REVISTA BRASILEIRA DE FRUTICULTURA

Published by the Brazilian Society of Fruit Crops

ISSN 0100-2945

Plant Protection

Original Article - Edited by: Ivan Herman Fischer

Banana horizontal and vertical resistance to the burrowing nematode depends on the level of aggressiveness or virulence of the nematode population

Jansen Rodrigo Pereira Santos[1], Fábio Gelape Faleiro[2], Dilson da Cunha Costa[3], Edson Perito Amorim[4], Sebastião de Oliveira e Silva[5], Juvenil Enrique Cares[6]

[1] Universidade Federal de Santa Maria, Santa Maria, RS, Brazil.
[2] Embrapa Cerrados, Planaltina, DF, Brazil.
[3] Embrapa Recursos Genéticos e Biotecnologia, Brasília, DF, Brazil.
[4] Embrapa Mandioca e Fruticultura, Cruz das Almas, BA, Brazil.
[5] Universidade Federal do Recôncavo da Bahia, Cruz das Almas, BA, Brazil.
[6] Universidade de Brasília, Brasília, DF, Brazil.
*Corresponding author. E-mail address: jansen.santos@ufsm.br

Abstract - The burrowing nematode *Radopholus similis* is among the most damaging pathogens. Resistant plants are one of the most promising approaches for nematode control, and knowledge of resistance and aggressiveness components is essential to understand resistance genetics and developing new cultivars. Therefore, this study aimed to assess the degree of resistance of eight banana accessions to populations of *R. similis* to verify differences in the reproduction capacity between nematode populations and to study the horizontal/vertical resistance and aggressiveness/virulence components of *Musa* spp. and *R. similis* pathosystem. The accessions 4249-05, 4279-06, Yangambi Km5, 0323-03, 0337-02, 1304-06, Borneo and Grande Naine were inoculated with one of three *R. similis* populations from the Brazilian states of Pernambuco, Distrito Federal, and Santa Catarina and kept in a greenhouse. Accessions 4249-05, Yangambi Km5, 0323-03, and 4279-06 showed different resistance levels, and the Pernambuco population had the highest reproductive capacity. Using Griffing Model IV, evidence of vertical and horizontal resistance was observed, with accessions 4249-05 and Yangambi km5 showing the highest levels of horizontal resistance.

Index terms: Capacity of reproduction, host-pathogen interaction, *Musa* spp., *Radopholus similis.*

Rev. Bras. Frutic., v.45, e-070 DOI: https://dx.doi.org/10.1590/0100-29452023070
Received 24 Jun, 2022 ● Accepted 02 Jan, 2023 ● Published Mar/Apr, 2023. Jaboticabal - SP - Brazil.

Resistência horizontal e vertical da bananeira ao nematoide cavernícola depende do nível de agressividade ou da virulência da população do nematoide

Resumo - O nematoide cavernícola, *Radopholus similis*, está entre os patógenos de banana mais prejudiciais. Plantas resistentes são uma das abordagens mais promissoras para o controle de nematoides. O conhecimento de componentes da resistência e da agressividade é essencial para entender a genética de resistência e para desenvolver novas cultivares. Portanto, o objetivo deste estudo foi acessar o grau de resistência de oito acessos de bananeira a populações de *R. similis*, verificar diferenças na capacidade de reprodução entre populações de nematoides e estudar os componentes de resistência horizontal/vertical e agressividade/virulência no patossistema *Musa* spp. e *R. similis*. Os acessos 4249-05, 4279-06, Yangambi Km5, 0323-03, 0337-02, 1304-06, Borneo e Grande Naine foram inoculados com cada uma das três populações de *R. similis* (Pernambuco (PE), Distrito Federal (DF) ou Santa Catarina (SC)) e mantidos em casa de vegetação. Os acessos 4249-05, Yangambi Km5, 0323-03 e 4279-06 expressaram diferentes níveis de resistência, e a população do nematoide de PE foi a que apresentou maior capacidade de multiplicação. Baseado no Modelo IV de Griffing, evidências de resistência vertical e horizontal foram observadas, sendo que os acessos 4249-05 e Yangambi km5 foram os que apresentaram maiores níveis de resistência horizontal.

Termos para indexação: Capacidade de multiplicação, Interação planta/patógeno, *Musa* spp., *Radopholus similis.*

Introduction

Banana (*Musa* spp.) is the most popular and widely consumed tropical fruit in the world. Nevertheless, banana crops are affected by a plethora of pests and diseases, including plant-parasitic nematodes that infect banana roots and lead to different consequences, restricting fruit yield (MENDOZA et al., 2008). Known as the burrowing nematode, *Radopholus similis* (Cobb, 1893) Thorne, 1949 is considered the most important plant-parasitic nematode to this crop (GOWEN et al., 2005).

Burrowing nematode's management in large-scale systems has mainly been performed by repeated application of nematicides (GOWEN et al., 2005). However, using these chemicals harms the environment and the user's health. More recently, nematode control in banana plantations has included other practices, such as micropropagated plants and crop rotation (QUÉNÉHERVÉ, 2009). Breeding for resistance to nematodes is an appropriate option for the sustainable management of these parasites; nevertheless, few studies have covered banana resistance to nematodes.

Few advances have been in breeding for resistance to the burrowing nematode in bananas and plantains due to the genetic complexity of *Musa* spp. and variability among *R. similis* populations (HAEGEMAN et al., 2010; COSTA et al., 2008). However, different cultivars and wild hybrids have been tested for nematode resistance (QUÉNÉHERVÉ et al., 2009).

Reactions of banana accessions to burrowing nematodes depend on the aggressiveness of the nematode population, which is linked to the reproductive capacity and virulence of such parasites. More aggressive *R. similis* populations reproduce rapidly, severely injuring banana roots. Various reports have indicated direct correlations between the number of burrowing nematodes in banana roots and root damage (FALLAS et al., 1995; MARIN et al., 1999; MOENS, 2004; SANTOS et al., 2013). Therefore, quantifying *R. similis* population levels in roots may be used to determine differences in aggressiveness among populations. Additionally, there is a lack of information regarding resistance mechanisms and plant-pathogen interaction. Given this scenario, understanding how the resistance alleles interact with pathogen's (a)virulence alleles is of the utmost importance for defining breeding strategies for resistance (VAN DER PLANK, 1968).

The genetic basis of resistance to *R. similis* in banana plants has not been established, although some researchers have shown that this characteristic is controlled by one or a few genes (PINOCHET et al., 1998). Moens et al. (2002) evaluated the progeny resulting from a cross between 'Pisang Berlin' and 'Calcutta 4' observed segregation of resistance to *R. similis*. Dochez et al. (2009) assessed the progeny resulting from a cross between the diploid hybrids TMB2 x 6142-1 and TMB2 x 8075-7 and found that two dominant genes controlled resistance, named A and B, both with additive and interactive effects, by which the recessive bb suppresses the dominant A. Moreover, genetic differences among *R. similis* populations in *Musa* accessions have been detected by DNA markers and phenotype evaluations (COSTA et al., 2008; SANTOS et al., 2010).

Melo and Santos (1999) tested a modified version of Griffing model IV (GRIFFING, 1956) that provides simplified information on horizontal and vertical resistance on the host and pathogen virulence and aggressiveness. Therefore, the objectives of this study were to evaluate the reaction of eight contrasting banana accessions (4249-05, 4279-06, Yangambi Km5, 0323-03, 0337-02, 1304-06, Borneo and Grande Naine) to three *R. similis* populations from different States/District of Brazil: Pernambuco (PE), Distrito Federal (DF), and Santa Catarina (SC), to determine differences in reproductive capacity between these nematode populations, and to initiate the characterization of the components of horizontal/vertical resistance and aggressiveness/virulence in *Musa* spp. vs *R. similis* pathosystem using the method described by Melo and Santos (1999).

Materials and methods

Eight contrasting *Musa* accessions (Borneo, Grande Naine, Yangambi Km5, 1304-06, 4279-06, 4249-05, 0323-03, and 0337-02) were obtained from the germplasm bank of the National Cassava and Tropical Fruits Research Center of Embrapa (Brazilian Enterprise for Agricultural Research). Plantlets produced by tissue culture were acclimated for three weeks in a growth chamber (27–28 °C) with a 12-h photoperiod, then transplanted into 1.5-L pots containing an autoclaved mixture of oxysol and sand (3:1). All banana accessions were previously evaluated with *R. similis* population from Pernambuco State (PE) (9º20'42.6"S, 40º32'52.7"W) by Santos et al. (2013). They were then reassessed with the same population (PE) and with two other *R. similis* populations from the Distrito Federal (DF) (15º44'46.3"S, 47º39'36.4"W) and Santa Catarina State (SC) (26º42'50.1"S, 48º54' 36.6"W). The population from Pernambuco was originally collected in Petrolina from roots of a cv. 'Pacovan' bananas, while the SC population was collected in Luis Alves from roots of a cv. 'Nanicão' bananas. The *R. similis* population from DF was collected at Núcleo Rural Rajadinha from roots of *Musa coccinea* Andrews and *Heliconia* spp. All *R. similis* populations were identified based on morphological and morphometric characteristics, according to Cares and Andrade (2006). The experiment was not repeated once we reproduced the results previously obtained by Santos et al. (2013), who used the PE population, one of the three we used in this study.

All three *R. similis* populations had been maintained in 'Grande Naine' banana plants (PE and SC) and *Musa coccinea* (DF) for four months. Each population was multiplied in the tissue culture of carrot cylinders for inoculation purposes (SANTOS et al., 2012). Fifteen days after transplanting, the roots of each plantlet of each *Musa* accession were inoculated with 1 ml of suspension containing 400 juveniles, females, and males of *R. similis* of one of the three populations mentioned above. Inoculated plants were maintained in 2-L pots (one plant per pot) in a greenhouse at the Experimental Station of Biology at the University of Brasilia in a completely randomized design with five replicates for each accession for 60 days.

Sixty days after inoculation, nematodes were extracted from the roots of each banana plant and the soil using the adapted methods described by Coolen and D'Herde (1972) and Jenkins (1964), respectively, to assess the levels of the three *R. similis* populations. The total roots of each plant were washed and weighed before the extraction process. Three replicates of 10 g of root and 100 cc of soil were used to estimate the total number of nematodes in the total root system or 1.5 L of soil of each pot. After extraction, the nematodes were counted using a stereomicroscope to determine *R. similis* population levels per plant.

The reaction of banana to *R. similis* infection was evaluated according to the reproduction factor (RF) estimated for each replication ('RF' is the ratio between the final and initial population of nematodes), in which the final population corresponds to the total number of nematodes recovered from soil and root system per pot. The analysis of the banana reaction to the nematode followed the scale of percent reduction on the RF (SASSER et al., 1987), in which the accession with the highest RF was considered the susceptible standard to data analysis (MOURA and RÉGIS, 1987). The accessions Grande Naine and Yangambi Km5 were included as susceptible and resistant standards, respectively. Variables such as the number of nematodes per gram of root, the number of nematodes per root system, the number of nematodes in the soil, and the total number of nematodes (soil + roots) were determined.

The original data were converted to log (x) for statistical analysis. To evaluate accession resistance, means were calculated and compared by Tukey's test ($p \leq 0.01$) after analysis of variance in a factorial 3 x 8 using the SISVAR software (FERREIRA, 2008). The RF was evaluated in each pathogen x host combination with four replications per treatment. Data analysis was performed using a modified version of Griffing Model IV in a partial diallel scheme described by Geraldi and Miranda Filho (1988) (MELO and SANTOS, 1999).

In its original version, partial diallel was proposed to access the capacity of a combination of genitors distributed in two groups, with inferences made for each group. In the modified version used in this study, one group is formed by the hosts and the second group by the different pathogen isolates. The goal is to evaluate the interaction based on the general and specific capacity of pathogen x host interaction combinations.

Three analyses of variance and three evaluations of general and specific combination capacity were performed using the Genes software (CRUZ, 2006). Considering the fixed model, a scheme of partial diallel variance involving a group of hosts and another group of pathogen isolates (physiologic races) was used (MELO and SANTOS, 1999).

Results and discussion

Analysis of variance showed significant differences ($p \leq 0.01$) between accessions for all variables considered (nematodes per gram of roots, nematodes in roots, nematodes in soil, total nematodes, and reproduction factor), independent of nematode population except for root weight. In the same way, nematode populations were statistically different ($p \leq 0.01$) for the variables tested, regardless of the banana accession evaluated. Considering possible interactions between different nematode populations and banana accessions, there was a significant difference only for the number of nematodes in the roots.

The number of nematodes per gram of roots ranged from 20 ('Yangambi Km5') to 130 ('Grande Naine'). The lowest means were observed in accessions 4249-05 and Yangambi Km5, and the highest in Grande Naine, 0337-02, and 1304-06. The total number of nematodes in the accessions ranged from 490 ('4249-05') to 7730 ('1304-06') (Table 1).

No nematode was found in soil in '1304-06' and 'Grande Naine', and only 11 were associated with 'Borneo'. Nonetheless, the greatest numbers of nematodes found in soil were recovered from 'Yangambi Km5', '0337-02', '4249-05', and '4279-06' (Table 1). The RF ranged from 1.22 ('4249-05') to 14.32 ('1304-06'), with the lowest means found in '4249-05' and 'Yangambi Km5' and the highest ones in '1304-06' and 'Borneo'. Based on the percent reduction of RF (Table 1), from eight accessions, two were classified as highly susceptible ('Borneo'; 13'04-06'), two as susceptible ('Grande Naine'; '0337-02'), two with low resistance ('4279-06'; '0323-03'), and two moderately resistant ('Yangambi Km5'; '4249-05').

'Grande Naine' and 'Yangambi Km5' were confirmed as standards of susceptibility and resistance, respectively. The RF in '1304-06' and 'Borneo' surpassed the RF in the standard of susceptibility ('Grande Naine'); therefore, they were considered highly susceptible, while '0337-02' had similar behavior to 'Grande Naine'. Among the accessions with some degree of resistance, only '4249-05' had similar behavior to 'Yangambi Km5' (Table 1).

Radopholus similis from PE was the population with the highest average values for the variables, nematodes in roots, nematodes per gram of root, total nematodes, and RF, thereby confirming its high reproductive capacity. The population from SC had the lowest means for all variables. The population from DF had intermediate means for nematodes in roots, nematodes per gram of root, total nematodes, and RF (Table 2).

Table 3 shows that 'Yangambi Km5', followed by '0323-03', '4249-05, and '4279-06', respectively, allowed the lowest number of nematodes in the root system for the DF

Table 1. The reaction of banana accessions to three *Radopholus similis* populations based on a percent reduction of the reproduction factor.

Accessions	Nematodes/ gram of root[a]	Nematodes in soil[a]	Total nematodes[a]	RF[a]	RRF/reaction
1304-06	105c	0a	7730c	14.32c	0/HS
Borneo	72c	11ab	3437bc	13.29bc	7/HS
0337-02	104bc	168c	3048abc	7.62bc	47/S
Grande Naine	130c	0a	3024abc	7.55abc	47/S
4279-06	38bc	116bc	2411abc	6.02ab	58/LR
0323-03	39bc	31ab	1688abc	4.21ab	71/LR
Yangambi Km5	20b	212c	775ab	1.93a	87/MR
4249-05	27a	162bc	490a	1.22a	91/MR

[a] Means followed by the same letter in the same column are not statistically different by Tukey's test ($p \leq 0.01$). RF (reproduction factor) = final population/initial population. Percentage reduction of the reproduction factor (RRF) = (100 – (RF x 100/14.32). Host reaction: MR = moderately resistant (76.0–95.0%); LR = low resistance (51.0–75.0%); S = susceptible (26.0–50.0%); HS = highly susceptible (0–25.0%) (SASSER et al., 1987).

Table 2. The effects of each *Radopholus similis* population on eight banana accessions.

Population (origin)	Nematodes/ gram of root[a]	Root weight (g)[a]	Nematodes in soil[a]	Total nematodes[a]	RF[a]
PE	161c	38a	171b	6289c	15.7c
DF	38b	28a	74b	1138b	2.85b
SC	12a	24a	17a	341a	0.85a

[a]Means followed by the same letter in the same column are not statistically different by Tukey's test ($p \leq 0.01$). RF = reproduction factor, DF = Distrito Federal, PE = Pernambuco, SC = Santa Catarina.

population. Except for ‘0323-03’, the other accessions had similar behavior when challenged by the SC population. The accession 4249-05 led to the lowest nematode number for the PE population. When comparing the nematode populations with respect to the ability to multiply in the root systems of the banana accessions evaluated, the PE population achieved the highest numbers in the roots of all accessions evaluated (Table 3). Contrarily, the SC population had the lowest counts in all accessions, except for ‘Borneo’. The DF population appeared in moderate numbers in ‘Borneo’, ‘0337-02’, ‘1304-06’, and ‘Grande Naine’, and in lower numbers in ‘Yangambi Km5’, ‘0323-03’, ‘4249-05’, and ‘4279-06’.

Table 3. Mean numbers of nematodes in the root system of eight banana accessions inoculated with three *Radopholus similis* populations.

Accessions	Populations		
	DF[a]	SC[a]	PE[a]
1304-06	1401 bcAB	309 cdA	15479 bB
‘Borneo’	1008 bcA	1229 dAB	8056 abB
‘Grande Naine’	3670 bcB	411 cdA	4990 abB
0337-02	1034 bcAB	135 bcA	7471 abB
4279-06	450 bAB	45 abA	6388 abB
0323-03	275 bA	406 cdA	4290 abB
‘Yangambi Km5’	9 aA	0 aA	1679 abB
4249-05	360 bAB	30 abA	595 aB

[a]Means followed by the same letter (lowercase) in the same column are not statistically different by Tukey’s test ($p \leq 0.01$). Means followed by the same letter (uppercase) in the same row are not statistically different by Tukey’s test ($p \leq 0.01$). DF = Distrito Federal, PE = Pernambuco, SC = Santa Catarina.

Diallelic analysis showed significant effects of the general reaction ability (GRA) and the general aggressiveness ability (GAA), indicating variability for horizontal resistance on the host and aggressiveness for the pathogen (Table 4). The specific interaction ability (SIA) was significant ($p < 0.01$), indicating the existence of interaction between nematode populations and host accessions, which characterizes vertical resistance. Nevertheless, as listed in Table 4, horizontal resistance is also indicated. Accessions with higher horizontal resistance levels were ‘4249-05’ and ‘Yangambi km5’, and accessions with the lowest horizontal resistance levels were ‘1304-06’ and ‘Borneo’ (Table 5). The PE population was the most aggressive compared to the SC and DF populations (Table 6).

Table 4. Diallelic analysis and mean of nematode reproduction factor evaluated in eight banana accessions inoculated with three different *Radopholus similis* populations.

Source of variation	DF[a]	MS[b]	F[c]	Prob.[d]
Treatments	23	361.976	361.976	0.01
GRA	7	276.945	276.945	0.01
GAA	2	1924.219	1924.219	0.01
SIA	14	181.313	181.313	0.01
Error	72	1		
Mean 7.02				

[a]Degree of freedom of the analysis of variance. [b]Mean square. [c]Freedom. [d]Probability. GRA = General reaction ability (horizontal resistance); GAA: general aggressiveness ability (aggressiveness); SIA = specific interaction ability (interaction).

Table 5. Estimates of the effect of general reaction ability (GRA) and relative horizontal resistance (RHR) of eight banana accessions inoculated with three *Radopholus similis* populations.

Accessions	GRA effect[a]	RHR (%)[b]
1- 4249-05	-5.8	100
2- ‘Yangambi Km5’	-5.086	94.54
3- 0323-03	-2.806	77.14
4- 4279-06	-1	63.35
5- ‘Grande Naine’	0.533	51.65
6- 0337-02	0.596	51.17
7- ‘Borneo’	6.26	7.93
8- 1304-06	7.3	0

[a]Negative values mean the accession had a negative effect over the reproduction factor (RF). [b]The RHR values were obtained by interpolation based on numeric distance, where -5.8 is 100% and 7.3 is 0%.

Table 6. Estimates of the effect of general aggressiveness ability (GAA) and relative aggressiveness (RA) of three *Radopholus similis* populations and eight banana accessions.

Nematode population	GAA effect[a]	RA (%)[b]
3. Pernambuco (PE)	8.700	100
2. Distrito Federal (DF)	-2.519	75.39
1. Santa Catarina (SC)	-6.181	0

[a]Negative values mean the accession had a negative effect on the reproduction factor. [b]The RA values were obtained by interpolation based on numeric distance, where 8.7 is 100% and -6.181 is 0%.

The SIA values on each pathogen x host combination allow inference on host vertical resistance and pathogen virulence (MELO and SANTOS, 1999). The SIA significance indicates that the host horizontal resistance expressed by GRA and isolate aggressiveness are insufficient to explain the nematode reproduction factor variation. Different banana accessions behave differently when inoculated with distinct *R. similis* populations and vice-versa. Therefore, SIA values are efficient indicators of the specific behavior of each pathogen x host combination, allowing the specific behavior of each host or each nematode population to be studied in detail.

Figure 1 shows the SIA values among eight banana accessions and three *R. similis* populations. When a resistant host presents little variation among SIA values, one can state that, for this host, horizontal resistance is more important than vertical resistance. Therefore, one can compare each host's behavior by analyzing SIA value variations. In this study, it is possible to observe smaller SIA variations in 'Grande Naine', 'Yangambi km5', and '4249-05' compared to the other five accessions. Thus, horizontal resistance strongly affects '4249-05' and 'Yangambi km5'. Accession 0323-03 had the most significant SIA variation; therefore, this accession has a higher effect on vertical resistance.

Figure 2 shows SIA variations of each nematode population regarding the eight banana accessions. The PE population showed the most significant variation in SIA values, indicating higher variations of this isolate's response to the banana accessions than the other isolates. It is also possible to affirm that the PE population shows the highest interactive effect with accession 0323-03, one of the resistant accesses to the DF and SC nematode populations. The PE population has a higher SIA value when infecting the accession 0323-03, indicating that this population is the most aggressive to this accession.

The banana accessions evaluated in this study expressed different levels of resistance. In some cases, the results showed that the three *R. similis* populations had different reproduction capacities in the same *Musa* accession. By considering different levels of resistance added to the different capacities of nematode reproduction, evidence of vertical and horizontal resistance was observed based on Griffing Model IV.

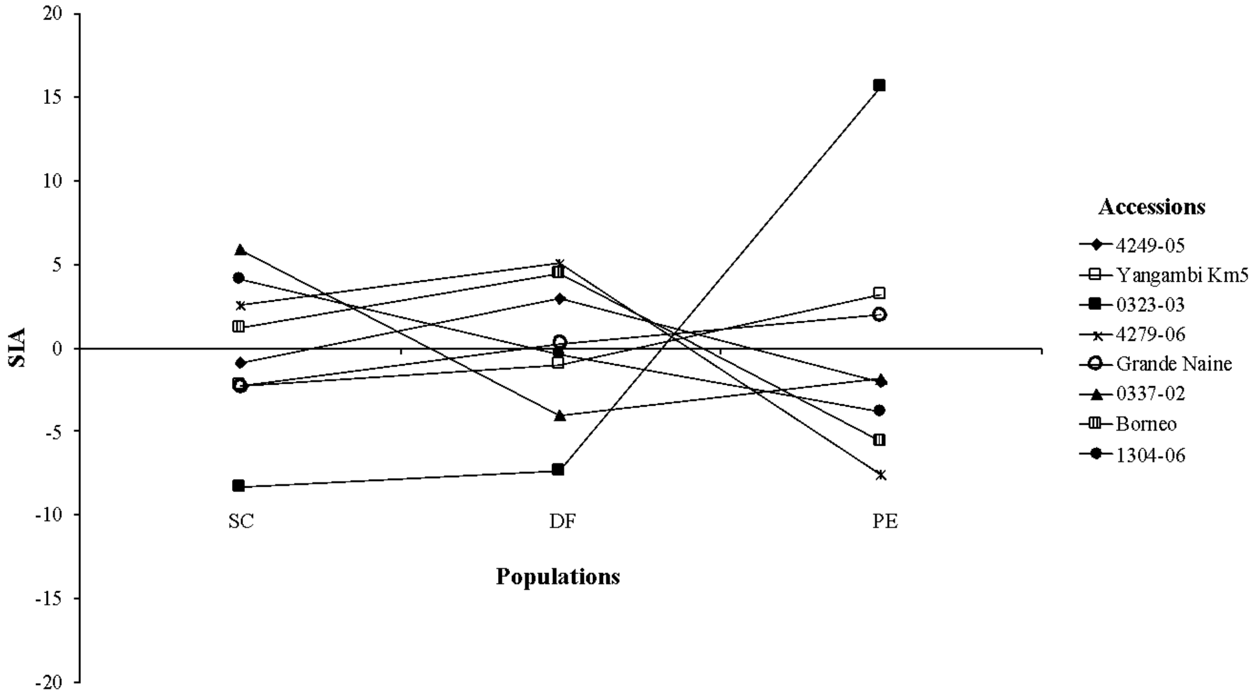

Figure 1. Specific interaction ability (SIA) of eight banana accessions inoculated with three *Radopholus similis* populations.

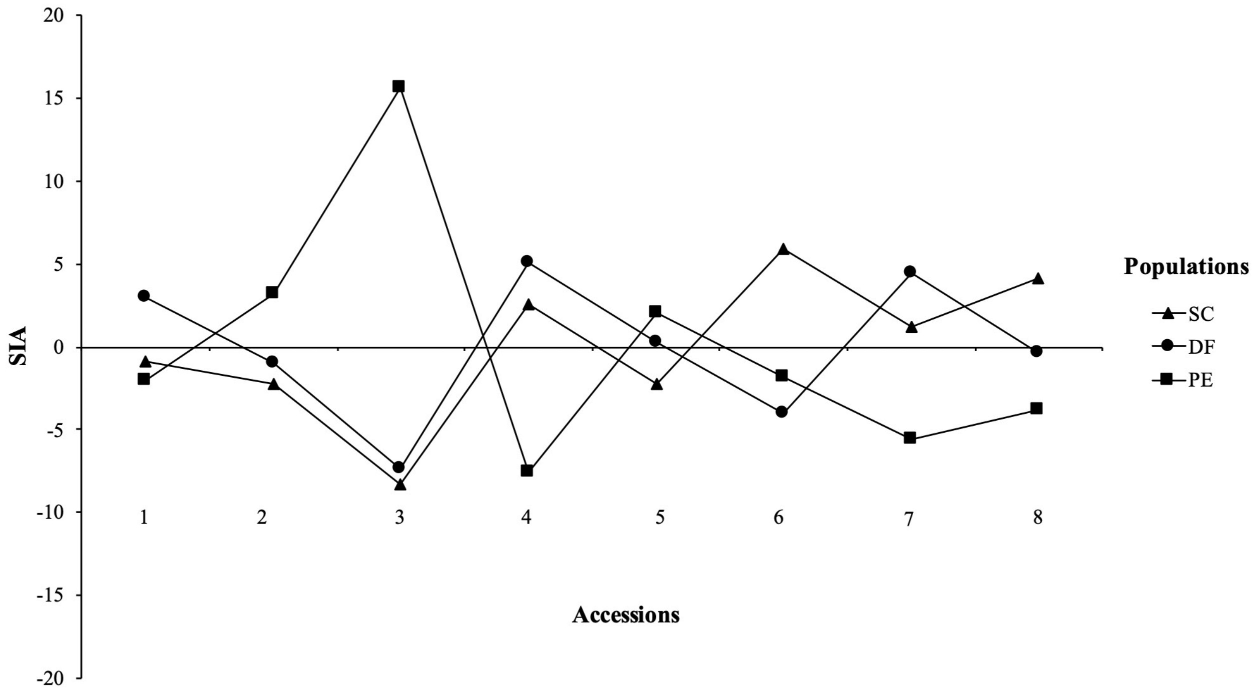

Figure 2. Specific interaction ability (SIA) of three Radopholus similis populations inoculated in eight banana accessions (1 - 4249-05, 2 – ‘Yangambi Km5’, 3 - 0323-03, 4 - 4279-06, 5 – ‘Grande Naine’, 6 - 0337-02, 7 – ‘Borneo’, and 8 - 1304-06).

In addition to confirming that the eight banana accessions evaluated had different reactions to parasitism by three different *R. similis* populations, significant differences in the reproductive capacity among the three nematode populations evaluated were also observed. This was evident when data from the eight accessions and three burrowing nematode populations were pooled. The PE population had the highest reproduction rate, which corroborates Costa (2004), who demonstrated that the PE population used in his study was among the most aggressive of the 12 populations evaluated from Brazil, Australia, Costa Rica, and Cuba. According to the author, except for having the highest RF, the PE population induced higher percentages of injured areas on the roots of banana plants and caused one of the highest percentages of dead roots.

As a result of this study, the SC population had the lowest RF; this contrasts with the results of Costa (2004), who evaluated other *R. similis* populations from SC (also from Luis Alves County) and noted that the population had high reproduction rates. However, the later population was less aggressive and caused less damage to banana rhizomes. It also emanated from this study that the *R. similis* population from DF occupied an intermediate position regarding its reproductive capability. Differences between *R. similis* populations were also confirmed in molecular studies (ELBADRI et al., 2002; COSTA et al., 2008). Therefore, the difference in the reproduction capacity between the three populations in this study was expected.

Nevertheless, all accessions had an RF higher than 1, and ‘Borneo’, ‘1304-06’, ‘Grande Naine’, and ‘0337-02’ were classified as highly susceptible to *R. similis* using the scale of Sasser et al. (1987). The accessions 1304-06 and Borneo were previously classified as susceptible to *R. similis* (COSTA et al., 1998; QUÉNÉHERVÉ et al., 2009; SANTOS et al., 2013; WEHUNT et al., 1978).

The hybrid 4249-05, classified as moderately resistant, has two accessions in its background (i.e., ‘M48’ and ‘M53’), which originate from Jamaica and have been used as a source of resistance to various pathogens (SILVA et al., 1998). Gowen (1976) found that the accession M48 was not a good host to *R. similis*, nor *Helicotylenchus multicinctus*

(Cobb, 1893) Golden, 1956. Additionally, the hybrid 4279-06, which is considered to have low resistance, in addition to having 'M53' as the female parent, has 'Calcutta 4' as ancestral, which has also been considered resistant to nematodes in previous studies (CARLIER et al., 2003; SANTOS et al., 2013). Santos et al. (2013) evaluated 26 banana accessions to an aggressive *R. similis* population and obtained similar results for accessions 4249-05 and 4279-06, which are classified as highly resistant and resistant, respectively. However, in our study, these accessions showed higher numbers of nematodes in soil and roots, a greater number of nematodes per gram of root, and a higher reproduction factor.

The accessions 0323-03 and 0337-02 have 'Calcutta 4' as female parents, although only the first accession expressed some degree of resistance in the present study. Previously, both accessions were classified as resistant, despite using only a single *R. similis* population and lower initial inoculum (SANTOS et al., 2013).

According to partial diallelic analysis, there is a high probability of horizontal and vertical resistance occurring among the accessions tested since the calculated GRA and SIA were statistically significant. Evidence of horizontal resistance was observed in accessions such as '4249-05' and 'Yangambi Km5' because they did not allow abundant reproduction of more than one of the nematode populations, suggesting the possibility of durable resistance in this pathosystem. In variance analysis, the highly significant interaction between races and cultivars indicates that the reaction of each cultivar is specific to a particular race. Similarly, the interaction in the current study can indicate vertical resistance. Nonetheless, the absence of interaction shows that the cultivars react similarly to distinct races, which means they differ in horizontal resistance but not vertical resistance (VAN DER PLANK, 1968). Nonetheless, the two types of resistance may occur in the same pathosystem, as shown previously in rice and *Xanthomonas oryzae* (Ishiyama) pathosystem (SWINGS et al., 1990; PARLEVLIET, 1981).

Indication of vertical resistance was shown according to SIA calculated for '0323-03', which shows a high level of resistance, although it seems to have a high interaction with the PE population. However, '0323-03' was also a stronger horizontal resistance effect based on the GRA. Pinochet et al. (1998) evaluated the genetic basis of *R. similis* resistance in banana plants and suggested that resistance is controlled by one or few genes. Dochez et al. (2009) assessed the progeny of diploid banana hybrids TMB2 x 6142-1 and TMB2 x 8075-7 and found that resistance is controlled by two dominant genes, A and B, both with additive and interactive effects, by which the recessive bb suppresses the dominant A.

The difference in aggressiveness was also confirmed by the diallelic analysis, as evidenced by a high significance of the general aggressiveness ability. The PE population had the highest aggressiveness among the *R. similis* populations tested. This population has shown a high RF in 'Grande Naine' and 'Pisang Jari Buaya', with a median rate in 'Yangambi Km5' (COSTA, 2004). Considering the data obtained by Costa et al. (2008), populations from Pernambuco and Santa Catarina States present a relevant genetic distance based on the complementation of the Nei and Li similarity coefficient, as calculated using RAPD markers.

This study contributes to investigating the interaction between *Musa* spp. and *R. similis* using the diallelic analysis method. Future investigations involving a larger number of nematode populations and banana accessions should be conducted to properly understand pathogen x host interaction and genetic resistance in order to support the identification of possible pathogen physiological races.

Conclusions

Accessions 4249-05, Yangambi Km5, 0323-03, and 4279-06 expressed some degree of resistance to *R. similis*, thereby having the potential to be considered for future breeding programs aiming to control the nematode. Additionally, these accessions seem to have high levels of horizontal resistance, and evidence of vertical resistance occurred among the accessions, with 0323-03 showing some interaction with the PE population.

There is a gradient of reproduction capacity among the populations of *R. similis* evaluated (PE > DF > SC), indicating that the PE population is the most aggressive and SC the least aggressive. Interaction between the reproduction capacity of the nematode with each accession resulted in different host reactions to the various populations of the pathogen. Thus, accessions with some degree of resistance may react with less damage when parasitized by a less aggressive *R. similis* population. Despite our promising findings, it is critical to conduct preliminary tests to assess the aggressiveness of nematode isolates before assessing the reaction of accessions of interest.

Acknowledgments

Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) is acknowledged for providing a scholarship for the first author during his Doctoral Program at the University of Brasilia and for the financial support (Proc. n. 474653/2008-0); FAP/DF (Fundação de Apoio à Pesquisa do Distrito Federal) for the financial support (Proc. n. 193.000.473/2008). We would also like to thank Atlas Assessoria Linguística for language editing.

References

CARES, J. E.; ANDRADE, E. P. Taxonomia do gênero *Radopholus.* **Revisão Anual de Patologia de Plantas**, Passo Fundo, v.14, p.113-49, 2006.

CARLIER, J.; DE WAELE, D.; ESCALANT, J. Global evaluation of *Musa* germplasm for resistance to Fusarium wilt, *Mycosphaerella* leaf spot diseases and nematodes. **INIBAP Technical Guidelines**, Montpellier, v.7, p.1-56, 2003.

COOLEN, W.A.; D'HERDE, C.J. **A method for the quantitative extraction of nematodes from plant tissue**. Ghent: Ministry of Agriculture, Agricultural Research Administration, State Agricultural Research Center, 1972. 77 p.

COSTA, D.C. **Variabilidade patogênica e genética de *Radopholus similis* em bananeira no Brasil**. 2004. Tese (Doutorado) - Departamento de Fitopatologia, Universidade de Brasília, Brasília, 2004.

COSTA, D.C.; FALEIRO, F.G.; CARES, J.E.; GOMES, A.C. Pathogenicity and genetic variability of *Radopholus similis* populations in bananas (*Musa acuminata* AAA and AA) based on RAPD analysis. **Nematologia Brasileira**, Piracicaba, v.32, n.4, p.303-16, 2008.

COSTA, D.C.; SILVA, S.O.; ALVES, F.R. Reação de genótipos de bananeira (*Musa* spp.) a *Radopholus similis* e *Meloidogyne incognita.* **Nematologia Brasileira**, Piracicaba, v.22, n.2, p.49-57, 1998.

CRUZ, C.D. **Programa genes**: estatística experimental e matrizes. Viçosa: Editora UFV, 2006. 285 p.

DOCHEZ, C.; TENKOUANO, A.; ORTIZ, R.; WHYTE, J.; DE WAELE, D. Host plant resistance to *Radopholus similis* in a diploid banana hybrid population. **Nematology**, Newcastle, v.11, n.3, p.329-35, 2009.

ELBADRI, G.A.; DE LEY, P.; WAEYENBERGE, L.; VIERSTRAETE, A.; MOENS, M.; VANFLETEREN, J. Intraspecific variation in *Radopholus similis* isolates assessed with restriction fragment length polymorphism and DNA sequencing of the internal transcribed spacer region of the ribosomal RNA cistron. **International Journal for Parasitology**, Amsterdam, v.32, n.2, p.199-205. 2002.

FALLAS, G.A.; SARAH, J.L.; FARGETTE, M. Reproductive fitness and pathogenicity of eight *Radopholus similis* isolates on banana plants (*Musa* AAA CV. Poyo). **Nematropica**, Auburn, v.25, n.2, p.135-41, 1995.

FERREIRA, D.F. SISVAR: um programa para análises e ensino de estatística. **Revista Symposium**, Recife, v.6, p.36-41, 2008.

GERALDI, I.O.; MIRANDA FILHO, J.B.D. Adapted models for the analysis of combining ability of varieties in partial diallel crosses. **Brazilian Journal of Genetics**, São Paulo, v.11, n.2, p.419-30, 1988.

GOWEN, S.R. Varietal responses and prospects for breeding nematode resistant banana varieties. **Nematropica**, Auburn, v.6, n.2, p.45-9, 1976.

GOWEN, S.R.; QUÉNÉHERVÉ, P.; FOGAIN, R. Nematode parasites of bananas and plantains. *In:* LUC, M.S.; BRIDGE, J.R.A. (ed.). **Plant parasitic nematodes in subtropical and tropical agriculture**. 2nd ed. Wallingford: CABI Publishing, 2005. p.611-44.

GRIFFING, B. Concept of general and specific combining ability in relation to diallel crossing systems. **Australian Journal of Biological Sciences**, Melbourne, v.9, p.463-93, 1956.

HAEGEMAN, A.; ELSEN, A.; DE WAELE, D.; GHEYSEN, G. Emerging molecular knowledge on *Radopholus similis*, an important nematode pest of banana. **Molecular Plant Pathology**, London, v.11, n.3, p.315-23, 2010.

JENKINS, W.R. A rapid centrifugal flotation technique for separating nematodes from soil. **Plant Disease Report**, St. Paul, v.48, p.692, 1964.

MARIN, D.H.; BARKER, K.R.; KAPLAN, D.T.; SUTTON, T.B.; OPPERMAN, C.H. Aggressiveness and damage potential of Central American and Caribbean populations of *Radopholus* spp. in banana. **Journal of Nematology**, College Park, v.31, n.4, p.377-85, 1999.

MELO, L.C.; SANTOS, J.B. Identification of resistant genotypes considering polygenic systems in host-pathogen interaction. **Genetics and Molecular Biology**, São Paulo, v.22, n.4, p.601-8, 1999.

MENDOZA, A.R.; KIEWNICK, S.; SIKORA, R.A. In vitro activity of *Bacillus firmus* against the burrowing nematode *Radopholus similis*, the root-knot nematode Meloidogyne incognita and the stem nematode *Ditylenchus dipsaci*. **Biocontrol Science and Technology**, London, v.18, n.4, p.377-89, 2008.

MOENS, T. **Variability in reproductive fitness and pathogenicity of *Radopholus similis* in *Musa*: Effect of biotic and abiotic factors**. 2004. (PhD Thesis) - Departement Biologie, Katholieke Universiteit Leuven, Leuven, 2004.

MOENS, T.; SANDOVAL, J.A.; ESCALANT, J.V.; DE WAELE, D. Evaluation of the progeny from a cross between ‘Pisang Berlin’ and *M. acuminata* spp. *burmannicoides* ‘Calcutta 4’ for evidence of segregations with respect to resistance to black leaf streak disease and nematodes. **Infomusa**, Montpellier, v.11, n.2, p.20-2, 2002.

MOURA, R.M.; RÉGIS, E.M.O. Reação de cultivares de feijoeiro comum (*Phaseolus vulgaris*) em relação ao parasitismo de *Meloidogyne* j*avanica* e *M. incognita* (Nematoda: Heteroderidae). **Nematologia Brasileira**, Piracicaba, v.11, p.215-25, 1987.

PARLEVLIET, J.E. Disease resistance in plants and its consequences for plant breeding. *In*: FREY, J.K. (ed.). **Plant Breeding II**. Iowa: The Iowa State University Press, 1981. p.309-64.

PINOCHET, J.; CAMPRUBÍ, A.; CALVET, C.; FERNÁNDEZ, C. Inducing tolerance to the root-lesion nematode *Pratylenchus vulnus* by early mycorrhizal inoculation of micropropagated Myrobalan 29 C plum rootstock. **Journal of the American Society for Horticultural Science**, Chicago, v.123, n.3, p.342-47, 1998.

QUÉNÉHERVÉ, P. Integrated management of banana nematodes. *In*: A. M. CIANCIO, A.M.; MUKERJI, K.G. (ed.). **Integrated management of fruit crops nematodes**. New York: Springer, 2009. p.3-62.

QUÉNÉHERVÉ, P.; VALETTE, C.; TOPART, P.; TEZENAS DU MONTCEL, H.; SALMON, F. Nematode resistance in bananas: screening results on some wild and cultivated accessions of *Musa* spp. **Euphytica**, Wageningen, v.165, n.1, p.123-36, 2009.

SANTOS, J.R.P.; ANDRADE, E.P.; COSTA, D.C.; GONZAGA, V.; CARES, J.E. Comparison of two methods for in vitro multiplication of *Radopholus similis* and *Pratylenchus brachyurus* in carrot cylinders. **Tropical Plant Pathology**, Brasilia, DF, v.37, n.4, p.266-70, 2012.

SANTOS, J.R.P.; TEIXEIRA, M.A.; CARES, J.E.; FALEIRO, F.G.; COSTA, D.C. Contrastant banana accessions for resistance to the burrowing nematode, based on molecular markers RAPD. **Euphytica**, Wageningen, v.172, n.1, p.13-20, 2010.

SANTOS, J.R.P.; TEIXEIRA, M.A.; COSTA, D.C.; SILVA, S.O.; FALEIRO, F.G.; CARES, J.E. Selection of *Musa* genotypes for resistance to *Radopholus similis* Cobb. **Nematropica**, Auburn, v.43, n.1, p.1-8, 2013.

SASSER, J.N.; HARTMAN, K.M.; CARTER, C.C. **Summary of preliminary crop germplasm evaluations for resistance to root-knot nematodes**. Raleigh: Department of Plant Pathology at North Carolina State University: United States Agency for International Development, 1987.

SILVA, S.O.; MATOS, A.P.; ALVES, E. J. Melhoramento genético da bananeira. **Pesquisa Agropecuária Brasileira**, Brasília, DF, v.33, n.5, p.693-703, 1998.

VAN DER PLANK, J. E. **Disease resistance in plants**. New York: Academic Press, 1968.

WEHUNT, E.J.; HUTCHISON, D.J.; EDWARDS, D.I. Reaction of banana cultivars to the burrowing nematode (*Radopholus similis*). **Journal of Nematology**, College Park, v.10, n.4, p.368-70, 1978.