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Host suitability of peppers to the false root-knot nematode *Nacobbus aberrans*

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The false root-knot nematode, *Nacobbus aberrans*, causes severe damage to field and greenhouse pepper crops in several localities of the American continent. No commercial peppers (*Capsicum annuum*) resistant to this nematode are available up to the present. Host suitability of 6 experimental and 3 commercial peppers (some of them carrying *Me1* and *Me7* resistance genes to *Meloidogyne* spp.) to two *N. aberrans* populations were evaluated under greenhouse experiments. None of the peppers was found to be resistant to the nematode. The evaluated parameters exhibited significant differences among some peppers tested within a single population and between populations for a single plant material. Some peppers carrying resistance showed higher nematode reproduction than some lines that did not possess resistance genes. These results confirmed that the genes conferring resistance to *Meloidogyne* spp. do not provide protection against this species of root-galling nematode. Host suitability of pepper lines carrying *Me1* or *Me7* resistance genes against *N. aberrans* is evaluated for the first time. Search for resistant genes against this nematode in wild peppers growing in areas where this nematode is indigenous should be promoted.

1. Introduction

Pepper (*Capsicum annuum* L.) is a valuable vegetable for human nutrition due to its content of bioactive nutrients, which are important dietary antioxidants (Navarro et al., 2006). In addition, pepper production is a good source of income for small producers in several developing countries worldwide (Bosland and Votava, 1999). The ban of the use of artificial colours and the rise in production costs has increased the international demand for this crop, resulting in a growing interest in the pepper crop in Argentina (Gonzalez Vera et al., 2002). The pepper cultivated area in the country is currently about 13000 ha in fields, representing a production of 65000 t.

Globally, pepper is cultivated in temperate, subtropical, and tropical areas where the root-knot nematodes (RKNs), *Meloidogyne* spp., complete several life cycles annually (Thies and Fery, 2000a), with *Meloidogyne incognita* being one of the major pests throughout the world. In the American continent, the pepper crop is also seriously affected by *Nacobbus aberrans* (Thorne, 1935) Thorne and Allen, 1944. This nematode is known as the false root-knot nematode because it also induces the formation of galls in the host roots. It is one of the top 10 plant-parasitic nematodes based on economic importance (Jones et al., 2013). The species is native to the Americas (Sher, 1970) and has quarantine importance (EPPO, 2009). This nematode causes severe damage to pepper production in Mexico and South America (Inserra et al., 1985); however, in most pepper production regions where the parasite occurs, losses have not been estimated. In Argentina, *N. aberrans* has been detected affecting the pepper crop in several provinces (Chaves and Sisler, 1980; Costilla and Ojeda, 1985; Del Toro et al., 2004; Doucet and Lax, 2005), with damage being more pronounced in greenhouses than in the field. Pepper cultivars commonly grown in Argentina are susceptible to the nematode. Managing this parasite is especially complex due to the variable behaviour observed

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among populations towards a single host and its wide host range (Costilla, 1990; Castiblanco et al., 1999; Lax et al., 2011).

Control of plant-parasitic nematodes mainly involves pre-plant fumigation with methyl bromide; however, due to increasingly strict policies on methyl bromide use and its inevitable loss of registration for pre-plant agricultural applications, genetically-based resistance is becoming increasingly important in the management of nematodes damaging pepper production (Thies and Ariss, 2009). One of the best alternatives to cope with nematode infestations relies on the deployment of resistance genes (R-genes), which represent an efficient, environmentally safe and economically sustainable control method (Djian-Caporalino et al., 2009). Resistance in *C. annuum* is associated with dominant *N* (Thies and Fery, 2000b), *Mech* (Djian-Caporalino et al., 2007), and *Me* genes (Djian-Caporalino et al., 1999, 2001; Berthou et al., 2003; Pegard et al., 2005). Some genes (*Me4*, *Mech1, and Mech2*) are specific to certain *Meloidogyne* species or populations, whereas others (*Me1*, *Me3*, and *Me7*) are effective against a wide range of *Meloidogyne* species, including *Meloidogyne arenaria*, *Meloidogyne javanica*, and *M. incognita*, the most common species in Mediterranean and tropical areas (Djian-Caporalino et al., 2007). However, nematode populations are able to break down plant resistance, and genetic resources in terms of R-genes are limited; sustainable management of these resources is thus important for R-gene durability (Barbary et al., 2014).

Screening and breeding for resistance to *N. aberrans* have focused mainly on potato, pepper, bean and tomato (Manzanilla-López et al., 2002). In pepper, some degree of resistance to the nematode has been detected in *Capsicum baccatum* L. var. *pendulum* (Willd.) (Brunner de Magar, 1967) and in three *C. annuum* cultivars (Sisler and Casaurang, 1983), but it was not associated with a specific gene. For this nematode species, only one study has evaluated the response of commercial and experimental pepper lines carrying *N* and *Me3* R-genes, showing that neither gene conferred resistance to *N. aberrans* populations (Lax et al., 2006). Screening of new germplasm, as well as of commercial cultivars commonly used in the country, and whose response to the nematode is still unknown, is of great importance for managing this parasite. The objective of this work was to evaluate the host suitability of commercial and experimental peppers (some of them carrying resistance to RKNs conferred by the *Me1* and *Me7* R-genes) under greenhouse, to *N. aberrans* populations.

2. Materials and methods

2.1. Nematode populations

Studies were conducted using two Argentine populations of *N. aberrans* from the localities of Río Cuarto (RC) (department of Río Cuarto, province of Córdoba) and Lisandro Olmos (LO) (La Plata district, province of Buenos Aires). The populations were selected based on their known aggressiveness to pepper (Lax et al., 2011). The nematodes were maintained on tomato cv. Platense. Egg masses were removed from infected roots and placed in Petri dishes containing water and maintained at room temperature (25 ± 2 °C) to allow egg hatching. After three days, active second-stage juveniles (J2) were collected and immediately used to inoculate pepper plants.

2.2. Plant material

The characteristics of the peppers evaluated are indicated in Table 1. California Wonder was used as a control because of its susceptibility to the nematode. Sakata Seed Sudamerica Ltd. (Brazil) provided the inbred experimental lines of *C. annuum*, some of them carrying *Me1* (AF 8724 and AF 8765) and *Me7* R-genes (AF 2739) to *M. arenaria, M. incognita* and *M. javanica* (Djian-Caporalino et al., 2007). Commercial peppers [Fyuco INTA, Fenomeno RZ (35–615), Yatasto] commonly used in Argentina and of unknown response to the nematode were also considered.

Seeds were germinated in trays with sterile soil. Four-leaf stage seedlings were transplanted individually into plastic pots (20 cm long × 4 cm wide) containing approximately 80 g of a mixture of sterile soil and sand (3:1). Plant roots were placed on this substrate, immediately inoculated with 1.5 mL of water containing 100 active J2 (Initial population = Pi), and covered with a similar amount of substrate. Pi density was selected based on previous experiments (Lax et al., 2006, 2011). A completely randomized experimental design was used with 8 plants for each pepper. Plants were watered as needed to maintain a soil moisture level similar to that in the field. The experiment was conducted twice under greenhouse at a mean temperature of 25 ± 2 °C and a 14-h photoperiod. Plants were watered as needed and were uprooted 60 days after inoculation. Roots were carefully washed to remove soil particles and observed under stereoscopic microscope; the number of galls and egg masses present in the entire root system were counted. To count the number of eggs per plant (Final population = Pf), egg masses were extracted and immersed in a 1% NaClO solution for 4 min (Hussey and Barker, 1973). Reproduction Factor (RF) was calculated for the different plant material (RF = Pf/Pi). Based on this parameter, a pepper was considered resistant at RF = 0, of intermediate resistance at RF < 1, and susceptible at RF ≥ 1 (Charchar et al., 2003). Reproduction index (RI) was used to assess the degree of resistance/susceptibility of the different germplasm; the index was calculated as the Pf on a plant material divided by the Pf on the susceptible cultivar × 100. Plants in which RI was more than 50% were considered susceptible; 25 ≤ RI ≤ 50%, slightly resistant; 10 ≤ RI ≤ 25%, moderately resistant; 1 ≤ RI ≤ 10%, very resistant; RI ≤ 1%, highly resistant; or immune when nematodes did not reproduce (Hadisoeganda and Sasser, 1982).

2.3. Statistical analyses

Normality and homogeneity assumptions were confirmed for all variables before statistical analyses. Data were normalized by transforming them into log_{10} (x + 1) for the analysis. Mean values were statistically compared using a Scott–Knott test ($p = 0.05$) with the aim of evaluating possible differences among plant materials for a single population and between populations for a single pepper. Data from each experiment were combined for analysis using InfoStat (2002). Host suitability of individual peppers was compared with that of the susceptible control California Wonder by the Dunnett's *t*-test (Dunnett, 1955), using XLSTAT version 2015; this test was performed with the RF and the RI values.

3. Results

Both populations of *N. aberrans* reproduced on all the pepper genotypes. The values of the assessed parameters differed among treatments (Tables 2 and 3). Differences in the behaviour of a single population on the different plant materials were observed; behaviour also differed among populations on a single pepper, especially in Fyuco INTA, AF 10742 and AF 10743, which do not possess resistance genes.

For both populations, the number of galls of all the peppers carrying resistance did not show significant differences from the susceptible control; the same result was obtained with non-resistant peppers AF 10744 (LO population), Fyuco INTA and Yatasto RZ (RC population). The number of galls in AF 10744 (RC), Yatasto RZ and Fyuco INTA (LO) was lower than in the control; the

Table 1
Main characteristics of the peppers used to determine variability in infection and reproduction of *Nacobbus aberrans* populations.

Plant material	Seed company	Availability	Nematode resistance[a]
California Wonder	Amsa Seed	Commercial	–
Fyuco INTA	Caps Seeds	Commercial	–
Yatasto RZ	Rijk Zwaan Seeds	Commercial	–
Fenomeno RZ (35–615)	Rijk Zwaan Seeds	Commercial	Ma, Mi, Mj
AF 2739	Sakata Seed Sudamerica	Experimental	Ma, Mi, Mj
AF 8724	Sakata Seed Sudamerica	Experimental	Ma, Mi, Mj
AF 8765	Sakata Seed Sudamerica	Experimental	Ma, Mi, Mj
AF 10742	Sakata Seed Sudamerica	Experimental	–
AF 10743	Sakata Seed Sudamerica	Experimental	–
AF 10744	Sakata Seed Sudamerica	Experimental	–

Abbreviations. *Meloidogyne arenaria* (Ma); *M. incognita* (Mi); *M. javanica* (Mj).
[a] Information from the seed companies' descriptions.

lowest values were observed in the experimental lines AF 10742 and AF 10743, especially for RC population. The number of egg masses per plant was found to be significantly lowest in the experimental lines AF 10742 and AF 10743 (both populations), Fyuco INTA (LO) and AF 10744 (RC population). The remaining evaluated peppers (including those carrying genes resistant to RKNs) did not exhibit significant differences from the susceptible control.

As observed for number of galls and of egg masses, the lowest RF was obtained in the experimental lines AF 10742 and AF 10743. In the RC population, RF values were below 1 (RF = 0.3–0.5), which is an indicator of intermediate resistance, whereas in the LO population, a susceptibility response was observed (RF = 8.3–10.0). The remaining evaluated peppers were susceptible, with RF values ranging between 10.5 and 49, regardless of being resistant or not to RKNs. The comparison of each plant material with the susceptible control showed that, in both populations, experimental lines AF 10742 and AF 10743, as well as AF 10744 in RC differed significantly because they presented the lowest reproduction values. In RC, Yatasto RZ also showed differences from California Wonder, given by its high susceptibility response, which was significantly higher than that of the control.

The comparison of Pf of each pepper with respect to control showed that RI ranged between 1.1–160.7% and 21.9–97.3% for the RC and LO populations, respectively. In LO, none of the peppers showed higher susceptibility than the control; however, in the RC population the peppers Fyuco INTA, Fenomeno RZ and Yatasto RZ were highly susceptible. The Dunnett's test showed that RI was significantly lower than the susceptible control in the experimental lines AF 10742 and AF 10743 (for both populations) as well as AF 10744 (RC) and Fyuco INTA (LO). According to this index, most of the evaluated peppers showed susceptible behaviour, except for AF 10742 (RC: very resistant; LO: moderately resistant), AF 10743 (RC: very resistant; LO: slightly resistant) and AF 10744 (RC: slightly resistant).

4. Discussion

The two *N. aberrans* populations were able to complete their life cycle in all the tested germplasms; however, different degrees of susceptibility/resistance to the nematode populations were observed. Although both populations belong to the same race (sugarbeet group: nematodes infecting sugarbeet, pepper and tomato but not potato) (Lax et al., 2011), they differed in their behaviour on a single host, as previously reported for other populations of the species (Toledo et al., 1992; Lax et al., 2006, 2011). Significant differences between RC and LO were evident mainly for AF 10742, AF 10743 and Fyuco INTA in all the tested parameters (number of galls, number of egg masses, RF and RI). The experimental lines AF 10742 and AF 10743 (not carrying R-genes to RKNs) showed the lowest values in all the measured variables. Considering the RF values, these lines exhibited intermediate resistance to RC population (RF < 1), whereas the response to LO nematode inoculation was susceptible (RF ≥ 1). According to the RI, these two experimental lines were very resistant ($1 \leq$ RI $\leq 10\%$) to RC nematodes, whereas AF 10742 and AF 10743 were moderately ($10 \leq$ RI $\leq 25\%$) or slightly ($25 \leq$ RI $\leq 50\%$) resistant to the LO population, respectively. Differences between populations based on RI were also observed in AF 10744, which behaved as slightly resistant to RC and susceptible (RI $> 50\%$) to LO. This shows the

Table 2
Mean values of number of galls (Galls) and egg masses produced by two *Nacobbus aberrans* populations in commercial and experimental peppers.[a]

Plant material	Galls		Egg masses	
	Río Cuarto	Lisandro Olmos	Río Cuarto	Lisandro Olmos
California Wonder[b]	14 aA	11.8 aA	9.2 aA	9.8 aA
Fyuco INTA[c]	17.3 aA	7.5 bB	13.7 aA	6.0 bB
Yatasto RZ[c]	19.7 aA	10.8 bB	13.8 aA	7.7 aB
Fenomeno RZ (35–615)[d]	18.0 aA	11.5 aA	11.7 aA	7.8 aA
AF 2739[d]	21.0 aA	18.0 aA	12.2 aA	13.5 aA
AF 8724[d]	15.3 aA	15.2 aA	10.2 aA	10.3 aA
AF 8765[d]	19.2 aA	12.8 aA	12.0 aA	8.8 aA
AF 10742[c]	0.7 cB	7.2 bA	0.3 bB	4.5 bA
AF 10743[c]	0.3 cB	8.0 bA	0.3 bB	3.8 bA
AF 10744[c]	7.8 bB	17.2 aA	4.7 bA	9.8 aA

[a] Means followed by different small letters (column) indicate significant differences among plant materials for the same population; means followed by different capital letters indicate significant differences between populations for that parameter (row) according to Scott–Knott's multiple range test ($p = 0.05$).
[b] Susceptible control.
[c] Pepper without resistance to *Meloidogyne* spp.
[d] Pepper with resistance to *Meloidogyne* spp.

Table 3
Reproduction factor and reproduction index of *Nacobbus aberrans* populations in commercial and experimental peppers.[a]

Plant material	Reproduction factor		Reproduction index (%)	
	Río Cuarto	Lisandro Olmos	Río Cuarto	Lisandro Olmos
California Wonder[b]	30.5 bA (S)	37.9 aA (S)	100.0 bA (S)	100.0 aA (S)
Fyuco INTA[c]	41.5 aA (S)	20.4 bB (S)	136.1 aA (S)	53.9 bB* (S)
Yatasto RZ[c]	49.0 aA* (S)	36.0 aA (S)	160.7 aA* (S)	95.0 aA (S)
Fenomeno RZ (35–615)[d]	44.8 aA (S)	29.6 aA (S)	146.9 aA (S)	78.1 aB (S)
AF 2739[d]	30.4 bA (S)	36.9 aA (S)	99.8 bA (S)	97.3 aA (S)
AF 8724[d]	28.0 bA (S)	23.0 bA (S)	91.8 bA (S)	60.7 bA (S)
AF 8765[d]	25.2 bA (S)	31.0 aA (S)	82.6 bA (S)	81.8 aA (S)
AF 10742[c]	0.3 dB* (IR)	8.3 cA* (S)	1.1 cB* (VR)	21.9 cA* (MR)
AF 10743[c]	0.5 dB* (IR)	10.0 cA* (S)	1.5 cB* (VR)	26.4 cA* (SR)
AF 10744[c]	10.5 cA* (S)	23.0 bA (S)	34.4 cA* (SR)	60.7 bA (S)

Abbreviations. Susceptible (S); intermediate resistance (IR); slightly resistant (SR); very resistant (VR); moderately resistant (MR).
[a] Means followed by different small letters (column) indicate significant differences among plant materials for the same population; means followed by different capital letters indicate significant differences between populations for that parameter (row) according to Scott–Knott's multiple range test ($p = 0.05$). Values in the same column with an* indicate differences between the pepper and the susceptible control California Wonder according to Dunnett's *t*-test ($p = 0.05$).
[b] Susceptible control.
[c] Pepper without resistance to *Meloidogyne* spp.
[d] Pepper with resistance to *Meloidogyne* spp.

importance of evaluating different populations when screening plant material for resistance to this nematode. The remaining tested peppers showed a highly susceptible response (RF $\geq$ 1 and RI > 50%).

The category of nematode resistance of a plant genotype can depend on the parameter/s considered and its/their respective scale to define the degree of resistance. In many cases, there is no correlation in the classification obtained for a single plant material considering different parameters; in the present work the designation obtained based on the RF and the RI showed some differences for some of the tested peppers. In a previous work with *N. aberrans,* there was not a close relationship between egg mass index (EMI) and the significance usually attributed to RF (Lax et al., 2011). Hadisoeganda and Sasser (1982) found that RI and EMI were significantly correlated in *Meloidogyne* spp.; those authors define a scale to design the degree of resistance based on EMI, assuming that differences in inoculum levels were not a factor. In this work, if we had used the scale defined by those authors, all the tested peppers would have been classified as very resistant (range of EMI = 1.1–3, data not shown), except for AF 10742 and AF 10743, which would have been defined as highly resistant lines (range of EMI = 0–1, data not shown) for the RC population. An evaluation of host suitability based on EMI is an indicator that the nematode completed its life cycle on the host; however, EMI does not measure nematode reproduction because it does not quantify the eggs produced. For that reason, an accurate determination of the degree of resistance/susceptibility of a plant material to this nematode can be obtained by estimating the RF (Lax et al., 2011).

The category of nematode resistance in a plant can also change depending on the experimental conditions set for screening, since nematode resistance is related to reproduction on a susceptible host. Thus, the choice of cultivar used as the standard for susceptibility is of great importance and seemed more crucial than the duration of the test (one or two generations) (Cortada et al., 2008). This is very important if RI is used to define the resistance level because this index compares the multiplication of each plant material in relation to the susceptible control. Therefore, its correct selection is crucial, especially in *N. aberrans* populations which show different behaviour, as observed in this work. The RI results obtained also showed that multiplication of the RC population on Fyuco INTA, Fenomeno RZ and Yatasto RZ was higher (between 36% and 67%) than on California Wonder (control).

In pepper, resistance to RKNs has been reported to be associated with at least 10 dominant genes (*N*, *Me1*, *Me2*, *Me3*, *Me4*, *Me5*, *Me6*, *Me7*, *Mech1* and *Mech2*). These genes induced different response patterns in root cells; in general, the resistance expression is characterised by a localised hypersensitive reaction, which consists of plant cell necrosis at the nematode infection site in response to the parasite attack, thereby preventing nematode development and reproduction (Gisbert et al., 2013). Some genotypes, such as *Me3* or *Me7*, have a locus controlling the penetration and migration of RKN juveniles in roots (Bleve-Zacheo et al., 1998; Pegard et al., 2005), and one genotype, *Me1*, has a locus that inhibits female development by conferring the development of defective giant cells (Bleve-Zacheo et al., 1998). Our results showed that the four pepper resistant genotypes to RKNs were as susceptible as the control (except for AF 8724 in LO), whereas in the RC population, Fenomeno RZ exhibited even significantly higher RF and RI values than California Wonder (control) and some of the peppers not carrying R-genes.

Previous studies of genes conferring nematode resistance have involved mainly sedentary nematodes whose infective J2 penetrate and establish permanent feeding sites in roots that were not already colonized by the nematode. *Nacobbus aberrans* is the only known species to have both migratory endoparasitic and sedentary endoparasitic stages within its life cycle; moreover, its sedentary stage appears to have characteristics of both the root-knot and the cyst nematodes (Eves van den Akker et al., 2014). In *N. aberrans,* infective immature females penetrate and establish feeding sites in roots that were already colonized by juveniles with endoparasitic migratory habits and which do not establish permanent feeding sites. It is not known if these differences in habits might interfere with the reaction of R-genes.

In the work reported here, host suitability of pepper lines carrying *Me1* or *Me7* resistance genes against *N. aberrans* populations is evaluated for the first time. To date, including the present results, four R-genes (*N*, *Me1*, *Me3*, and *Me7*) have been evaluated in *N. aberrans* and none of them have shown resistance to this parasite (Lax et al., 2006). Unfortunately, no commercial pepper cultivars resistant to *N. aberrans* are available up to the present. This fact favours the increase of nematode populations in contaminated plots, especially in greenhouses. The results obtained indicate the need to evaluate new pepper cultivars to detect resistant -or at least tolerant- genes with the aim of reducing yield losses in fields and greenhouses infested with this nematode. Search for resistance against *N. aberrans* in wild peppers growing in areas where the parasite is indigenous should be promoted.

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