan, & Rajendran, 2002).

Among G- (Gram-negative) bacteria, *Pseudomonas fluorescens* suppressed Indian populations of *R. reniformis* by up to 70% (Jayakumar, Ramakrishnan, & Rajendran, 2003). Unidentified agents in three soils from cotton fields in the Texas Lower Rio Grande Valley, whose effects were removable by 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 and A. F. Robinson, unpublished data). Exploitation of knowledge regarding biological control of nematodes is an opportunity for the future.

5.2.4. Cultural Control

Any practice that tends to reduce water and nutrient stress tends to reduce yield losses due to nematodes. A very old deep tillage practice that is called in-row subsoiling in the southeastern United States and precision tillage in California (Garber et al., 1996), is often used to allow cotton roots to penetrate deeper than normal and thereby partly offset deleterious effects of *M. incognita* on water and nutrient uptake. This practice involves pulling a ripping shank through the soil where the future cotton beds will be located, generally at least 45 cm deep, and is made more precise by the advent of laser guided tractors and global positioning systems. Plowing up old roots in the fall also tends to reduce populations.

Organic soil amendments can be considered for nematode management in cotton if materials are abundant and labor is cheap. Toxic amendments have been explored for management of *R. reniformis* and *M. incognita* on cotton in pots in India, and several are highly effective, including presmud, fresh Azolla, farm yard manure and neem cake (Patel, Patel, & Thakar, 2003). Identification of active components in highly effective amendments could lead to new nematicide chemistry with application to regions where the raw products for making those amendments are not available. In the United States, municipal solid waste application consistently improved tilth, suppressed *H. columbus* populations and increased cotton yield for 3 years in a row in South Carolina (Khalilian et al., 2002). The populations of *H. columbus* in cotton also were suppressed by poultry litter in North Carolina (Koenning & Barker, 2004) and Georgia (Riegel & Noe, 2000). Incorporation of shellfish waste and crop residues that contain chitin or generate biofumigants, highly effective against plant nematodes, has shown economic potential in cotton in Alabama (Hallmann, Rodríguez-Kábana, & Kloeper, 1999). One goal of chitin addition is the attack of chitin in nematode egg shells by augmented chitinolytic microflora, but chitin amendments also alter the C:N ratio and other components of microbiotic interactions in soil. Because *R. reniformis* symptoms in cotton mimic potassium deficiency, potassium supplementation has been explored as an amelioration strategy, but without significant effects on yields (Pettigrew, Meredith, & Young, 2005).

5.2.5. Crop Rotation

In the southeastern United States, the primary crop rotations recommended for managing nematodes in cotton are peanut or groundnut (*Arachis hypogaea*), American corn (*Zea mays*) and soybean (*Glycine max*) (Brathwaite, 1974; Gazaway, Akridge, & Rodriguez-Kabana, 1998; Gazaway, Akridge, & McLean, 2000; Davis, Koenning, Kemerait, Cummings, & Shurley, 2003; Thames & Heald, 1974). Peanut is excellent because *M. incognita*, *R. reniformis* and *H. columbus* all reproduce poorly on peanut (Blasingame, 1994), and the peanut root-knot nematode,

M. arenaria, reproduces insignificantly on cotton (Starr, 1998). Where they are an economic option, sorghum (*Sorghum bicolor*) and small grains can be used to suppress *R. reniformis*.

Great care must be taken in using corn and soybean rotations for nematode management in cotton. Most corn hybrids are highly resistant to *R. reniformis* (Windham & Lawrence, 1992) but support good reproduction by *M. incognita* (Davis & Timper, 2000). Soybean cultivar selection is complex because cultivars differ with respect to resistance to *M. incognita*, *R. reniformis* and soybean cyst nematode, *Heterodera glycines* (Gilman et al., 1978, 1979; Hartwig & Epps, 1977; Harville, 1985; Robbins et al., 2001; Westphal & Scott, 2005). In addition, soybean cultivars fall into maturity groups adapted to specific latitudes, necessitating availability of a specific nematode resistance gene in a specific maturity group for use in nematode management in a specific growing region. In Brazil, sorghum and velvet bean (*Stizolobium deeringianum*) can be used to manage *R. reniformis* (Farias, Barbosa, Vieira, Sánchez-Vila, & Ferraz, 2002). In North American fields infested with *M. incognita*, clover (*Trifolium* spp.) and vetch (*Vicia* sp.) winter cover crops can increase nematode populations, but rye (*Secale cereale*) (McBride, Mikkelsen, & Barker, 1999; Timper, Davis, & Tillman, 2006) and the vetch cultivar Cahaba White (Timper et al., 2006) do not, and have been shown to be acceptable winter cover crops in infested fields.

In California, peanut and nematode-resistant cultivars of soybean and corn are generally not considered suitable rotational crops. However, most varieties of alfalfa (*Medicago sativa*) grown in California and Arizona are resistant to *M. incognita* and can be used in rotation with cotton (Garber et al., 1996; Goodell, et al., 1996). Grain sorghum is recommended for reducing *M. incognita* populations in Arkansas but not on the High Plains of Texas (Blasingame, 1994; Thomas & Kirkpatrick, 2001). Rotational crops recommended for control of *M. acronea* in Africa include pearl millet (*Pennisetum typhoides*), finger millet (*Eleusine coracana*), corn (*Zea mays*), peanut, guar bean (*Cyanopsis tetragonoloba*), and leucaena (*Leucaena glauca*) (Starr & Page, 1990).

5.2.6. Sanitation/Weed Management

Meloidogyne incognita has a wide host range and reproduces on more than 1 000 plant species. In the United States, *M. incognita* reproduces on many of the weeds commonly encountered in cotton fields. *R. reniformis* has a similarly wide host range, reproducing on 87% of more than 350 plant species tested as potential hosts (Birchfield & Brister, 1962; Linford & Yap, 1940; Robinson et al., 1997). Many common weeds in all cotton production regions of the world support prolific reproduction by *R. reniformis* (Carter, McGawley, & Russin, 1995; Inserra, Dunn, McSorley, Langdon, & Richmer, 1989; Lal, Yadav, & Nandwana, 1976; Quénehervé, Drob, & Topart, 1995). Thus, effective weed management in the crop, during winter fallow, and during crop rotations is critical for managing both of these nematodes in cotton.

In practice, recognizing and removing weeds that interfere with nematode management has been shown to be easier than might be predicted by the host ranges of *M. incognita* and *R. reniformis*. Recent studies in Alabama and Georgia have

shown that only a small proportion of weeds found in cotton fields are problematic to nematode management in cotton production because, although most dicotyledonous weeds in cotton in the southeastern United States are hosts, only a few are better hosts than cotton (Davis & Webster, 2005; Dismukes, Lawrence, Price, Lawrence, & Akridge, 2006). In some cases, plants that support high populations of one nematode do not support the other nematode, so it is important to know which weed is a good host for which nematode. Some are sufficiently good hosts to sustain populations in fields planted to non-host corn (Dismukes et al., 2006).

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 (Davis & Webster, 2005), only purple nutsedge (*Cyperus rotundus*), sicklepod, Florida beggar weed (*Desmodium tortuosum*) and smallflower morninglory were comparable to cotton, with populations (expressed as a percentage of that on cotton) of 454%, 81%, 73% and 33%, respectively.

Also *M. incognita* 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. Weed species also differ through the year. Thus, weed management for nematode control in cotton requires knowing which weeds support which nematodes as well as when they are present during the cropping cycle. Weed hosts, however, do not appear to explain the gradual increase that has been documented in the incidence of *R. reniformis* in the central part of the United States cotton belt (Robinson, 2007).

One other important point regarding sanitation should be made. The use of cotton seed hulls or husks produced by cotton gins and oil mills as a soil amendment and or as cattle feed is practiced in many parts of the world and has been documented to spread infestations of *Fusarium* (Hillocks & Kibani, 2002).

5.3. Genetic Resistance to Nematodes in Cotton

Host plant resistance is the most efficient way to manage nematodes (Starr, Bridge, & Cook, 2002). There are very few nematode-resistant cotton cultivars available, and those are not widely adapted. Currently, host plant resistance is an area of intense investigation in cotton nematology research.

5.3.1. Terminology

In principle, nematode resistance and tolerance should be clearly distinguished as genetic traits (Cook & Evans, 1987). Resistance refers to the ability of a plant to

limit a nematode's reproduction; tolerance has no necessary relationship to resistance and refers to the ability of the plant to grow and yield in soil where the nematode is present (Cook & Evans, 1987). In practice, tolerance in cotton often appears to be accompanied by partial resistance (Davis & May, 2003, 2005), and resistance makes plants more tolerant (Zhou & Starr, 2003).

5.3.2. Resistance and Tolerance Mechanisms

In resistant plants, the *M. incognita* J2 invades roots, migrates through tissue, and attempts to feed on the same cells as in susceptible plants. However, a hypersensitive response by the plant results in the collapse and death of cells probed by the nematode (Carter, 1981; Creech, Jenkins, Tang, Lawrence, & McCarty, 1995; Jenkins et al., 1995; Shepherd & Huck, 1989). Normal root penetration by *R. reniformis* with failure to induce a syncytium also characterizes the resistant response of *Gossypium longicalyx* and *G. hirsutum* hybrids carrying *R. reniformis* resistance from *G. longicalyx* (Agudelo, Robbins, Stewart, Bell, & Robinson, 2005a).

In cotton roots infected by *M. incognita*, toxic terpenoid aldehydes accumulate around the nematode head more rapidly in resistant than in susceptible plants (Veech & McClure, 1977; Veech, 1978, 1979). Roots of the susceptible cotton germplasm line M-8 develop more extensive cracking of the epidermis and cortex as they grow than roots of the resistant line Auburn 623 RNR (Shepherd & Huck, 1989). The resultant leachates and increased physical access to the root interior were hypothesized to explain the greater susceptibility of M-8 to the root-knot nematode and Fusarium-wilt disease complex (Shepherd & Huck, 1989).

An *M. incognita* resistance-specific protein (*MIC-3*) produced in response to nematode infection, has been sequenced and determined to belong to a novel gene family with six members (Zhang et al., 2002). The existence of numerous host differentials between *M. incognita* and *R. reniformis* suggests different resistance mechanisms.

Bacillus thuringiensis delta-endotoxin transgenes encoding for the *Cry 1 Ac* protein do not confer nematode resistance in cotton, and resistance may be lost when transgenes are transferred into resistant genotypes, if resistance inheritance is not monitored during backcrossing (Colyer, Kirkpatrick, Caldwell, & Vernon, 2000). The *Cry 2 Ab* toxins await testing.

5.3.3. Resistant and Tolerant Cultivars and Resistance Sources

5.3.3.1. *M. incognita*

Early germplasm evaluations (Jones et al., 1958) focused on the *M. incognita* and Fusarium wilt disease complex. Finding resistance to the complex was confusing since resistance to the nematode and resistance to the fungus were inherited independently. Thus, cultivars with resistance to the disease complex in the field often supported high levels of nematode reproduction (Starr & Martyn, 1991; Starr & Veech, 1986) and genotypes that were wilt-resistant, when stem-inoculated with

the fungus in the greenhouse, often showed little resistance to the fungus under field conditions if the nematode was present (Shepherd, 1986a; Shepherd & Kappelman, 1986). Wilt resistance has been incorporated into many cultivars, and *M. incognita* resistance remains an important component of resistance to the disease complex in contemporary resistant cultivars (Koenning et al., 2004).

Today, there are at least five independently developed sources of resistance to *M. incognita* available in agronomic types of *G. hirsutum*. The first one came from a cross made by R.L. Shepherd in Alabama in the 1960s (Shepherd, 1974a, 1974b) between the Fusarium wilt resistant cv. Cleve-wilt 6, and a root-knot nematode-resistant primitive *G. hirsutum* accession from Mexico, registered in the USDA National Cotton Collection as Wild Mexican Jack Jones. The F₁₀ selection Auburn 623 RNR, which was more resistant than either parent, was backcrossed to wilt-resistant Auburn 56. Nematode resistance was recovered in the selection Auburn 634, which in turn was backcrossed to obsolete cvs. Deltapine 61, Coker 201, Coker 310 and Stoneville 213 to produce the highly resistant Auburn M lines (M. Robinson et al., 1997; Sheperd 1982, 1986b, 1989; Shepherd & Huck, 1989). This material was used as the source of resistance for Arkot 9111, recently released by the Arkansas Agricultural Experiment Station (Bourland & Jones, 2005), as well as GA161, released by the Georgia Agricultural Experiment Station (May, Davis, & Baker, 2001), and several breeding lines to be released by Mississippi State University in cooperation with USDA. Resistance in the Auburn M lines appears to be inherited as a two-gene system, one dominant and one partial. Significant progress has been made toward discovery of DNA markers suitable for marker-assisted selection and mapping of the resistance genes (Hinchliffe et al., 2005; Shen et al., 2006).

A second source of resistance developed in Brazil has Auburn 56 as a key parent. Auburn 56 is also in the background of the Auburn M lines, and is generally thought to be a source of Fusarium but not root-knot nematode resistance in those lines. Genotypes within the resistant Brazil group include the highly resistant IAC/414 and the moderately resistant IAC98/708 and IAC98/732 (Carneiro et al., 2005). The cultivar CD405, also developed for Brazil but apparently unrelated to IAC/414, is reported nematode tolerant (Bélot et al., 2005).

A third source of root-knot nematode resistance came from a cross made by J. E. Jones (Jones, Wright, & Newsom, 1958; Jones, Beasley, Dickson, & Caldwell, 1988; Jones et al., 1991) in Louisiana between Cleve-wilt 6 and Deltapine 15, ultimately leading to the moderately root-knot nematode-resistant Bayou 7769 (Jones & Birchfield, 1967). Bayou 7769 was in turn crossed with Deltapine 16 and nematode-resistant progeny selected from this cross led to LA 434-RKR, crossed in turn with DES 11-9 to produce the once widely planted, moderately root-knot nematode-resistant cultivar Stoneville LA 887 and the related Paymaster (formerly Hartz) 1560 (Jones et al., 1991). These cultivars combined root-knot nematode resistance with high yield, high fiber quality, medium maturity, high lint percentage and wide adaptation. They also showed excellent field resistance to the *M. incognita* and Fusarium wilt disease complex. A closely related nematode-resistant transgenic cultivar, Stoneville 5599 BR, is currently commercially available and planted in the central United States cotton belt. LA 434-RKR was also used to develop four breeding lines (Jones et al., 1988) adapted to Louisiana that combine root-knot

nematode resistance with reniform nematode tolerance. Three of those lines were utilized in turn, to develop seven additional, high yielding breeding lines adapted to South Texas growing conditions, which also are root-knot nematode resistant and reniform nematode tolerant (Cook, Namken, & Robinson, 1997; Cook, Robinson & Namken, 1997; Cook & Robinson, 2005; Koenning, Barker, & Bowman, 2000). Stoneville LA887 and the Auburn M line 240 RNR were both used as parents in the development of GA96-211, recently released by the Georgia Agricultural Experiment Station (May, Davis, & Baker, 2004).

A fourth independently derived source of root-knot nematode resistance in cotton was developed by Angus Hyer with the USDA in California, leading to the development of a resistant breeding line C-225, which was released after his death as the cultivar NemX by California Planting Cotton Seed Distributors (CPCSD) and the University of California (Ogallo et al., 1997). The details of this rather complex lineage are given by Robinson et al. (2001). NemX meets fiber quality as well as yield standards of the Acala cotton types grown in California (Garber et al., 1996) and is resistant to the *M. incognita* and Fusarium wilt disease complex. However, it is not widely adapted and cannot be grown for profit in most other production regions of the United States, but might be adaptable to regions of the world with conditions similar to California. NemX has been the subject of intensive recent investigations in California that have identified DNA markers for the resistance and made substantial progress toward fine-mapping of the recessive resistance gene (Wang, Matthews, & Roberts, 2006). Markers will enable marker assisted selection, facilitating the use of NemX as a source of resistance for cultivars adapted to conditions outside California, and mapping could eventually lead to resistance gene cloning.

A fifth source of resistance, effective against *M. incognita* race 4, is the South African cultivar Gamka, developed from N9311, thought to have come out of Gus Hyer's breeding program in California, but of uncertain relation to NemX.

There is already some evidence of the development of populations of *M. incognita* able to reproduce on NemX in California. NemX was compared with LA887 and an Auburn line in North Carolina (Koenning, Barker, & Bowman, 2001) and suppressed the field population tested well. At least one population on the Texas High Plains, however, induces galls and reproduces on NemX (T. A. Wheeler, personal communication). Thus, it seems likely that resistance-breaking populations will develop, and additional resistance sources may prove invaluable. Most primitive accessions of *G. hirsutum* are good hosts for *M. incognita* but resistance to the nematode is not uncommon in primitive *G. hirsutum*. Additional sources of resistance to *M. incognita* have been identified among accessions of *G. hirsutum* from Mexico, Central America and the Caribbean Basin. Eighteen of 471 accessions examined by the USDA at Mississippi State University in 1983 had a level of resistance intermediate to the moderately resistant Cleve-wilt 6 and the highly resistant Auburn 623 RNR (Shepherd, 1983). Twelve of those accessions were used to develop day-neutral isolines by crossing with cv. Deltapine 16, and selecting for day neutrality across recurrent backcrosses onto primitive accessions (Shepherd, 1988). Nine more resistant accessions were discovered in 1996 (Robinson & Percival, 1997). It is not known yet if the resistance genes in these sources differ.

5.3.3.2. *R. reniformis*

Resistance to *R. reniformis* has been hard to find. Of 2 000 *G. hirsutum* genotypes evaluated in the search for resistance (Robinson, Bridges, & Percival, 2004; Robinson & Cook, 2001; Robinson, Cook, & Percival, 1999; Robinson & Percival, 1997; Yik & Birchfield, 1984), only 19 were scored as potentially resistant in the first examination, of which nine (Yik & Birchfield, 1984) were reclassified as susceptible in a subsequent screen (Robinson & Percival, 1997), and four (TX-110, TX-502, TX-1347, TX-1348) were reclassified as *G. barbadense*, leaving only six moderately resistant *G. hirsutum* accessions (TX-25, TX-748, TX-1586, TX-1828, TX 1860, TX-2469). Several additional weakly to moderately resistant primitive accessions of *G. hirsutum* have been found recently (D. Weaver, personal communication).

Stronger levels of resistance than in *G. hirsutum* occur in one or more accessions of *G. barbadense*, *G. arboreum*, *G. herbaceum*, *G. longicalyx*, *G. somalense* and *G. stocksii* (Carter, 1981; Robinson & Percival, 1997; Stewart & Robbins, 1995, 1996; Yik & Birchfield, 1984), which in some cases suppress *R. reniformis* populations in pots 90–100%, compared to susceptible upland cotton, and also suppress populations in the field (Robinson et al., 2006). Currently, projects are underway at the 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 primitive *G. hirsutum*, *G. barbadense*, *G. longicalyx* and *G. arboreum* into agronomic *G. hirsutum* (Avila, Stewart, & Robbins, 2006; Bell & Robinson, 2004; Dighe et al., 2007; Moresco, Morgan, Ripple, Smith, & Starr, 2004; Robinson et al., 2005; Silvey, Ripple, Smith, & Starr, 2003; J. N. Jenkins, E. Sacks, D. Weaver, L. D. Young, personal communication). These are challenging, long term projects, as the requisite transfers of DNA within the genus *Gossypium* are complex involving differences in ploidy and different genomes and sub-genomes, with in many cases low or no intercompatibility, due to chromosome inversions, deletions, etc. (Percival, Wendel, & Stewart, 1999).

Probably the most advanced of the projects, which is being carried out by the USDA at College Station, Texas, in collaboration with Texas A&M University, has employed two tri-species hybrids of *G. hirsutum* (Bell & Robinson, 2004) with *G. longicalyx*, and either *G. armourianum* or *G. herbaceum* as bridges, to introgress virtual immunity to *R. reniformis* from diploid *G. longicalyx* into allotetraploid *G. hirsutum* (Robinson, Jenkins & McCarty, 2007). 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.

By making literally thousands of attempted crosses, 689 first-backcross generation progeny were generated from the two male-sterile 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 again three to six

times to *G. hirsutum* to derive agronomically suitable types, selecting for nematode resistance by bioassay at each backcross, as well as within segregating progeny from selfed plants at selected generations. This was an arduous process, involving the evaluation of nematode resistance in ca. 3000 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, 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.

More than 500 segregating phenotyped plants in the USDA-Texas A&M University *G. longicalyx* project were utilized to discover six SSR markers co-segregating with the trait. One of the markers is co-dominant, allowing it to be used to distinguish homozygous from heterozygous resistant plants, and resides within ca. 1 centiMorgan of the resistance gene (Dighe et al., 2007). Seed of two genetic stocks, Lonren-1 and Lonren-2 were released by USDA, Texas A&M University, and Cotton Incorporated in May of 2007.

In other introgression projects, resistance to *R. reniformis* is being transferred into cotton from *G. barbadense* TX-110 (Moresco et al., 2004), *G. barbadense* GB-713 (Robinson et al., 2005), *G. arboreum* (Avila et al., 2006; 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 the likelihood of ultimately confronting linkage drag between resistance genes and agronomically unacceptable traits in each case 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 is already ample evidence of much variability within *R. reniformis* (Agudelo, Robbins, Stewart, & Szalanski, 2005b; Dasgupta & Seshadri, 1971b; McGawley & Overstreet, 1995; Nakasono, 1983).

5.3.3.3. *H. columbus* and *B. longicaudatus*

Agronomically useful levels of resistance to the sting and Columbia lance nematodes have not been found in *G. hirsutum*. However, one or more cultivars with good tolerance to the Columbia lance nematode have been identified in North Carolina (Koening, Edmisten, Barker, & Morrison, 2003). Tolerance is found in both late and early maturing cultivars. However, among late cultivars the highest yielding were the most tolerant, whereas among early cultivars, high yielding cultivars were least tolerant (Koening & Bowman, 2005).

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