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Interaction among *Meloidogyne incognita* and *M. enterolobii* with *Pratylenchus zeae* in Sugarcane[1]

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ABSTRACT

Plant-parasitic nematodes *Meloidogyne incognita* and *Pratylenchus zeae* are commonly associated to sugarcane in Brazil causing serious problems. Thus, the objectives of this study were to determine the reproductive rate of *M. incognita* and *M. enterolobii* in sugarcane when inoculated in isolation and together with *P. zeae* and the effects of this interaction on the early development of two varieties of sugarcane. Two experiments were performed. In the first experiment, three different population densities of *M. incognita* and *M. enterolobii* were inoculated in both sugarcane varieties. In the second experiment, inoculation of *P. zeae* followed by inoculation with *M. incognita* or *M. enterolobii* was carried out. *Meloidogyne enterolobii* did not show good development in both sugarcane varieties after 120 days of infestation; contrary to *M. incognita*, which reached high population levels. Fresh and dry shoot biomasses were lower under joint infestation of *P. zeae* and *Meloidogyne*. In mixed infections, *P. zeae* suppressed the development of *M. incognita* and increased the multiplication of *M. enterolobii* in the variety RB867515 whereas the contrary was observed in the variety RB92579, demonstrating once more the resistance reaction of this variety to *M. enterolobii*.

Keywords: mixed interaction, root-knot nematode, root-lesion nematode, *Saccharum* spp.

INTRODUCTION

Sugarcane (*Saccharum* spp. L.) is strongly related to the socioeconomic development of Brazil which is responsible for 45% of world production[1] mainly used for the bioethanol and sugar production. Around the world sugarcane is significant for charcoal production, fertilizers and also for animal feed being a valuable crop in the trade balance of many countries.[2]

Plant-parasitic nematodes (PPN) are one of the main causes for sugarcane yield reduction in Brazil.[3] Most common and damaging genera are root-knot nematode (*Meloidogyne* spp. Goeldi) and lesion nematodes (*Pratylenchus* spp. Filipjev). *P. zeae* Graham, *M. incognita* (Kofoid & White) Chitwood and *M. javanica* (Treub) Chitwood are highly pathogenic and the most important to sugarcane production due to significant crop losses.[4-6]

Meloidogyne enterolobii Yang & Eisenback, synonym to *M. mayaguensis* Rammah & Hirschmann, is a highly aggressive nematode that is causing severe damage to several crops worldwide. The population density of PPN, soil type and sugarcane variety influence the intensity of the parasitism damage,[7] which, in turn, is determined by initial population density and development and yield of the crop. The increase in initial nematode population density is negatively correlated with plant development.[8,9] Plant responses due to nematode parasitism vary with initial inoculum of the pathogen and the level of resistance/tolerance of the species. High levels of initial infestation of nematodes exerts an inoculum pressure on the plants capable of increasing their susceptibility or break their resistance, increasing nematode penetration and development inside roots.[10,11]

Mixed nematode infestation in sugarcane fields is very common and monoculture, intense soil use, low fertility and long drought seasons aggravate the situation [8,7]. The simultaneous parasitism of different species plant-parasitic nematodes negatively interferes in crop yield, resulting in greater damages when compared to single species infestation.[12,13]

Studies addressing mixed infestation and damages caused by polyspecific nematode communities are sparse and restrict to some crops as soybean, onion and sugarcane. [7,14,15] Therefore, we aimed to determine the reproductive rate of *M. incognita* and *M. enterolobii* when inoculated in isolation or together with *P. zeae* in sugarcane and the effects of such interaction on the early development of sugarcane varieties RB867515 and RB92579.

MATERIAL AND METHODS

Experiment conduction

Two experiments were carried out under greenhouse conditions at the Plant Nematology Laboratory from the Department of Agronomy at the Federal Rural University of Pernambuco (Recife, Pernambuco State, Brazil). Sugarcane varieties RB867515 and RB92579 were used on both experiments. These varieties are among the most produced in Brazil. In Experiment 1 stalks from both varieties were obtained from the Estação Experimental de Cana-de-açúcar de Carpina (Carpina, Pernambuco State, Brazil) for seedling production. For Experiment 2, seedlings were obtained from shoot apex cultivation developed by the Programa de Melhoramento Genético de Cana-de-açúcar – RIDESA, produced and donated by Biofábrica of Santa Tereza Mill, Goiana-PE.

Seedlings were kept under greenhouses conditions throughout the experiments. After nematode inoculation, irrigation was suspended for five days to avoid inoculum leaching. Later, plants were transplanted to seedling bags (5 L capacity) with autoclaved soil, until evaluations time. The plants were watered and fertilized as needed.

Nematode inoculum

Populations of *M. incognita* were obtained from roots of naturally infected sugarcane fields. Preliminary identification of nematode species was performed by esterase enzyme electrophoretic patterns in 7% polyacrylamide gel in a horizontal electrophoresis system using *M. javanica* as reference, according to Carneiro & Almeida.[16] When the species was identified, eggs were inoculated in tomatoes (*Solanum lycopersicum*, variety 'Santa Clara') for multiplication.

M. enterolobii was obtained from guava roots from the São Francisco Valley (09°23'54" S 40°29'54" W). The roots were washed free of debris and females were collected and identified by esterase enzyme electrophoretic patterns, as previously described. Later, eggs were extracted and inoculated into 'Santa Clara' tomatoes for multiplication.

The eggs extraction was according to Hussey and Barker,[17] modified using blender for 30 seconds. Egg suspensions were counted in Peters' slides under an optical microscope.

The population of *P. zeae* was obtained from infested soil grown with sugarcane at Santa Teresa Mill, Goiana-PE

(7°33'39" S 35°00'10" W), and it was previously identified through morphometry.[18] Nematodes were maintained in shoot apex seedlings of sugarcane varieties RB 867515 and RB 92579. For the experiment, the nematodes were extracted from the roots through sucrose centrifugal flotation technique.[19] Individuals were quantified using Peters' slides under optical microscope.

Experiment 1: Reproduction of Meloidogyne incognita and Meloidogyne enterolobii in single inoculation

Sugarcane stalks were cut in 60-mm pieces, with a single bud per billet, and sown into 500 mL plastic cups with sterile soil. Plants that showed better development after 15 days were selected and inoculated with egg of either *M. incognita* or *M. enterolobii*. The inoculum was poured over two different holes equidistant to the plant stalks. The plants were completely randomized in a factorial design, with two varieties of sugarcane (RB867515 and RB92579) and three inoculum density (5,000, 10,000 and 20,000 eggs per plant) with five replicates for each nematode species beyond the negative control which was composed by plants without nematodes.

Roots were rinsed in tap water 120 days after inoculation (DAI) for evaluations. Egg extraction followed the protocol proposed by Hussey and Baker,[17] modified by Bonetti and Ferraz,[20] using a blender for 30 seconds. Eggs counting of each experimental unit was done using Peters' slides under optical microscope. The following parameters were evaluated: total final population of nematodes within sugarcane roots and reproduction factor (RF) calculated by the relation between final population and initial population of each *Meloidogyne* species.[21]

Experiment 2: Early development of sugarcane and reproduction of Meloidogyne incognita, Meloidogyne enterolobii and Pratylenchus zeae

All plants were previously inoculated with 2,000 eggs + J_2 of *P. zeae*. After seven days, the same plants were inoculated with 2,000 eggs + J_2 of *M. incognita* or *M. enterolobii*, through two equidistant holes near the plant stalks. Plants were completely randomized under a factorial design with two mixed inoculations (*P.* zeae + M. *incognita* and *P. zeae* + M. *enterolobii*) and two sugarcane varieties (RB867515 and RB92579) with five replicates. Evaluations were performed at 100 DAI.

Plants were uprooted and washed thoroughly with tap water. Root systems were separated and chopped in a blender with water, then centrifuged in sucrose solution.[19] Nematode suspensions were quantified using Peters' slides under optical microscope. The following parameters were evaluated: fresh and dry shoot biomass (FSB and DSB, respectively), fresh root biomass (FRB), plant height and number of eggs and J_2 of each *Meloidogyne* species and eggs, J_2 and adults of *P. zeae* inside sugarcane roots.

Statistical Analysis

Data were analyzed by normality and variance homogeneity. For each plant/nematode combination, the reproduction factor (RF) was calculated as RF = FP/IP, where FP=final population density and IP=initial population density. Population density and reproduction factor were transformed in log (x + 1) and ($\sqrt{x}$ + 1) for analysis of variance (ANOVA). Tukey test at 5% of probability was used to compare means among significantly different factors and interaction.

RESULTS

Experiment 1: Reproduction of Meloidogyne incognita and Meloidogyne enterolobii in single inoculation

M. enterolobii showed the lowest population densities when inoculated in sugarcane, keeping a low reproductive stability regardless of initial inoculum density ($p > 0,05$) in both sugarcane varieties; whereas the population density of *M. incognita* increased proportionally to the initial inoculum density, reaching high reproduction values with the inoculum of 10,000 eggs + J_2 per plant, and a population reduction with 20,000 eggs + J_2 inoculum (Table 1).

The initial inoculum density of *M. incognita* significantly influenced the reproduction factor only for sugarcane variety RB867515, were we observed the greatest population level, when 10,000 eggs + J_2 were inoculated with RF = 120.95; whereas there was no significant difference among the inoculum densities used for the variety RB92579 (Table 1). When comparing the sugarcane varieties, we observed that plants of RB867515 inoculated with 10,000 eggs + J_2 showed higher multiplication of *M. incognita*. There was no difference on the reproduction of nematodes when plants were inoculated with 5,000 and 20,000 eggs + J_2 per plant (Table 1).

Table 1. Population density and reproduction factor (RF) of *Meloidogyne incognita* and *M. enterolobii* at 120 days after inoculation on sugarcane varieties RB 867515 and RB 92579

Inoculum density	*Meloidogyne incognita*			
	Population Density		RF	
	RB 867515	RB 92579	RB 867515	RB 92579
5,000	29,200bA	103,860aA	5.84	20.77
10,000	120,948aA	371,400aB	12.10	37.14
20,000	54,860bA	85,410aA	2.74	4.27
p-value	< 0.005	< 0.005		
CV (%)	7.93			
Inoculum density	*Meloidogyne enterolobii*			
	Population Density		RF	
	RB 867515	RB 92579	RB 867515	RB 92579
5,000	512^{ns}	300^{ns}	0.10	0.06
10,000	192	600	0.01	0.06
20,000	488	550	0.02	0.02
p-value	< 0.005	< 0.005		
CV (%)	65.07			

Means within columns followed by the same lowercase letter and within lines followed by the same uppercase letter are not statistically different (P > 0.05 ANOVA followed by Tukey test). Analysis was performed on log (x + 1) - transformed data. Original means are displayed. ns – not significant

Experiment 2: Early development of sugarcane and reproduction of Meloidogyne incognita, Meloidogyne enterolobii and Pratylenchus zeae

No interaction between sugarcane varieties and nematode species was observed. *M. incognita* and *M. enterolobii* when inoculated together with *P. zeae* significantly decreased fresh and dry shoot biomasses when compared to nematode-free seedlings (Table 2). However, fresh root biomass and plant height did not differ statistically between treatments ($p < 0.05$). Regarding sugarcane varieties, we observed increases in dry shoot biomass and plant height of variety RB 867515 (Table 2).

We observed that the population densities of both *M. incognita* and *M. enterolobii* were not high when plants were previously inoculated with *P. zeae.* The FP of *M. enterolobii* has decreased in sugarcane variety RB92579; whereas there was an increase in the population of *Meloidogyne* species in variety RB867515 (Table 3). The population density of *M. incognita* in sugarcane variety RB92579 was significantly greater when compared to the one observed in RB867515 (Table 3). The Reproduction factor (RF) values observed for mixed infestation of *M. incognita* and *P. zeae* in RB 92579 was 1.99 and *M. enterolobii* and *P. zeae* in RB 867515 was 3.28. Reproduction factors of *Meloidogyne* sp. were always below 1 (Table 3).

DISCUSSION

The varieties tested in this study although susceptible to root-knot nematodes have good agronomic attributes as well as resistance to environment with high solar radiation and water shortage.[5,22,23] Because are extensively used in Brazil hence the importance of testing the effect of interaction between plant parasitic nematodes in these varieties.

Initial population densities of *M. incognita* influenced its reproduction, that is, low inoculum density resulted in greater multiplication rates. High nematode reproduction factors in low inoculum levels might be due to abundant food resources, reduction in the competition levels with other organisms and the host's ability to tolerate nematode populations.[24] The inoculum of 20,000 eggs + J_2 of *M. incognita* per plant can be considered too high, which leads to competition among specimens, decreasing the FP and, consequently, the reproduction factor.

Silva et al.[23] report that *M. enterolobii* does not reproduce easily in sugarcane. Thomazelli et al.[25] evaluated thirteen varieties of sugarcane for their resistance to *M. enterolobii* based on the nematode reproduction factor. All sugarcane cultivars were found to be immune to *M. enterolobii*. Our results confirm such studies since the reproduction factor of this species was low even after 120 DAI. The exposure time of a host to nematodes influences its response to

Table 2. Shoot fresh biomass (SFB), dry shoot biomass (DSB), fresh root biomass (FRB) and plant height of sugarcane, varieties RB 867515 and RB 92579, inoculated with *Meloidogyne incognita* or *Meloidogyne enterolobii* and previously infected with *Pratylenchus zeae*

Treatments (T)	SFB	DSB	FRB	Height
M. incognita	147.63b	27.63b	59.45^{ns}	189.2^{ns}
M. enterolobii	174.25b	32.29b	64.88	184.6
Control	209.85a	41.15a	58.57	199.7
p-value (T)	< 0.001	< 0.001	0.489	0.232
Variety (V)				
RB 867515	187.63^{ns}	35.57a	64.53^{ns}	201.5a
RB 92579	166.85	31.80b	57.41	180.9b
p-value (V)	0.057	0.030	0.134	0.008
p-value (TxV)	0.903	0.201	0.808	0.231
CV (%)	16.08	13.32	20.65	10.28

Means followed by the same letter within columns are not statistically different (P > 0.05 ANOVA followed by Tukey test). ns – not significant

Table 3. Population density and reproduction factor of *Pratylenchus zeae* and *Meloidogyne* sp. in sugarcane RB varieties, 100 days after inoculation with *M. incognita* or *M. enterolobii*

	Population density			
Nematode	*Pratylenchus zeae*		*Meloidogyne* sp.	
	RB 867515	RB 92579	RB 867515	RB 92579
M. incognita	4,580bB	6,562aA	75bB	1,480aA
M. enterolobii	3,982aA	9,834bB	1,500aA	54bB
CV(%)	5.85		28.7	
	Reproduction factor			
Nematode	*Pratylenchus zeae*		*Meloidogyne* sp.	
	RB 867515	RB 92579	RB 867515	RB 92579
M. incognita	2.29	3.28	0.04	0.74
M. enterolobii	1.99	4.92	0.75	0.03

Means followed by the same letter, lowercase within columns and uppercase within lines, do not differ (P > 0.05 ANOVA followed by Tukey test). Original data are shown, but analysis was performed on log (x + 1) - transformed data

parasitism.[26] In our experiment, *M. enterolobii* was not able to multiply normally at 120 DAI, which indicates the resistance degree of both varieties to *M. enterolobii*.

In mixed infestations with plant parasitic nematodes in susceptible variety, both nematode species suppress each other due to decrease and interspecific competition of feeding sites.[15] This behavior can be attributed to the feeding habits of these species; *P. zeae* is a migratory endoparasite and *M. incognita* is a sedentary endoparasite. While *P. zeae* has rapid penetration and can move through the intracellular tissues of the host, *M. incognita* becomes sedentary after all the ecdysis and it is a highly specialized parasite, frequently having a systemic effect over the feeding of other nematodes within the same root.[27]

The decrease of *M. incognita* population in the presence of *P. zeae* demonstrate a competition between the nematodes for root penetration and feeding sites.[7,15] Furthermore, under high infestation, biochemical response of a stressed host might be harmful to the nematode.[28,29]

Despite the presence of mixed populations in sugarcane fields along Brazilian territory, specially Pernambuco state, it is possible to recognize regular prevalence of *P. zeae* in relation to species of *Meloidogyne*.[22] *P. zeae* and *M. incognita* have also been reported as the most recurrent genera in surveys of soil and root samples collected from sugarcane plantations in Alagoas, Brazil.[30]

Mixed infestation of migratory and sedentary endoparasitic nematodes is normally additive, however it does not always result in greater damage to the host when compared to single infestation.[31] Despite it is an agressive plant-parasitic nematode, *M. enterolobii* in the RB92579 variety combined with the competition for feeding site with *P. zeae* did not have a good development neither contributed to the enhancement of damage symptoms.

The increase in the FP of *M. enterolobii* in variety RB867515 might be due to the previous infection with *P. zeae*. This behavior may be caused by current host stress[32] and attraction of other nematodes to the penetration path made by *P. zeae*, where it was observed that nematodes aggregate around damaged areas.[33] On account of such population increase, we speculate that *M. enterolobii* was not able to infect roots with all its potential; and the low reproduction factor after 120 DAI in our experiment shows the delay and difficulty on the development of this species.

Pratylenchus zeae and *M. incognita* are nematodes that live together in the soils of sugarcane fields in Brazil.[34] In fact, some authors address the difficulty of developing a resistant variety of sugarcane due to mixed infestation under natural conditions.[22,35] As sugarcane plants are parasitized concomitantly by different species of plant-parasitic nematodes under field conditions, it is believed that in some situations different nematodes parasitize and feed on the same plant.[27]

Sugarcane varieties used in our experiment were inoculated with *P. zeae* and a few days later they were inoculated with *M. incognita* or *M. enterolobii*. The time between inoculations might have enabled a slight advantage of *P. zeae* over *Meloidogyne* sp. in terms of parasitism, since its rapid penetration and migratory ability might have left fewer feeding sites for both root-knot nematode species.

Mixed infestation of sugarcane caused shoot biomass reduction. The decrease of dry shoot biomass due to nematode parasitism might be explained by the water build-up in shoot tissues of an infested plant because of *Meloidogyne* sp. Parasitism.[36] Parameters such as plant height and root system weight might be an indicative of good development even under parasitism of plant-parasitic nematodes.[37] Our results suggest an initial tolerance response of both sugarcane varieties (RB92579 and RB867515) to *M. incognita* and *M. enterolobii*.

Environmental factors such as temperature, humidity, and the chemical and physical properties of the soil influence the development of plant-parasitic nematodes, and in a scenario of climate change, it is essential to consider and explore these variables in the dynamics of the interaction between different species of plant-parasitic nematodes in sugarcane cultivation.

CONCLUSIONS

The results of our experiments elicit new evidences of the potential of mixed infestation of plant-parasitic nematodes and add up to the scarce literature on the subject. Our results support the ease of interaction among different species of nematodes in production fields. They also show that these nematodes, even though living together, may suppress or improve infection of species that are not mutually adapted. Future studies must be performed to improve our knowledge of how the interaction between *Meloidogyne* and *Pratylenchus* affect both species and plant development.

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DATA AVAILABILITY STATEMENT

The authors declare that all relevant data are included in this manuscript.

AUTHOR CONTRIBUTIONS

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