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Characteristics of mixed *Meloidogyne arenaria* and *M. incognita* populations in flue-cured tobacco

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Summary – Two years of field experiments were conducted to characterize the association of *Meloidogyne arenaria* race 2 (populations Pelion and Govan) and *M. incognita* race 3 in tobacco resistant to *M. incognita* races 1 and 3 and tobacco susceptible to both *Meloidogyne* species. Experiments also studied whether host resistance to *M. incognita* races 1 and 3 was modified by *M. arenaria* infection. Tobacco plants were simultaneously inoculated with eggs of *M. incognita* and *M. arenaria*. Species identity of *Meloidogyne* was determined at harvest by lengths of second-stage juveniles. *M. arenaria* race 2 infection did not predispose the *M. incognita*-resistant tobacco to *M. incognita* parasitism. Root galling of *M. incognita*-resistant tobacco was more severe with the *M. arenaria* population Pelion than with Govan. In infestations of susceptible tobacco with *M. arenaria* and *M. incognita*, *M. arenaria* Govan proportions at end season were greater ($P = 0.05$) than Pelion proportions in similar treatments.

Résumé – ***Charactéristiques de populations mixtes de* Meloidogyne arenaria *et* M. incognita *parasitant le tabac*** – Des expériences en champ ont été poursuivies pendant deux ans afin de caractériser l'association de *Meloidogyne arenaria* race 2 (populations Pelion et Govan) et de *M. incognita* race 3 sur des plants de tabac résistant à *M. incognita* races 1 et 3 ainsi que sur des plants de tabac sensible aux deux espèces. A été également étudié l'effet potentiel de l'infestation par *M. arenaria* sur la résistance de l'hôte à *M. incognita* races 1 et 3. L'identité spécifique des *Meloidogyne* a été établie à la récolte en se fondant sur la longueur des juvéniles de deuxième stade. Les plants de tabac résistants à *M. incognita* ne se sont pas montrés prédisposés à l'infestation par *M. incognita* lorsqu'ils étaient infestés par *M. arenaria* race 2. Le développement des galles sur les racines de tabac résistant à *M. incognita* est plus important dans le cas de la population Pelion que dans celui de la population Govan de *M. arenaria*. Lors d'infestations mixtes par *M. incognita* et *M. arenaria*, et avec des traitements équivalents sur plants de tabac sensible, la proportion de la population Govan de *M. arenaria* est toujours plus importante ($P = 0,05$) que celle de la population Pelion.

Key-words : *Meloidogyne*, root-knot nematode, tobacco, resistant, susceptible, interaction.

Flue-cured tobacco is an important cash crop in the southeastern USA. More than 20 000 ha are planted to tobacco in South Carolina yearly. South Carolina farm income from tobacco is nearly $ 200 million per year (Gooden *et al.*, 1991). Root-knot nematodes (*Meloidogyne* spp.) are serious pests of flue-cured tobacco and account for approximately 15 % annual loss in tobacco production world wide (Schneider, 1991). Root-galling interferes with normal root functions and reduces vigor of afflicted plants. Futhermore, root-knot nematodes predispose plants to secondary saprophytic and pathogenic invaders resulting in a variety of disease complexes with fungi and bacteria (Powel, 1971, 1979). Incidence and severity of certain diseases such as Black Shank *(Phytophthora parasitica)* and Granville Wilt *(Pseudomonas solanacearum)* are increased by root-knot nematode infection (Shepherd & Barker, 1989; Schneider, 1991). In addition to influences of *Meloidogyne* on other pathogens, interactions may be present between different species of root-knot nematodes (Johnson & Nusbaum, 1970; Kinloch & Allen, 1972). Different *Meloidogyne* species have diverse host requirements, but are, however, similar enough for their ecological niches to overlap. The resulting interspecific competition influences relative species proportions in mixed populations (Nusbaum & Barker, 1971).

Meloidogyne javanica and *M. arenaria* are regarded as the most damaging root-knot nematode species in the southeastern U.S. tobacco production area, followed by *M. incognita* (Barker *et al.*, 1981). No resistant cultivars are commercially available in the U.S. for the first two species and both are also more tolerant to certain nematicides than is *M. incognita* (Barker *et al.*, 1981; Nordmeyer *et al.*, 1982; Nordmeyer & Dickson, 1985). *M. incognita* host races 1 and 3 are reliably controlled with resistant tobacco cultivars. The incidence of *M. arenaria* has increased and this species frequently occurs in mixed infestations with *M. incognita* in flue-

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cured tobacco in South Carolina and other southeastern states (Fortnum *et al.*, 1984; Rich & Garcia, 1985; Schmitt & Barker, 1988; Barker, 1989; Johnson, 1989; Young, 1992). Shifts in species ratios of polyspecific populations in favor of *M. incognita* isolates which can be controlled effectively by chemical means and host plant resistance are desirable (Fortnum & Currin, 1993). Wide-spread use of *M. incognita*-resistant tobacco cultivars has led to selection of virulent *M. incognita* isolates (Graham, 1969) and to increased proportions of *M. arenaria* and *M. javanica* in mixed infestations (Fortnum *et al.*, 1984; Barker, 1989; Young, 1992). Interactions between *Meloidogyne* species must be identified and understood in order to more effectively manage nematode communities.

Loss of *M. incognita*-resistance in *M. incognita*-resistant tobacco after infection with *M. arenaria* has been reported (Eisenback, 1983; Tedford, 1986; Tedford *et al.*, 1986; Ibrahim, 1987). This phenomenon challenges current nematode management practices because the benefit of resistant tobacco cultivars may be diminished. Two years of field experiments were conducted with susceptible and resistant tobacco cultivars infested with isolates of *M. arenaria* race 2 and *M. incognita* race 3. The objectives were to : *i)* assess the influence of *M. arenaria* parasitism on *M. incognita*-resistance in tobacco : *ii)* analyse how mixed *M. arenaria* and *M. incognita* populations interact in a susceptible tobacco cultivar, and *iii)* determine potential differences between *M. arenaria* isolates with respect to objectives *i* and *ii*.

Materials and methods

Nematode isolates

M. arenaria race 2 isolates Govan and Pelion from Bamberg and Lexington Counties, South Carolina, respectively, and one *M. incognita* race 3 isolate from Florence County, South Carolina, were used throughout this study. Cultures were maintained in the greenhouse on tomato (*Lycopersicon esculentum* Mill.) cv. Rutgers. Eggs were extracted from 40 to 60-day-old galled roots with 0.05 % sodium hypochlorite and washed in tap water (Hussey & Barker, 1973). Egg suspensions were diluted to allow infestation of soil and plants with 10 ml of egg suspension of each *Meloidogyne* species in the desired population densities.

Tobacco cultivars and experiment design

In the first year, tobacco (*Nicotiana tabacum* L.) cvs Coker 176 (resistant to *M. incognita* races 1 and 3) and Coker 319 (susceptible to all *M. incognita* and *M. arenaria* races) were tested. For the second year, NC 95 (resistant to *M. incognita* races 1 and 3) was included.

Experiments were designed in approximately 100 m long rows under field conditions. Raised planting beds were 75 cm wide and spaced 150 cm apart. Whole rows were fumigated with Terr-o-Gas (67 % methyl bromide and 33 % chloropicrin) at a rate of 408 kg/treated hectare to control nematodes and soil fungi. The fumigant was applied approximately 15 cm deep with three chisels per bed. Rows were immediately covered with plastic and sealed with soil on all sides. Fumigated rows alternated with untreated spacer rows. After 9 days, plastic covers were removed, and tobacco plants were transplanted on April 27, 1990 and May 2, 1991. Spacing between the plants was 60 cm.

Planting material was produced in seed beds following recommended practices (Gooden *et al.*, 1991). Within the first week after transplanting, soil around individual plants was infested with nematode eggs by pipetting 5 ml of egg suspension each in two holes adjacent to each plant. Control plants without nematodes received extracts prepared from uninfected tomato roots. Holes were filled with soil to prevent desiccation of eggs. Infested plants within rows were separated from each other by two border plants to prevent cross contamination through mechanical weed control measures. Experiment plants received 0, 5, or 15×10^3 eggs of *M. incognita* and 0, 5, 15, or 30×10^3 eggs (highest level added only in the second year) of *M. arenaria* in all combinations applied simultaneously. The experiments were designed as split-split-plots with four replications; tobacco cultivars were tested as the main group, followed by infestation levels and *M. arenaria* isolate. Each treatment consisted of four plants.

Harvest and assessment

Roots were removed from the soil in late August to September. Harvest was staggered by cultivar and replication to allow processing of the large amounts of sample material. In the laboratory, roots were washed free of soil, and root-knot severity was rated on a 0 to 10 scale where : 0 = healthy, and 10 = dead (Zeck, 1971). Random root samples of *ca.* 20 g were taken from each root system and second-stage juveniles (J2s) were hatched in a mist chamber for 7 days (Seinhorst, 1964). J2s from each treatment were heat relaxed with hot water and preserved in 2.5 % formaldehyde and measured for species identification as follows (Tedford, 1986; Tedford *et al.*, 1986; Fortnum & Currin, 1993). From each treatment, 200 J2s were traced with a Leitz Dialux 20 microscope equipped with a Leitz drawing tube (Ernst Leitz Inc., Wetzlar, Germany), and nematode lengths were determined using a Zidas digitizing board (Carl Zeiss, Inc., Thornwood, NY). Length measurements between 300 µm and 560 µm were grouped in 20 classes of 13-µm increments to yield length distributions for individual treatments. Two hundred length values from monospecific populations were mixed in predetermined ratios of *M. arenaria* and *M. incognita*. Observed length distributions of J2s from experimental treatments were compared to length distributions of these simulated species mixtures by χ^2 analysis. Species proportion of the best fitting simulated distribution was

used to give an estimated value for the species proportion of the experimental treatment. Results were subjected to ANOVA and T-tests to determine significant effects. Analyses were conducted using SAS (SAS Institute Inc., Cary, NC).

Results

Abundant root-galling and egg masses were observed in all compatible nematode-plant interactions. Infestations of Coker 176 and NC 95 with *M. incognita* eggs showed only neglectable root-knot nematode reproduction, confirming the resistance to the selected *M. incognita* isolate. Root-galling of these two resistant cultivars in response to *M. arenaria* Govan infestation was less ($P = 0.05$) than observed on Coker 319, indicating an inhibitory effect of the *M. incognita*-resistance on this isolate (Table 1). The *M. arenaria* isolate Pelion produced more root-galling ($P = 0.05$) than the Govan isolate in treatments of *M. incognita*-resistant cvs Coker 176 and NC 95. This was not true in *M. incognita*-susceptible cv. Coker 319, where both *M. arenaria* isolates led to equally high root-galling ratings. In mixed *M. incognita* and *M. arenaria* infestations of the *M. incognita*-resistant cvs Coker 176 and NC 95, *M. incognita* was without influence on the observed root-galling ratings.

Length measurements of the *M. arenaria* and *M. incognita* isolates used in this study resulted in the J2-length distributions shown in Figure 1. The two species were characterized by distinct means with bell-shaped distribution curves which, however, substantially overlapped. Estimates of species proportions of monospecific *M. arenaria* or *M. incognita* control infestations by χ^2 analysis of J2 length measurements showed satisfactory accuracy, particularly in the resistant cultivars (Tables 2, 3). Estimates of species proportions of control infestations of resistant cultivars with either *M. arenaria*

Table 1. *Root-galling indices of* Meloidogyne incognita-*resistant tobacco cultivars NC 95, Coker 176, and susceptible Coker 319 after infestation with* M. arenaria *race 2 isolate Govan or Pelion at 5 000, 15 000 or 30 000 eggs per plant.*

No. eggs ($\times 10^3$)	NC 95	Coker 176	Coker 319
1st year			
Govan			
5	–	3.8 *b*	8.3 *a*
15	–	6.0 *a*	8.8 *a*
Pelion			
5	–	6.5 *a*	6.8 *b*
15	–	7.0 *a*	7.8 *ab*
2nd year			
Govan			
5	4.3 *b*	3.0 *c*	9.0 *a*
15	5.5 *b*	4.3 *b*	9.0 *a*
30	4.3 *b*	4.5 *b*	9.0 *a*
Pelion			
5	8.5 *a*	8.3 *a*	8.5 *b*
15	9.0 *a*	9.0 *a*	9.0 *a*
30	9.0 *a*	8.5 *a*	9.0 *a*

Within columns, means with the same letter are not different ($P = 0.05$). Analyses were separate for the 2 years and each cultivar.

Table 2. *Estimated* Meloidogyne arenaria *(MA) and* M. incognita *(MI) proportions using length of second-stage juveniles hatched from roots of the resistant tobacco cultivar Coker 176 and the susceptible cultivar Coker 319 after mixed infestation with eggs of* M. arenaria *race 2 isolates Pelion or Govan and* M. incognita *race 3 at different initial population densities in the first year.*

No. eggs ($\times 10^3$)		Proportion (%)	
MA	MI	MA	MI
Coker 176			
Ma-Govan			
5	0	95	5 *b*
15	0	94	6 *b*
5	5	74	26 *a*
15	5	88	12 *b*
5	15	90	10 *b*
15	15	89	11 *b*
MA-Pelion			
5	0	100	0 *b*
15	0	100	0 *b*
5	5	95	5 *ab*
15	5	85	15 *a*
5	15	90	10 *ab*
15	15	90	10 *ab*
Coker 319			
MA-Govan			
0	5	13	87 *a*
0	15	17	83 *a*
5	0	97	3 *e*
15	0	93	7 *de*
5	5	73	27 *c*
15	5	73	27 *c*
5	15	50	50 *b*
15	15	80	20 *cd*
MA-Pelion			
0	5	13	87 *a*
0	15	17	83 *a*
5	0	95	5 *b*
15	0	88	12 *b*
5	5	13	87 *a*
15	5	33	67 *a*
5	15	30	70 *a*
15	15	28	72 *a*

Means with the same letter are not different ($P = 0.05$). Analyses were separate for each cultivar and each *M. arenaria* isolate.

Table 3. *Estimated* Meloidogyne arenaria *(MA) and* M. incognita *(MI) proportions using length of second stage juveniles hatched from roots of the resistant tobacco cultivars Coker 176 and NC 95 and the susceptible cultivar Coker 319 after mixed infestation with eggs of* M. arenaria *race 2 isolates Pelion or Govan and* M. incognita *race 3 at different initial population densities in the second year.*

No. eggs ($\times 10^3$)		Proportion (%)	
MA	MI	MA	MI
Coker 176			
MA-Govan			
5	0	99	1 *a*
15	0	100	0 *a*
30	0	98	2 *a*
5	5	100	0 *a*
15	5	95	5 *a*
30	5	95	5 *a*
5	15	100	0 *a*
15	15	100	0 *a*
30	15	98	2 *a*
MA-Pelion			
5	0	97	3 *b*
15	0	97	3 *b*
30	0	90	10 *b*
5	5	98	2 *b*
15	5	93	7 *b*
30	5	91	9 *b*
5	15	99	1 *b*
15	15	95	5 *b*
30	15	66	34 *a*
NC 95			
MA-Govan			
5	0	92	8 *bcd*
15	0	93	7 *bcd*
30	0	99	1 *d*
5	5	98	2 *d*
15	5	88	12 *bc*
30	5	84	16 *ab*
5	15	75	25 *a*
15	15	95	5 *cd*
30	15	100	0 *d*
MA-Pelion			
5	0	96	4 *cd*
15	0	86	14 *b*
30	0	89	11 *bc*
5	5	96	4 *cd*
15	5	70	30 *a*
30	5	80	20 *b*
5	15	83	17 *b*
15	15	98	2 *d*
30	15	100	0 *d*
Coker 319			
MA-Govan			
0	5	0	100 *a*
0	15	2	98 *a*
5	0	80	20 *cde*
15	0	80	20 *cde*
30	0	83	17 *de*
5	5	50	50 *bcd*
15	5	63	37 *bcd*
30	5	63	37 *bdc*
5	15	42	58 *b*
15	15	48	52 *bc*
30	15	70	30 *bcde*
MA-Pelion			
0	5	0	100 *a*
0	15	2	98 *a*
5	0	85	15 *d*
15	0	84	16 *d*
30	0	40	60 *c*
5	5	2	98 *a*
15	5	9	91 *ab*
30	5	21	79 *abc*
5	15	7	93 *ab*
15	15	27	73 *bc*
30	15	16	84 *ab*

Means with the same letter are not different ($P = 0.05$). Analyses were separate for each cultivar and *M. arenaria* isolate.

isolate (Govan or Pelion) resulted in values very close to the expected 100 % *M. arenaria* proportion. Some treatments of susceptible tobacco (Coker 319) were slightly less accurate, but still within tolerable limits.

Mixed infestations of resistant tobacco with *M. arenaria* and *M. incognita* generally resulted in low *M. incognita* proportion estimates (Tables 2, 3). Only five out of 32 mixed *M. arenaria* and *M. incognita* infestations were significantly different from *M. arenaria* control infestations. Cv. NC 95 tobacco showed higher estimated *M. incognita* proportions than cv. Coker 176. No particular infestation level or *M. arenaria* isolate reproducibly led to higher *M. incognita* proportions.

The two *M. arenaria* isolates interacted very differently with *M. incognita* in roots of the susceptible cultivar Coker 319 (Tables 2, 3). Estimates of species proportions indicated that *M. incognita* became the predominant isolate over *M. arenaria* Pelion, when both coinhabited the same root system. Frequently, exclusively *M. incognita*-sized juveniles were recovered from susceptible roots inoculated with both isolates. This effect was not observed with the Govan isolate and *M. incognita,* where *M. arenaria*-sized juveniles represented at least half of the recovered nematodes and in most cases this species was the predominant taxon.

Discussion

In contrast to earlier reports (Eisenback, 1983; Tedford, 1986; Tedford *et al.,* 1986; Ibrahim, 1987), our results demonstrate that the two *M. arenaria* isolates had no predictable or consistent influence on *M. incognita*-resistance in Coker 176 and NC 95. The presence of *M. incognita* proportions in resistant tobacco did not follow an ordered pattern. Rather, there was no *M. arenaria* infestation level beyond which a loss of *M. incognita*-resistance occurred, and no consistent effect of *M. arenaria* infestation level on *M. incognita* resistance was observed.

NC 95 tobacco repeatedly showed higher *M. incognita* proportions than Coker 176. These findings do not fully resolve whether a loss of *M. incognita*-resistance in tobacco due to *M. arenaria* infection occurs or not. If a real phenomenon, it does not take place regularly or predictably. Sporadic *Meloidogyne* reproduction and detection of *M. incognita*-sized root-knot nematodes in resistant cultivars after *M. incognita* infestation may have resulted from residual hot spots of *M. incognita* race 2 or 4 that were not totally eliminated by fumigation. It is also possible that the genotype of *M. incognita*-resistant tobacco, especially NC 95, is variable and could allow sporadic *M. incognita* reproduction (J. D. Eisenback, pers. comm.). In the majority of treatments in this study, however, *M. arenaria* was without significant influence on *M. incognita*-resistance. The fact that two distinct *M. arenaria* isolates and two separate tobacco cultivars produced comparable results supports this finding. We

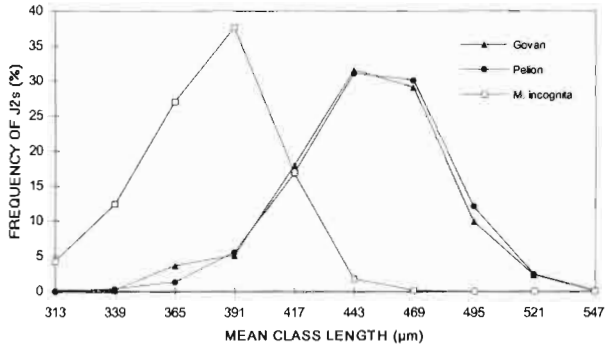

Fig. 1. *Length distributions of second-stage juveniles hatched from eggs on tobacco roots infected with* Meloidogyne arenaria *(Govan or Pelion) or* M. incognita.

therefore conclude from our work that the use of tobacco cultivars with *M. incognita*-resistance is of benefit even in fields with mixed infestations of *M. arenaria* and *M. incognita* (races 1 and 3), as long as *M. arenaria* levels are below damage threshold levels.

Where *M. arenaria* infestation levels increase, the implementation of alternative measures such as rotation with non-host crops, fallow, or the application of nematicides has to be considered. The strategy of deliberately shifting species proportions through cultural practices towards *M. incognita* races 1 or 3 (Fortnum & Currin, 1993), which can be controlled by resistant cultivars, appears as a promising control scheme for root-knot nematodes in the production of tobacco.

Two years of field experiments revealed fundamental differences between the two *M. arenaria* isolates in aggressiveness and competitiveness. The Govan isolate produced fewer galls and egg masses than *M. arenaria* Pelion in both resistant tobacco cultivars. In cv. Coker 319 this observation was not evident and both isolates led to similar root-galling ratings. This suggests that the ability of *M. arenaria* to reproduce on *M. incognita*-resistant tobacco is a quantitative trait.

Pelion and Govan also differed in their ability to compete with *M. incognita* in susceptible tobacco. Although Pelion proved to be more damaging and prolific than Govan in resistant tobacco cultivars, this isolate was not able to become established in mixed populations with *M. incognita* in the susceptible cv. Coker 319. Govan, which was less aggressive in resistant tobacco, surprisingly became the predominant species when competing with *M. incognita* in cv. Coker 319. The Govan population apparently has the potential to be more aggressive and competitive than Pelion. The lack of aggressiveness in resistant tobacco could indicate that the genotypic basis for reproduction on resistant germplasms is superimposed on the general parasitic abilities to infect and reproduce, comparable to the concept discussed by Heath (1981). As soon as resistance constraints are removed, as is the case in cv. Coker 319, Govan competes better with *M. incognita* than does Pelion.

The finding that one *M. arenaria* isolate was less aggressive in *M. incognita*-resistant cultivars than in susceptible tobacco indicates that this resistance also confers inhibition of certain *M. arenaria* isolates. Barker and Melton (1990) report similar findings in their testing of selected tobacco cultivars with several *Meloidogyne* species and isolates. They found that *M. incognita*-resistant tobacco cultivars carry some tolerance or resistance against species other than *M. incognita,* particularly *M. arenaria* race 1.

The results clearly indicate that different *M. arenaria* isolates are distinct in their biological capabilities, suggesting that identification of root-knot nematodes to the species levels is not always satisfactory. Carpenter and Lewis (1991), Noe (1992), and Ibrahim and Lewis (1993) reported differences among *M. arenaria* isolates that would warrant different agricultural recommendations for different *M. arenaria* isolates. Such differences have been shown to occur between the two *M. arenaria* race 2 isolates employed in the present study on tobacco. It is desirable to recognize groups of such nematode biotypes and to work out identification systems. In future work, testing of more *M. arenaria* isolates, including host race 1, for their ability to break *M. incognita*-resistance should be considered. Accordingly, screening *M. incognita* isolates for their ability to benefit from physiological changes elicited by *M. arenaria* is important, since only one isolate was included in this study.

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