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Inheritance of resistance to *Meloidogyne incognita* race 3 in cotton accession TX 25

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ABSTRACT. Cotton producers worldwide suffer with the losses caused by the presence of phytonematodes. The aim of the present study was to investigate the inheritance of resistance to *Meloidogyne incognita* race 3 in *Gossypium hirsutum* variety punctatum accession TX 25. Accessions of *Gossypium* sp. were obtained from the germplasm bank of Embrapa Cotton. Two experiments were performed in two consecutive years. In the first experiment, a susceptible parental line, FiberMax 966, a resistant parental line, TX 25, and their F_1, F_2 and backcross generations were tested. In the second experiment, parental lines FiberMax 966 and TX 25, their F_2 generation, and genotypes M315 (resistant), LA887 and DeltaOpal (moderately resistant) were tested. In both experiments, plants were inoculated with 2000 eggs and J2 of *M. incognita* race 3. The gall index, egg mass index and reproduction factor were evaluated 120 days following inoculation. In the first experiment, plants from the F_1 and backcross generations were susceptible. Plants from the F_2 generation presented a 3:1 resistant-to-susceptible ratio in the two experiments, indicating oligogenic resistance.

Keywords: *Gossypium hirsutum*, gall nematode, gene segregation.

Herança da resistência do acesso TX 25 de algodoeiro a *Meloidogyne incognita* raça 3

RESUMO. Os cotonicultores do mundo inteiro sofrem com as perdas causadas pela presença de fitonematoides nas lavouras. Assim o objetivo deste trabalho foi estudar a herança da resistência do acesso TX 25 de *Gossypium hirsutum* raça punctatum a *Meloidogyne incognita* raça 3. Foram utilizados acessos de *Gossypium* sp. pertencentes ao Banco de Germoplasma da Embrapa Algodão. Foram realizados dois experimentos em dois anos consecutivos. No primeiro ano foram testados FiberMax 966 e TX 25 como parentais suscetível e resistente, respectivamente, e as gerações F_1, F_2 e retrocruzamento. No segundo experimento foram testados os parentais FiberMax 966 e TX 25, a geração F_2 além dos genótipos M315 (resistente) LA887 e DeltaOpal (moderadamente resistentes). Em ambos experimentos as plantas foram inoculadas com 2000 ovos e J2 de *M. incognita* raça 3. As avaliações ocorreram aos 120 dias após a inoculação, e avaliou-se índice de galhas, índice de massa de ovos e fator de reprodução. No primeiro experimento as plantas da geração F_1 e do retrocruzamento se mostraram suscetíveis, As plantas da geração F_2 nos dois experimentos apresentaram uma proporção de três plantas resistentes para uma suscetível indicando resistência de caráter oligogênico.

Palavras-chave: *Gossypium hirsutum*, nematoide de galhas, segregação gênica.

Introduction

In spite of their high productivity, cotton producers suffer crop losses due to the presence of phytonematodes. Main are of cotton plant-parasitic nematode species *Meloidogyne incognita* (Kofoid & White, 1919, Chitwood, 1949), *Rotylenchulus reniformis* (Linford & Oliveira, 1940) *Pratylenchus brachyurus* (Godfrey, 1929) Filipjev & Sch. Sttekhoven, 1941 (Galbieri et al. (2009) evaluated the resistance of 22 cotton genotypes against *M. incognita* and observed that 21 genotypes allowed nematode reproduction. The most affected genotypes generated a 65% loss of production when compared to the resistant genotypes.

The use of resistant cultivars is the most affordable method for the control of nematodes, because it do not increase production costs, do not interfere with the environment, and do not lead to environmental imbalances (Davis & Stetina, 2016). Genetic resistance is therefore the safest method for decreasing damages caused by *M. incognita* to cotton crops (Barbosa et al., 2009). In Brazil, however, there are currently no cotton varieties that combine

interesting agronomical characteristics and a level of resistance against this nematode. It is therefore important to identify and characterize sources of resistance and include them in improved germplasm.

Cotton cultivars with moderate resistance to the gall nematode have been previously identified, but are not used on a commercial scale because of their low production potential (Ogallo, Goodell, Eckert, & Roberts, 1997). In the USA, there are three commercial cultivars with moderate resistance to *M. incognita*. The first source of resistance, Acala NemX, and the second source of resistance, Clevewilt 6, are considered only moderately resistant, and these sources are now used as commercial cultivars. The third source of resistance, Wild Jack Jones, did not become a commercial cultivar but was used to produce cultivar Auburn 623 (cross between Clevewilt 6 and Will Jack Jones), which is highly resistant (Shen et al., 2006). Subsequently, the commercial cultivars Stoneville LA887 and Paymaster 1560 were generated from the second resistance source. Of these three sources, only Acala NemX continues to be used by cotton producers in the USA. The remaining two sources are considered obsolete because their agronomic characteristics do not meet the productivity and quality standards of the current market (Robinson et al., 2001).

In Brazil, the Agronomy Institute of Campinas (Instituto Agronômico de Campinas – IAC) introduced a resistant cultivar, IAC 20, originating from the cross between Auburn 56, which is resistant to the *Fusarium* sp. and root-knot nematode disease complex, and GH 11-9-75 (Carneiro, Neves, Falcão, Paes, Cia, & Sá, 2005). This cultivar was introduced in 1983 and grown until 1996. The IAC later introduced cultivars 96/414, IAC 22 and IAC 23, all of which are IAC 20 hybrids and originated from the Auburn 56 source of resistance. Thus, sources of resistance are scarce and present resistance mechanisms that are similar and therefore easy to overcome (Carneiro et al., 2005).

The continued use of varieties with the same resistance sources can accelerate the nematodes selection pressure and compromise the durability of resistance. Therefore, it is essential to search for new sources, preferably combining different resistance genes.

Recently were identified two main cotton genes that confer resistance to *M. incognita*. These genes were identified from the RNR Auburn 623. The source of resistance genes are on chromosomes 11 and 14 and appear to have different mode of action, resulting in a resistance mechanism with two stages. While the gene present on chromosome 11 do not prevent the penetration of the second-stage juveniles, however, soon after penetration prevents the development of these juveniles (Gutierrez et al., 2010; He et al., 2014). Already this gene on chromosome 14, expresses the resistance later form. Not prevent the formation of galls, but prevents or reduces the production of eggs (Gutierrez et al., 2010; He et al., 2014). Thus these two genes are complementary to allow the cotton presents a resistance response to *M. incognita*.

Another study of cotton genotypes CIR 1348 and TX-25, which have common ancestors known Auburn 623 RNR, was resistant to two similar stages. A hypersensitive response during the first week after infection *M. incognita* which stopped the development of the nematode and consequently the formation of galls. It also showed a delayed resistance reaction, about two to three weeks after infection, allowed the formation of larger giant cells galls, and development of nematodes, however prevented nematodes progressed to adult females (Mota et al., 2013).

Given the reduced number of resistant genotypes and the increase in areas contaminated with nematodes, especially *M. incognita*, studies focused on identifying new resistance sources and evaluating the possibility of their introduction into genetic improvement programs for the development of new cultivars are essential. The aim of this study was to investigate the resistance of wild cotton accession TX 25 to *M. incognita* race 3.

Material and methods

Two experiments were conducted using *Gossypium hirsutum* accessions obtained from the germplasm bank of Embrapa Cotton. The species used and their origins are presented on Table 1. The nematodes *M. incognita* race 3 inoculum was obtained from roots of tomato (*Solanum lycopersicum*) cultivar Santa Clara from the Santa Cruz group. The inoculum, with nematodes previously identified by species and race, was supplied by the Laboratory of Nematology of Embrapa Genetic Resources (Embrapa Recursos Genéticos - Cenargen).

The first experiment was conducted in a greenhouse. Seeds were sown in 5-L plastic pots containing a mix of soil, sand and commercial substrate (1:1:1) that was previously autoclaved. One seed was sown per pot. The experiment consisted of twenty backcross (BC), seven F_1, two hundred F_2, seven TX 25, and seven FiberMax 966 plants in a completely randomized experimental design (Table 1).

Table 1. Origin and response of *Meloidogyne incognita* race 3 on *Gossypium* sp. genotypes tested in two experiments conducted in 2011 and 2012. Goiania, Goiás State, 2015.

Genotypes/Generations	Specie/race	Origin	Company owner	Reaction to *M. incognita*	Experiment 2011	Experiment 2012
FiberMax 966	*G. hirsutum* race latifolium	Commercial cultivar	Bayer	S[1]	X	X
DeltaOpal	*G. hirsutum* race latifolium	Cultivar commercial	Monsanto	MR		X
LA887	*G. hirsutum* race latifolium	USA / Stoneville/Cultivar commercial obsolete	LA AES	MR		X
M315	*G. hirsutum* race latifolium	USA	-	R		X
TX 25	*G. hzrsutum* race punctatum	México/Wild acess	NPGS PI no. 154035	R	X	X
F1	*G. hirsutum*	FiberMax 966 (♀) x TX 25(♂)	CNPA*	--	X	
F2	*G. hirsutum*	FiberMax 966 (♀) x TX 25(♂)	CNPA*	--	X	X
BC (Backcross)	*G. hirsutum*	F_1 x FiberMax 966	CNPA*	--	X	

Centro Nacional de Pesquisa em Algodão. [1]S - susceptible; R- resistant; MR - moderately resistant.

When plants were approximately 20 cm high, which occurred on average twenty days after emergence, 5 mL of a suspension containing 5,000 eggs and J2 were inoculated per plant. The experiment was conducted between June and November at 2011. Plants were watered daily. Fertilization and pest control were performed as needed.

Evaluations were performed 120 days after inoculation. The plants were removed from the pots, the shoots were discarded, and the roots were taken to the laboratory where they were washed and the root fresh weight was measured. The roots were then stained by immersion in 0.15 g L^{-1} Phloxine B dye (dissolved in water) for twenty minutes and then washed to remove the excess.

Following staining, the gall index and egg mass index were quantified according to Hartman and Sasser (1985): 0 = no galls or egg masses; 1 = 1-2 galls or egg masses, 2 = 3 to 10 galls or egg masses; 3 = 11 to 30 galls or egg masses; 4 = 31 to 100 galls or egg masses; and 5 = more than 100 galls or egg masses. The total number of eggs per plant was quantified according to Hussey and Barker (1973). The reproduction factor (RF) was calculated for each plant by dividing the total number of eggs per plant (PF) by the number of eggs inoculated (PI = 5,000).

The second experiment was also conducted in a greenhouse. The treatments consisted of five plants of each genotype: FiberMax 966, TX 25, DeltaOpal, M315 and LA887. Cultivars DeltaOpal, LA887 and M315 The genotypes DeltaOpal, M315 and LA887. Cultivars DeltaOpal, LA887 and M315 were included in the experiment because their behavior against *M. incognita* is well-known, thereby enhancing the reliability of the results. A Federer's augmented block experimental design was used (Federer, 1956) with six blocks. Each block consisted of 34 F_2 plants and one plant of each of the controls Delta Opal, FiberMax 966, LA887, M315 and TX 25 for a total of 39 plants. Each block therefore included 34 plants with unknown behavior and five with known behavior.

Seeds were placed in 2-L plastic seedling bags. The substrate, sowing conditions, experimental period since inoculation, and evaluations were performed as described for the first experiment.

The data obtained from the first experiment were subjected to a Pearson's chi-squared test to measure the discrepancy between the observed and expected frequencies under the proposed hypothesis. A goodness of fit test was used to test for monogenic inheritance, double recessive epistasis, and oligogenic or polygenic character in the F_2 genotypes by testing the following distributions at $p < 0.01$: 3S:1R, 1S:2MR:1R, 9S:7R and 9S:3MR:4S. The hypotheses were accepted or rejected based on the χ^2 test.

To better visualize of the behavior of the F_2 generation plants, histograms were plotted using the RF data obtained for the two experiments. Nematode reproduction in the F2 generation genotypes were compared to a standard susceptible cultivar and classified as resistant, moderately resistant or susceptible according to the method of Starr and Mercer (2010). Plants with a nematode multiplication of 0 to 5%, 5 to 25%, 25 to 50%, and greater than 50% relative to the standard susceptible cultivar were considered highly resistant, resistant, moderately resistant, and susceptible, respectively.

Results and discussion

Cultivar FiberMax 966 was confirmed to be susceptible, presenting a high gall index, egg mass index and nematode RF in both experiments (Tables 2 and 3). The RF values for this cultivar were 24.5 and 59.5 for experiments 1 and 2, respectively, indicating a high susceptibility. Genotype TX 25 presented the lowest gall index and egg mass index and an RF of less than 1, thereby confirming the resistance of this genotype (Oostenbrink, 1966). Genotype TX 25 was highly resistant when compared to the standard susceptible control, FiberMax 966, according to the Starr and Mercer (2010) classification (Table 2).

Table 2. Average gall index (GI), egg mass index (EMI), reproduction factor (RF), and percentage decrease in the percentage decrease in the reproduction factor (PD) of *M. incognita* race 3 in different *Gossypium hirsutum* genotypes in the fisrt experiment. Goiania, Goiás State, 2015.

Tratament	GI	EIM	RF	PD[1]
FM966	5.0	5.0	24.5	0%
TX 25	4.0	2.0	0.6	97.56%
F_1	5.0	3.0	4.6	81.23%
BC	5.0	4.0	13.6	44.49%
F_2	5.0	3.0	6.0	75.52%

[1]Percentage decrease in the reproduction factor according to Starr and Mercer (2010).

Table 3. Average gall index (GI), egg mass index (EMI), reproduction factor (RF), and percentage decrease in the reproduction factor (PD) of *M. incognita* race 3 in different *Gossypium hirsutum* genotypes in the second experiment. Goiania, Goiás State, 2015.

Tratament	GI	EIM	RF	PD[1]
FiberMax 966	4.83	4.83	59.5	100%
TX 25	3.66	1.83	0.2	0.38%
M 315	1.33	1.00	0.4	0.62%
LA 877	4.66	4.00	4.9	8.30%
Delta Opal	5.00	4.83	8.4	14.12%

[1]Percentage decrease in the reproduction factor according to Starr and Mercer (2010).

Plants from the F_1 generation were 100% resistant according to the Star and Mercer (2010) classification. According to the Oostenbrink (1966) classification, the F_1 generation was susceptible, as it presented a high egg mass index and gall index and an RF greater than 1 (Table 2), showing that female reproduction was affected. Plants originating from backcrossing were susceptible, presenting a high gall index and egg mass index, an RF of 13.6 (Table 2) and an average percentage decrease in RF of 55.65%. These results were expected because the F_1 generation used for backcrossing was backcrossed with a susceptible parental line. Plants from the F_2 generation presented a decrease in RF of 24.72%, being classified as resistant to *M. incognita* race 3 according to the classification of Star and Mercer (2009).

The results of the second experiment also confirmed the known behavior of the genotypes used as controls (Table 3). Cultivar FiberMax 966 was susceptible to *M. incognita* and presented the highest RF (59.48). The genotype TX 25 and M315 presented the lowest RF values (0.2 and 0.4, respectively) and a 99% decrease in nematode reproduction relative to FiberMax 966. The resistance of genotype M315 is known to effectively control of *M. incognita* race 3. This resistance is conferred by two genes, one dominant gene, MiC 11, derived from accession Auburn 623 and located in chromosome 11 (Gutierrez et al., 2010; Shen et al., 2010), and one recessive gene, MiC 07, derived from the moderately resistant cultivar Clevewilt 6-1 and located in chromosome 7 (Shen et al., 2006).

Although genotype TX 25 presented intermediate root gall index and egg mass index values (3,66 and 1,83, respectively), it had a low RF (0.2) (Table 3). This indicates that the resistance mechanism present in this genotype interferes with the biology of female nematodes, decreasing their fecundity.

A resistance mechanism that affects the penetration, development and fecundity of female nematodes has been previously reported for other TX genotypes, also originating from Mexico (Faske & Starr, 2009). However, this is a slow mechanism, which allows nematodes to penetrate and become established in the root, and the decrease in nematode population occurs gradually over several nematode generations. Genotypes TX 25 and M315 are highly resistant to *M. incognita* (Starr & Mercer, 2010) and efficient in decreasing nematode populations.

According to Mendel's first law, if the F_1 generation is phenotypically similar to one of the genitors, that genitor is dominant relative to the other (Griffiths, Wessler, Lewontin, & Caroll, 2016). Segregation in the F_1 generation occurs because the resistance in genitor TX 25 is associated with two alleles, and the haploid cells formed during gamete formation possess only one allele of each pair, half of the information of genitor TX 25 and half the information of genitor FiberMax 966. These results indicate that genotype TX 25 is dominant relative to FiberMax 966, resulting in an F_1 generation that is 100% resistant. Resistance may therefore be monogenic. However, none of the ratios tested using the chi-squared test, were significant (Table 4). This may be due to the low number of plants in the F_1 generation: seven plants do not appear to be sufficient to confirm the behavior of a generation. Therefore, the possibility of monogenic inheritance should not be discarded based only on the analysis of the results for the F_1 generation.

According to the goodness-of-fit test, the phenotypic segregation for F_2 did not fit a 3:1 or 1S:2MR:1R ratio and, therefore, does not indicate monogenic resistance (Table 4). The F_2 generation fit a 9R:3MR:4S ratio, indicating oligogenic inheritance.

Table 4. Chi-squared (χ^2) test for F_1 and F_2, originated in parental FiberMax 966 (♀) x TX 25(♂) segregation patterns based on the reproduction factor, considering one or two genes involved in the control of resistance, in the first experiment. Goiania, Goiás State, 2013.

Crossing	3S:1R	1S:2MR:1R	9S:7R	9S:3MR:4R
F_1	ns	ns	ns	ns
F_2	ns	ns	ns	**

** significant according to the χ^2 test, at $p < 0.01$; ns: not significant.

The behavior of the F_2 generation is presented in Figure 1. Most genotypes were classified as resistant, with RF values between 0.01 and six. Genotypes with RF values between 6.1 and 12 were classified as moderately resistant, and those with RF values greater than 12 were considered susceptible.

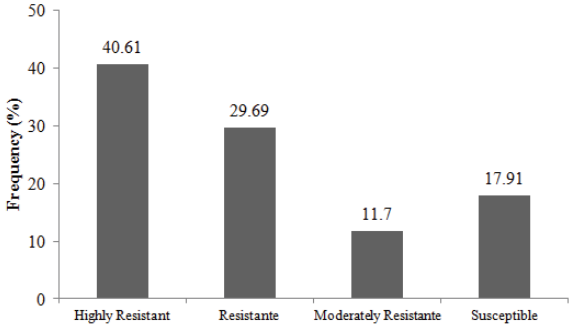

Figure 1. Frequency of reproduction factor of *Meloidogyne incognita* plants in the F_2 generation cotton genotypes in the first experiment. Goiania, Goias State, 2015. *Genotypes with RF values between 0.01 and 1 = highly resistant; genotypes with RF values between 1.1 and 6.0 = resistant; genotypes with RF values between 6.1 and 12 = moderately resistant, and those with RF values greater than 12 were considered susceptible.

Cultivars LA887 and DeltaOpal have been previously classified as moderately resistant (Mota et al., 2013). However, according to the classification of Starr and Mercer (2010) adopted in this study, these cultivars were classified as resistant, presenting percentage decrease in the reproduction factor of 8.34% and 14.12% for LA887 and DeltaOpal, respectively (Table 3).

The genes for *M. incognita* resistance in cotton are located on chromosome 11 (Wang, Ulloa, & Roberts, 2006) and chromosome 14 (Ynturi, Jenkins, Mccarty, Gutiérrez, & Sasha, 2006). The gene on chromosome 14 plays a role in polygenic resistance expression (Ynturi et al., 2006). The resistance mechanism in DeltaOpal is slow, as it allows nematode juveniles to penetrate the roots, establish their feeding site, inject the toxins responsible for cell hyperplasia and hypertrophy, cause galls, and cause disease to some degree. In LA887 this moderate resistance originates from accession Clevewilt 6, which presents a recessive resistance gene (Robinson, Bridges, & Percival, 2004). Although M315 and LA 887 had one genitor in common, they presented different behaviors.

It was recently demonstrated that cotton plants that were sensitive to *M. incognita* induced to express the MIC-3 protein (*Meloidogyne* Induced Cotton 3), become resistant to *M. incognita* and reduced egg production, although galls have not been reduced compared with the sensitive plants (Wubben, Callahan, Velten, Burke, & Jenkins, 2015). The reduction of egg production without a concomitant reduction in the galls, suggest that the MIC 3 is somehow mediated resistance gene on chromosome 14 (Wubben et al., 2015), which has a similar effect. This protein seems to be comum or exclusive the genus *Gossypium* (Wubben, Callahan, Hayes, & Jenkins, 2008). The quantity of MIC-3 protein produced in the tissue increases the infected root according to the increased resistance to *M. incognita* level (Davis & Stetina, 2016).

The mechanism of action of the MIC-3 explains the behavior of the LA887 and M315 genotypes in this study. For these genotypes showed lower rates of eggs index and higher galls index, probably showing that the MIC-3 is present in the LA 887 and M315 in moderate amounts, then have moderate resistance.

Similar to the observed results in the first experiment, most genotypes from the F_2 generation in the second experiment were found to be highly resistant (Figure 2). The histograms plotted for the two experiments (Figures 1 and 2), together with the goodness-of-fit test performed in the first experiment, indicate that the plants present oligogenic inheritance. Considering that there are two genes involved in the control of resistance and that they are located on different chromosomes, an independent distribution of these two genes can be expected.

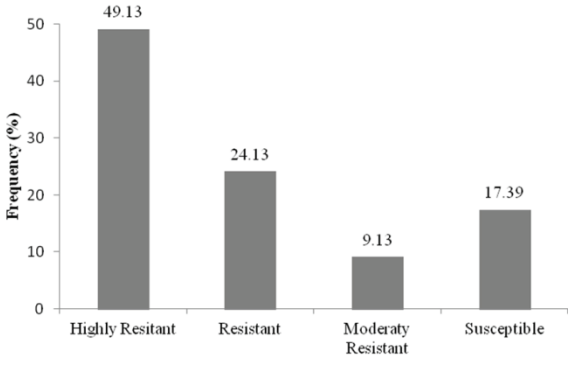

Figure 2. Frequency of reproduction factor of *Meloidogyne incognita* in plants in the F_2 generation cotton genotypes in the second experiment. Goiania, Goiás State, 2015. *Genotypes with RF values between 0.01 and 1 = highly resistant; genotypes with RF values between 1.1 and 6.0 = resistant; genotypes with RF values between 6.1 and 12 = moderately resistant, and those with RF values greater than 12 were considered susceptible.

Polygenic and oligogenic resistance are interesting and necessary tools for plant disease management. Although they result in different levels of resistance, from high susceptibility to high resistance, they are more stable than monogenic resistance.

Assuming the same environmental and genetic conditions, genetic changes in several pathogenicity *loci* are needed for pathogens to overcome plant resistance and become virulent. The cotton genotypes tested in this study likely present oligogenic resistance, which tends to decrease disease severity in cultivated areas, and their inclusion in improvement programs is recommended.

Conclusion

Genotype TX 25 presents resistance against *M. incognita* race 3. Genotype M315 presents resistance against *M. incognita* race 3. The genetic control of *M. incognita* race 3 resistance in genotype TX 25 is predominantly oligogenic. The F_2 generation genotypes present oligogenic resistance to *M. incognita*.

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