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Full Length Research Paper

Indications of variation in host suitability to root-knot nematode populations in commercial tomato varieties

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The host suitability of 21 local, commercial tomato varieties were evaluated in concurrent greenhouse trials for resistance to *Meloidogyne incognita* race 2 and *Meloidogyne javanica*, respectively. *M. incognita* race-2-resistance identified in variety 'Rhapsody' during the latter study was subsequently verified in a follow-up microplot trial using differential initial population (Pi) densities and as well as in a field trial with four soil amendments. Substantial variation existed among the tomato varieties in the greenhouse screening with regard to resistance to the respective root-knot nematode species. Comparison of the different indicators of resistance used for the two species showed that labelling of specific varieties as resistant should not only be based on one criterium, since it could be insufficient. Strong non-linear relationships were shown in the microplot trial between Pi and Pf in the roots of both tomato varieties but nematode reproduction was poor on the resistant 'Rhapsody'. Significantly lower Pf in roots and J2 in soil was obtained for 'Rhapsody' compared to the susceptible Moneymaker. In the soil-amendment field trial, 'Rhapsody' also maintained significantly lower *M. incognita* numbers compared to 'Moneymaker' in all treatments. These results confirm the superior resistance of 'Rhapsody' to local *M. incognita* race-2 populations used in this study. More frequent and extensive screenings of commercial tomato material are recommended in order to provide resource-poor producers with better options for improved and sustainable yields.

Key words: Initial densities, *Meloidogyne incognit*a, *Meloidogyne javanica*, resistance, susceptible, root-knot nematodes, screening, tomato, varieties.

INTRODUCTION

Vegetables are high-value cash crops that constitute a major portion of human diets in many parts of the world and are, therefore, integral in agriculture (Potter and Olthof, 1993; Sikora and Fernandez, 2005). Yield and consumption of vegetables have expanded rapidly throughout the world during the past few decades, with a 32% increase recorded from 1990 to 2002 for Africa (Sikora and Fernandez, 2005). Tomato (*Solanum lycopersicon* L.) is one of the most common vegetables and hosts a wide variety of plant-parasitic nematodes including root-knot nematode species (Overman, 1991; Sikora and Fernandez, 2005; Bridge and Starr, 2007). *Meloidogyne incognita* (Kofoid and White, 1919) Chitwood, 1949 is the predominant root-knot nematode species parasitising this crop worldwide but ranks second

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to *Meloidogyne javanica* (Treub) Chitwood in tropical and subtropical regions (Nono-Womdim et al., 2002). Both parasites attack tomato crops almost wherever they are grown and cause major yield reductions when proper nematode management strategies are not applied (Sikora and Fernandez, 2005; Bridge and Starr, 2007). Estimated yield losses in excess of 50% (Nono-Womdim et al., 2002) and between 20 and 40% (Bridge and Starr, 2007) have been reported in tomato because of infection by *Meloidogyne* spp. However, depending on biotic, abiotic and management factors, the impact of root-knot nematode infection on tomato globally is highly variable (Nono-Womdim et al., 2002; Bridge and Starr, 2007).

The development and constant availability of root-knot nematode resistant crops such as tomato are crucial (Hussey and Janssen, 2002; Williamson and Roberts, 2009). This particularly applies to small-scale farmers who have limited infrastructure and financial resources for effective control against these plant parasites (Nono-Womdim et al., 2002). The availability of resistant vegetable varieties also remains one of the most viable and environmentally friendly options for limiting crop yield and quality losses due to parasitism by plant-parasitic nematodes (Hussey and Janssen, 2002; Williamson and Roberts, 2009). Although a number of root-knot-nematode-resistant tomato varieties are available in the world (Roberts, 1992; Sikora et al., 2000; Cook and Starr, 2006; Williamson and Roberts, 2009); the host suitability of the two most common *Meloidogyne* spp. and races in many, particularly third-world countries is generally unknown. However, the presence of the *Mi* gene; whether it is dominant or recessive (Godzina et al., 2010); whether its expression is affected by temperature (Devran et al., 2010) and possible differences in virulence of root-knot nematode populations on *Mi*-gene-bearing tomato varieties are all factors to be considered (Karajeh et al., 2005). A nematode survey of rural and peri-urban home, community and school gardens as well as small fields showed that root-knot nematodes are the predominant biotic constraint in vegetable production, including tomato, in 48 of 51 sites sampled (Mtshali et al., 2001). This indicates that root-knot nematodes could be a widespread problem in this country, at least in resource-poor farming. According to the aforementioned survey, tomato varieties grown in this sector seemingly do not have sufficient levels of resistance to these nematode parasites. Many producers that were interviewed during the aforementioned survey indicated that they purchase commercial seed for planting at some stage, although they regularly use second and even third-generation seed.

The objectives of this study were, therefore, to test tomato varieties that are commercially available in South Africa for their host suitability to local *M. incognita* race 2 and *M. javanica* populations. These species are the most common root-knot nematodes in South Africa (Keetch and Buckley, 1984; Kleynhans, 1991; Riekert, 1996).

Resistance indicated by the greenhouse screening was verified under semi-controlled microplot as well as a field trial.

MATERIALS AND METHODS

Greenhouse screening of commercial tomato varieties

Twenty-one tomato varieties that were commercially available at the time in South Africa were evaluated for their host suitability to local *M. incognita* race 2 and *M. javanica* populations in separate but concurrent greenhouse trials during 2005 on the premises of the Agricultural Research Council's Grain Crops Institute (A.R.C.-G.C.I.; 26.73° S, 27.08° E), North West Province, South Africa. In both trials the commercial variety 'Moneymaker' (Anwar et al., 1994; Hadisoeganda and Sasser, 1982; Nono-Womdim et al., 2002) was considered representative of susceptible varieties to these root-knot nematode species, while the variety MFH 9343 was selected as resistant check based on claims by the seed company that owns the breeder's rights (Anonymous, 2005). At the onset of this study, there was no substantiated evidence available on the host status of any of the local commercial varieties to root-knot-nematodes. Since seed supply of the line FA 1454 was limited, it was used only in the *M. incognita* trial and replaced by 'Rodade' in the M. javanica trial. An ambient temperature regime of 19±1°C minimum (night) and 26±1°C maximum (day), with a 14:10LD photoperiod was maintained in the greenhouses for both trials. The study was realized in a randomised-complete block design, with six replicates per entry (variety). Plastic pots (4 cm^3) were filled with a methyl-bromide-fumigated (1,162 g a.s./2 m^2 soil) and steam-pasteurised, sandy-loam soil (ca. 94% sand, 4% clay, 2% silt and 0.5% organic material). The soil pH (H2O) was 6.55. Fertiliser was applied according to a soil nutrient analysis and the optimal nutritional requirements for tomato (A.R.C.-Vegetable and Ornamental Plant Institute, Roodeplaat). Two seeds of each tomato genotype were planted per pot and seedlings were thinned to one per pot 14 days after plant emergence. The pots were watered by hand three times a week into the trays of each pot for the duration of the trials.

Populations of *M. incognita* race 2 and *M. javanica* were created and maintained on the tomato variety 'Moneymaker' in separate greenhouses. These populations were originally established from root-knot-nematode-infected material collected from groundnut (Vaalharts Irrigation Scheme in the Northern Cape Province; 27.95° S, 24.85° E) and pumpkin fields (Loskop Dam Irrigation Scheme in the Limpopo Province; 25.88° S, 29.89° E), respectively. After morphological (Taylor and Sasser, 1978) as well as molecular nematode species identification using the SCAR-PCR method (Zijlstra *et al.,* 2000), tomato seedlings were inoculated each with a single egg mass from the respective nematode source material, that is *M. incognita* or *M. javanica*. After the third tomato generation, random checks were done whereafter the identity of the respective root-knot nematode species was confirmed using the aforementioned molecular techniques. After the fourth generation of each root-knot nematode population, the 'North Carolina Differential Host Range Test' was performed for every population (Taylor and Sasser, 1978). These tests confirmed the identity of the two nematode populations and that they were monospecific. The *M. incognita* population was also confirmed as race 2, which is the most common of this species in South Africa (Kleynhans, 1991). Eggs and second-stage juveniles (J2) of each appropriate species were used to inoculate tomato seedlings in the respective greenhouse trials. Inoculation was performed 14 days after crop emergence by pipetting approximately 5 000 eggs and J2 of the respective population on exposed roots of each tomato seedling. The roots were covered again with soil after inoculation. The trials were terminated 56 days after inoculation (DAI). This period of screening allowed completion of at least one nematode generation

during the growing period of the tomato varieties(Kleynhans, 1991; Milne and Du Plessis, 1964; Fourie, 2005). At trial termination, the aboveground plant parts were removed and discarded. The root systems of each plant were washed under a gentle tap-water stream and stained by immersing each root system for 20 min in a 0.1% phloxine-B solution to facilitate counting of egg masses (Hussey and Boerma, 1981). The number of egg masses, representing the egg-laying females (E.L.F) per root system was counted under a commercial magnifying glass. Counting was stopped when there were more than 100 eggs masses on a particular root system. E.L.F indices per root system were rated on a scale from 0 to 5, where 0 = no egg masses; 1 = 1 to 2 egg masses; 2 = 3 to 10 eggs masses; 3 = 11 to 30 eggs masses; 4 = 31 to 100 eggs masses and 5 = more than 100 eggs masses per root system (Hussey and Boerma, 1981). After having counted the eggs masses, eggs and J2 were extracted from each root system using the adapted NaOCl method of Riekert (1995), which consists of a 1% NaOCl solution. Nematode eggs and J2 were subsequently counted under a dissection microscope (60x magnification). The reproductive potential of each nematode population on each tomato variety screened was determined according to Oostenbrink's reproduction factor (Windham and Williams, 1988), Rf = final egg and J2 numbers (Pf)/initial egg and J2 numbers (Pi).

In addition to this the resistance percentages (number of eggs and J2 per root system/the highest number of eggs and J2 numbers/root system in the batch x 100) (Hussey and Janssen, 2002) were also calculated for each genotype and used as an additional criterion of resistance.

Verifying the difference in host suitability observed in the preceding greenhouse trials in a microplot trial

A microplot trial was conducted during the next growing season (2005/2006) in Potchefstroom on the premises of the A.R.C.-G.C.I. to verify the difference in host suitability observed in the greenhouse between varieties 'Moneymaker' and 'Rhapsody' to the *M. incognita* race-2 population used in the latter. This trial was not repeated with *M. javanica* since no variety evaluated in the greenhouse trial had Rf values ≤ 1 to this species. The microplots used in this study consisted of 70 circular concrete tubes, 1.0 m in diameter, partially buried vertically 1.25 m deep in the soil in a field adjacent to the greenhouse complex where the previous screenings were done. The microplots were filled with methyl-bromide-fumigated soil (1,162 g a.s./2 m^2). The soil used in this trial was a sandy-loam, Hutton-type soil [ca. 94% sand; 4% clay; 2% silt and 5.0 g/kg organic material, pH (H_2O) 7.43], purchased from a commercial supplier. Soil analysis was done by the Soil Laboratory of the Institute for Industrial Crops of the A.R.C. in Rustenburg (North-West Province). Commercially available NPK (2:3:2) and super phosphate (10% phosphorous) were fertilisers applied according to a soil-nutrient analysis and the optimal nutritional requirements for tomato (A.R.C.-Vegetable and Ornamental Plant Institute, Roodeplaat). Seedlings of the respective cultivars tested in this trial were obtained from seedling trays filled with sterile vermiculite and planted to seeds from the same sources than those used in the greenhouse study. Twenty, two-week-old plants of each cultivar were transplanted into each microplot according to a randomised-complete block in a split-plot trial plan. The two tomatoes varieties represented the main factor and the seven treatments (including untreated control) the sub-factors, each replicated five times. The 20 seedlings in each plot were planted in three rows with intra-row spacing of 10 cm and inter-row spacing of 25 cm. Plots were irrigated three times a week for 15 min through micro sprayers fitted in each; delivering 25±4 mm water during this period. To prevent water logging, irrigation was rescheduled when it rained.

M. incognita race-2 inoculum used for this trial was from the same source as used in the greenhouse trial. A range of initial nematode inoculum levels (Pi) consisting of ca. 100, 500, 1,000, 5,000, 10,000 and 20,000 *M. incognita* race 2 eggs and J2 per seedling was prepared in tap water and inoculated on the exposed root systems of each tomato seedling in each microplot, except the uninoculated controls. Together with the different Pi-level treatments each tomato variety had replicated, nematode-free (Pi = 0) treatments included. Nematode sampling was done at crop maturity, 86 DAI. The roots of all 20 tomato plants in each microplot were carefully removed with a spade and rinsed free of adhering soil and debris. Each root system was kept separately, cut in pieces and used for nematode extraction. The eggs and J2 were extracted from each tomato root system as described for the greenhouse trials. Soil adhering to each root system was collected when the root systems were removed and these samples per plot were combined to make a composite soil sample per plot. Each soil sample was thoroughly mixed and a 200 g sub-sample per plot was collected for nematode extraction using the adapted decanting-and-sieving method (Cobb, 1918; Hooper et al., 2005; Khan, 2008). This was followed by the adapted sugar flotation method (Caveness and Jensen, 1955; Hooper et al., 2005). Nematode J2 and eggs were counted as described earlier and Rf values were calculated separately for roots.

Field trial

During the 2007/2008 growing season, a follow-up field trial was done with the tomato varieties 'Moneymaker' (susceptible) and 'Rhapsody' (resistant) in combination with four soil-amendment treatments. The field in Potchefstroom on the premises of the A.R.C.-G.C.I. was specially prepared to have a relatively uniform infestation of *M. incognita* race 2. Preparation of this field started during the 2003 and 2004 season by removing the top 50 cm soil of a 50 × 50 m piece of land. This was replaced by the same soil source used in the aforementioned microplot trials. Prior to planting for the first time, the soil was fumigated with methyl bromide at the same rate than in the microplots to eliminate all unwanted organisms. Nematode infestation of the soil was initially done by incorporating 2.0 cm chopped pieces of *M. incognita*-infected beetroot tubers obtained from the Loskop Dam area (25.35° S, 29.38° E). Maize and tomato crops were rotated on this field during the summer seasons of the 2004/2005, 2005/2006 and 2006/2007. A relatively high infestation of this *M. incognita* population was thus established and maintained before the tomato field trial commenced. In addition to the established *M. incognita* population in this field, ca. 2 000 J2 and eggs of the *M*. *incognita* population used in the greenhouse and microplot trials were inoculated on exposed roots of each two-week-old seedling of the susceptible tomato variety 'Moneymaker'. Each treatment consisted of 26 tomato plants spaced in 4 m rows, with 1 m inter- and 15 cm intra-row spacing. Precautions were taken to prevent contamination by other root-knot nematodes species by avoiding human and animal movement, movement of soil either by natural or human intervention and irrigation procedures were restricted to the bare essential.

The trial had a randomised-complete, split-plot layout, with 'Rhapsody' (resistant) and 'Moneymaker' (susceptible) tomato varieties as main factor, chicken manure (40 t/ha), cattle manure (40 t/ha), green Napier grass (*Pennisetum purpureum* Schumach) mulch (33 t/ha), the synthetic nematicide aldicarb (300 g/m) and an untreated but nematode-infested control as sub-factors, each repeated six times. The manure was purchased from an egg farm and a cattle feeding-pen, respectively, where only processed feed and fodder are used. The Napier grass mulch was prepared by cutting grown-out bunches of grass from on-station nurseries at A.R.C.-G.C.I. and carving up the stalks and leaves with a motorised carver. This material was prepared on the day this trial was planted.

Table 1. Reproduction of *Meloidogyne incognita* race 2 on tomato varieties as determined 56 days after inoculation (DAI) with ±5 000 eggs and second-stage juveniles (J2) in a greenhouse trial.

Tomato variety	E.L.F. index	Number of eggs and J2/root system	Rf value	Resistance (%)
1) Rhapsody	0.8^{ab}	1 674^{a}	0.3^{a}	1
2) MFH 9324	0.5^{a}	2 853^{a}	0.6^{a}	2
3) FA 1454	1.8^{cd}	3 728^{a}	0.7^{a}	2
4) FA 593	0.8^{ab}	3 728^{a}	0.7^{a}	2
5) Primepak	1.6^{bc}	6 078^{a}	1.2^{a}	4
6) FA 1418	1.5^{bc}	7 122^{a}	1.4^{a}	4
7) FA 1419	2.7^{def}	11 935^{a}	2.4^{a}	7
8) Roma	2.0^{cde}	14 368^{a}	2.9^{a}	9
9) MRS 0457	3.0^{fg}	14 770^{a}	2.1^{a}	9
10) Floradade	1.3^{abc}	21 975^{a}	4.4^{a}	13
11) MFH 9318	3.7^{gh}	32 258^{ab}	6.5^{ab}	20
12. Heinz	4.0^{hi}	61 833^{bc}	12.4^{bc}	38
13) Star 9030	4.2^{hi}	63 058^{bcd}	12.6^{bc}	38
14) Star 9001	4.0^{hi}	68 600^{bcde}	13.7^{bcd}	42
15) Fransesca	4.0^{hi}	81 427^{cde}	14.0^{bcd}	49
16) MFH 9343[1]	4.2^{hi}	78 400^{cde}	15.7^{cd}	48
17) FA 1453	2.8^{efg}	94 967^{cdef}	19.0^{cde}	58
18) Star 9006	4.5^{hi}	100 392^{def}	20.1^{cde}	61
19) Brilliante	4.2^{hi}	106 692^{ef}	21.3^{de}	65
20) FA 1410	4.8^{i}	124 950^{f}	25.0^{e}	76
21) Moneymaker[2]	4.5^{hi}	164 792^{g}	33.0^{f}	100
P value	0.0000	0.0000	0.0000	
F ratio	18.62	12.37	11.97	
SD	1.58	56 790.27	11.35	

[1]Resistant standard; [2]Susceptible standard.

The manures and grass mulch were broadcast in each plot in aliquots of the required rates per hectare and lightly worked into the 30-cm top-layer of soil with a gardening fork. The granular formulation of commercial aldicarb (Temik 15G®) was applied in the rows at the required rate by means of a specially developed wheelbarrow applicator (Mc Donald, 1998). All these applications as well as application of fertiliser at the same rates than in the microplot trial were done before transplanting of the tomato seedlings. Seedlings of both varieties were produced by planting seed from the same sources that were used in the preceding trials in pasteurised vermiculite in seedling trays. Two-week-old seedlings were transplanted to each row in which holes were made after application of the fertiliser and respective treatments. Immediately after planting semi-permanent irrigation lines with evenly spaced micro sprayers were placed in the field and irrigation at a rate of ca. 25 ml/h was applied three times a week for the duration of the trial unless it rained in adequate quantities. At termination of the trial, 86 days DAI two randomly selected plants were taken from each of the two rows per plot with their root systems intact. The roots of these four plants per replicate were cut in ca. 2 cm pieces, combined and a 50 g sub-sample per plot was taken for extraction of J2 and eggs as described earlier.

Soil samples were also taken and subjected to the same extraction methods as described earlier.

Statistical analyses

Data obtained from the respective glasshouse trials were subjected to an analysis of variance (ANOVA). Means were separated by the Tukey test ($p \leq 0.05$) for significance. E.L.F. indices and the Rf values as well as percentage resistance were calculated for the greenhouse screening data as described earlier.Non-linear regression analyses of the range of Pi levels (independent variables) in the microplot trial (verification of resistance) were done using the rational, linear-divided-by-linear model, $\hat{y} = A+B/(1+D*X)$, the exponential model $\hat{y} = A+B*(R\hat{}X)$ as well as the quadratic model $\hat{y} = A + B*(R\hat{}X)$. For the soil-amendment field trial, Pf in the soil and roots and Rf values where applicable, were analysed by means of a factorial analysis of variance. All nematode data were loge(x+1) transformed before analysis. Means were separated by Tukey's test ($p \leq 0.05$).

RESULTS

Greenhouse screening of commercial tomato varieties. Egg masses were present and eggs and J2 of *M. incognita* or *M. javanica* were extracted from the roots of all the varieties included in the study (Tables 1 and 2). E.L.F. indices in the *M. incognita* trial ranged from 0.5 to 4.5 and from 2 to 5 in the *M. javanica* greenhouse trial. Numbers of eggs and J2 extracted from the roots of the genotypes in the *M. incognita* trial ranged from 1,674 to 164,792 and from 8,925 to 1,075,610 in the *M. javanica*

Table 2. Reproduction of *Meloidogyne javanica* on tomato varieties as determined 56 days after inoculation (DAI) with ±5 000 eggs and second-stage juveniles (J2) in a greenhouse trial.

Tomato variety	E.L.F. index	Number of eggs and J2/root system	Rf value	Resistance (%)
1) Rhapsody	2.0[a]	8 925[a]	1.8[a]	1
2) Star 9030	2.2[ab]	10 681[a]	2.1[a]	1
3) FA 1410	2.7[bc]	10 833[a]	2.2[a]	1
4) FA 593	2.7[bc]	11 830[a]	2.4[a]	1
5) FA 1453	2.8[c]	13 195[a]	2.6[a]	1
6) Star 9006	3.0[c]	133 989[ab]	24.3[ab]	12
7) FA 1419	3.2[c]	276 617[abc]	55.3[abc]	26
8) Star 9001	4.0[d]	302 598[abc]	60.5[abc]	28
9) FA 1418	4.7[e]	323 867[abc]	64.8[abc]	30
10) MFH 9324	4.8[e]	342 008[abc]	68.4[abc]	32
11) MFH 9318	4.8[e]	476 558[bcd]	95.3[bcd]	44
12)Rodade	4.8[e]	555 742[cde]	111.1[cde]	52
13) Primepak	4.8[e]	866 453[def]	116.7[cde]	81
14) Fransesca	4.8[e]	584 033[cde]	116.8[cde]	54
15) MRS 0457	4.8[e]	596 225[cde]	119.2[cde]	55
16) Brilliante	5.0[e]	645 633[cde]	129.1[cde]	60
17) MFH 9343[1]	5.0[e]	798 642[def]	159.7[def]	74
19) Heinz	5.0[e]	871 383[ef]	174.3[ef]	81
18) Moneymaker[2]	5.0[e]	1 039 910[f]	207.9[f]	98
20) Floradade	5.0[e]	1 055 780[f]	211.2[f]	98
21) Roma	5.0[e]	1 075 610[f]	215.1[f]	100
P value	0.000	0.0000	0.0000	
F ratio	22.38	7.808	7.203	
SD	1.2	471 771.3	94.3	

[1]Resistant standard; [2]Susceptible standard.

trial. Rf values ranged from 0.3 to 33.0 and 1.8 to 215.1, respectively, in the *M. incognita and M. javanica* trials. Analysis of variance showed significant differences between many of the genotypes or groups of them for all the aforementioned variables in both greenhouse trials. Resistance percentage which is a relative measurement (Hussey and Janssen, 2002) within each trial showed trends of resistance (>10%) against both species (Tables 1 and 2).

With the exception of varieties 'Rhapsody', 'Francesca', 'Moneymaker', 'FA 593', 'FA 1419' and 'MFH 9318' no other variety held its relative position in terms of host suitability to the two nematode populations based on E.L.F. index, numbers of eggs and J2 per root system, Rf value and resistance percentage (Tables 1 and 2).

Verifying the difference in host suitability observed in the preceding greenhouse trials

The results on the host suitability of the two selected varieties to the *M. incognita* race-2 population in the microplots over increasing Pi's (Figure 1), as well as the results in the *M. incognita* race-2-infested, soil-amendment field trial (Figure 2 and Table 3) confirmed the significant differences in host suitability that was shown in the greenhouse trials. Nematode multiplication as expressed in number of eggs and J2/root system (Figure 1A), J2/200 g soil (Figure 1B) and Rf values (Figure 1C) of the two varieties differed significantly over the range of Pi that was applied in the microplot trial. The difference between the two varieties in the soil-amendment field trial with regard to number of eggs and J2/50 g roots and 200 g soil was also highly significant (Table 3) over all the treatments and untreated control (Figures 2A and B). Different amendments and the aldicarb treatment on the tomato varieties resulted in significant differences in nematode numbers/50 g roots but variety × treatment effects were not significant (Table 3).

DISCUSSION

Since nematode eggs and J2 occurred on all, none of the tomato varieties screened during this study were immune

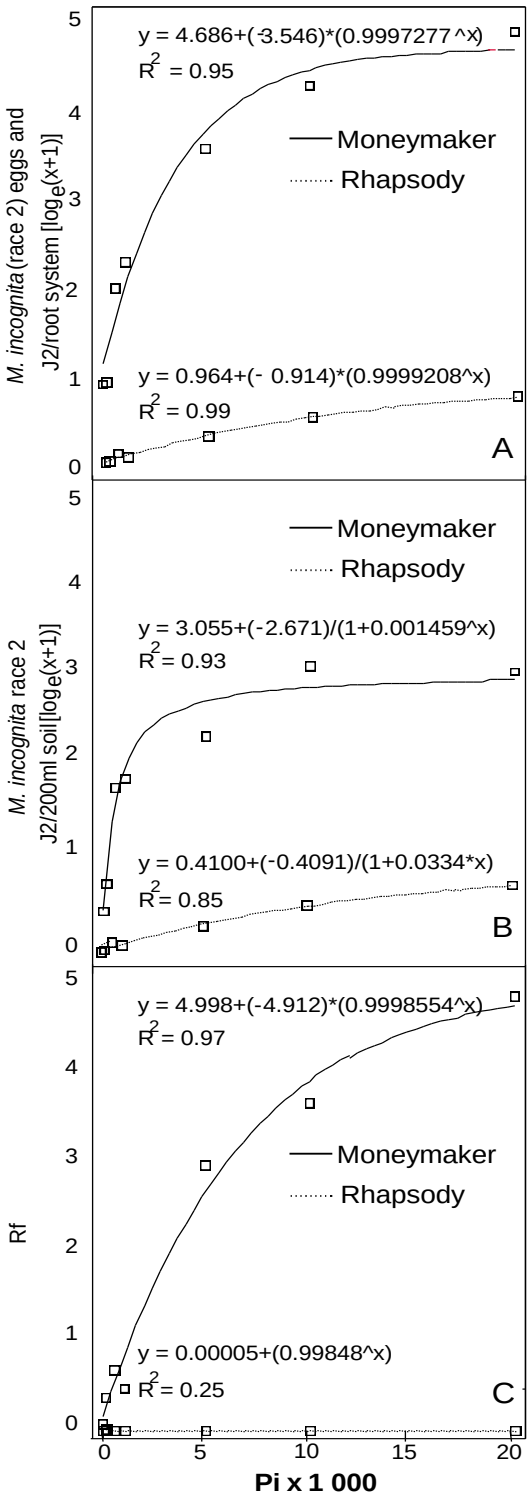

Figure 1. Non-linear relationships between initial (Pi) and final *Meloidogyne incognita* race 2 populations (Pf) in 50 g tomato roots (A), 200 ml soil (B) and reproduction factor (Rf) at 86 days after inoculation (DAI) for a susceptible ('Moneymaker') and a resistant ('Rhapsody') tomato variety in a microplot trial at Potchefstroom during the 2005/2006 growing season.

to either nematode species they were inoculated with. The genotypes screened in both glasshouse trials ranged from highly susceptible to both root-knot nematode species' populations to highly resistant to the *M. incognita* race-2 population based on the various parameters reported by Cook and Starr (2006), Hussey and Janssen (2002) and Starr and Mercer (2009). According to these results, the *M. javanica* population seemed more aggressive than *M. incognita* race 2 on average for all tomato genotypes screened. *M. javanic*a outscored *M. incognita* race 2 in terms of all variables determined in this study, from the most resistant to the most susceptible genotype. The root-knot nematode inoculum rate, procedures and conditions for the two trials were the same but the tomato genotypes reacted differently to the two nematode populations. Several authors (Cook and Starr, 2006; Starr and Mercer, 2009) cautioned about variable resistance such as the highly variable levels of reaction of these tomato varieties to the two nematode populations used in this study. It is a particular problem in South Africa, inter alia because both nematode species often occur together in local soils where crops such as tomato are grown (Kleynhans, 1991; Riekert, 1996). This trend in variable resistance will need to be verified by screening more tomato varieties to more and different populations of the two nematode species. Comparison of the various indicators of resistance of several tomato varieties against two root-knot nematode species under similar conditions also suggests that labelling of specific varieties as resistant based on one or even more criteria could sometimes be insufficient.

A good example of this is the tomato variety 'MFH 9343' that is claimed to be root-knot nematode resistant (Anonymous, 2005) but turned out to be highly susceptible to both local nematode populations. Other examples are 'FA 593' and 'FA 1454' that have significantly different E.L.F indices but had the same number of eggs and J2 per root system for *M. incognita* race 2. This could indicate that fewer eggs are produced per egg mass on the latter genotype. Similar cases were evident in the second greenhouse trial, for example, varieties 'Star' and 'FA 1410' evaluated against *M. javanica*. In terms of resistance percentage, these results further demonstrate the need for using several criteria when a batch of genotypes are screened, particularly when the level of resistance of the standard that is used had not been verified beforehand, as happened in these trials. Firstly, this criterion does not have the same meaning in the two trials, even where 'Rhapsody' turned out least susceptible in both. This genotype had far better scores for all the other variables measured in the *M. incognita* than in the *M. javanica* trial, while 'Moneymaker' had been the most susceptible genotype in both greenhouse trials although its susceptibility to *M. javanica* was almost 10-fold that of *M. incognita* race 2. The authors concede that nematode resistance is not the only important trait growers would be looking for when

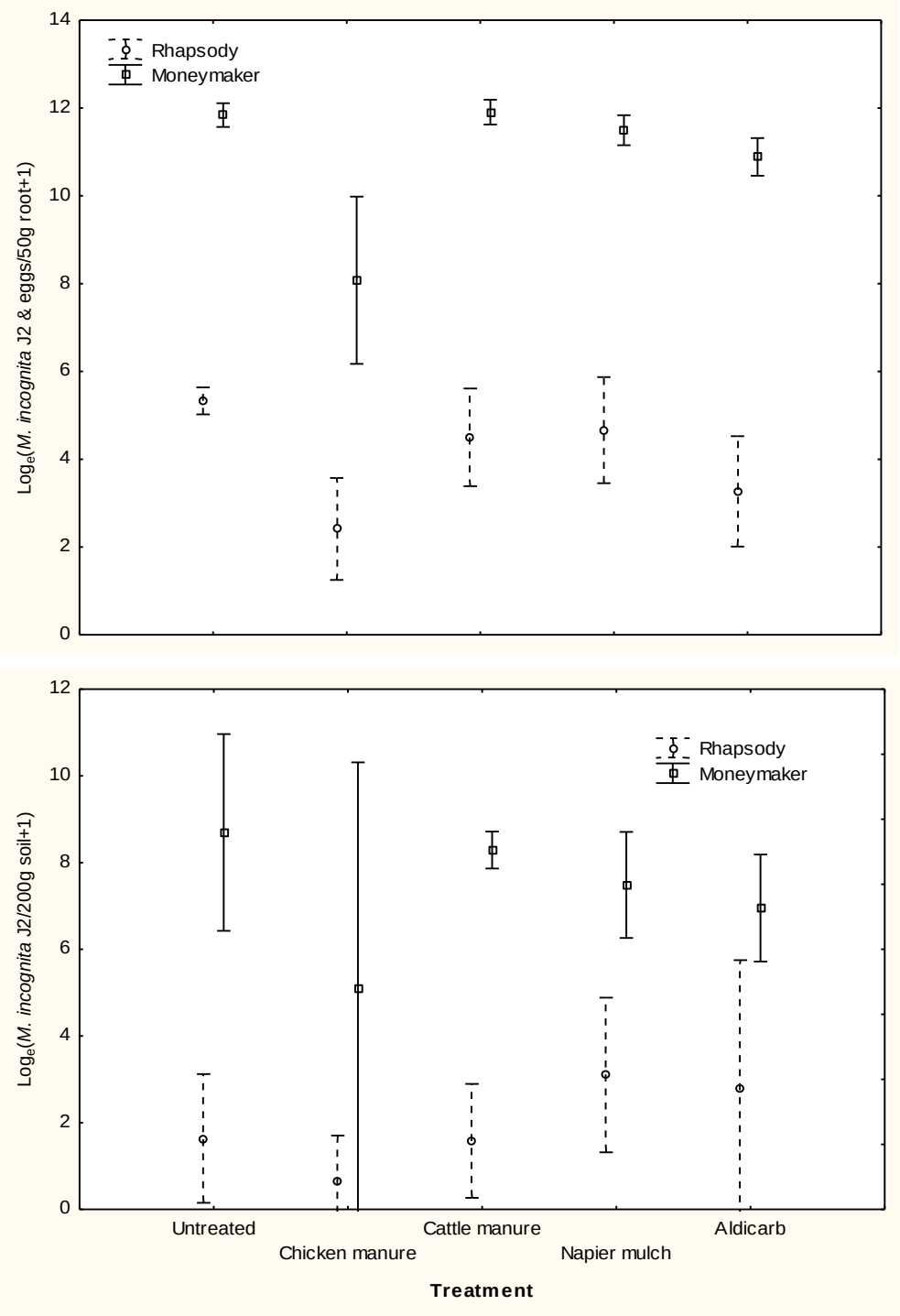

Figure 2. The effect of *Meloidogyne incognita* race-2 resistant variety 'Rhapsody' in combination with four soil amendments on population levels of this parasite compared to the susceptible variety 'Moneymaker' in a field trial at Potchefstroom during the 2006/2007 growing season.

selecting suitable varieties. When the yield of nematode-infected and uninfected varieties would be compared,another form of resistance, namely tolerance (Roberts, 2002; Cook and Starr, 2006) will come into effect. The authors accept that this study was done on a limited range of tomatoes genotypes and with only two *M. incognita* populations that might be considered 'domesticated' in a sense. However, it is maintained that

Table 3. Analyses of variance (ANOVA) statistics on the nematode data analyses of root and soil samples from the two tomato varieties Moneymaker (susceptible) and Rhapsody (resistant) subjected to four different treatments and an untreated control in a field trial infested with a *Meloidogyne incognita* race-2 population.

	Effect	Sum of squares	Degrees of freedom	Mean square	F	p
Log_e (*M incognita* eggs and J2/50 g roots	Intercept	3318.95	1	3318.9540	617.3683	0.0000
	Variety (V)	695.030	1	695.0300	129.2846	0.0000
	Treatment (T)	87.0070	4	21.7520	4.0461	0.0065
	V x T	7.2350	4	1.8090	0.3074	0.8717
	Replicate	38.0380	5	7.6080	1.4151	0.2354
	Error	263.423	49	5.3760		
Log_e (*M incognita* J2/200 g soil	Intercept	1285.77	1	1285.7670	284.9855	0.0000
	Variety (V)	430.007	1	430.0070	95.3094	0.0000
	Treatment (T)	47.3210	4	11.8300	2.6221	0.0459
	V x T	735E7	4	184E7	1.1068	0.3425
	Replicate	40.5380	5	8.1080	1.7970	0.1309
	Error	221.073	49	4.5120		

tomato that is often grown under conditions similar to those of this study. Rural, resource-poor people have very limited land available and will most likely grow tomato repetitively in one field. They rarely have access to commercial crop varieties and theirs could be highly susceptible to nematode populations that may also have become habituated. A recent survey of rural and peri-urban home and school gardens as well as small fields showed 89% infection and incidence rates of root-knot nematodes on tomato (Fourie and Mc Donald, 2002).

As suggested earlier, the situation might be exacerbated further when tomato field infestations consist of mixed populations of *M. incognita* and *M. javanica* or other root-knot nematode species (Keetch and Buckley, 1984; Kleynhans, 1991; Riekert, 1996). The particular gene (-s) encoding resistance identified in the varieties screened in this study is unknown to the authors. The *Mi*-1 gene that confers resistance to *M. incognita*, *M. javanica* and *Meloidogyne arenaria* in particular, is incorporated in a wide range of tomato varieties worldwide (Cook and Starr, 2002; Williamson and Roberts, 2009). It is, however, known that this gene is ineffective at high soil temperatures (>28°C) and it is not effective against *M. hapla* and some other root-knot nematodes species (Cook and Starr, 2006; Williamson and Roberts, 2009) that occur in local agricultural and horticultural soils (Keetch and Buckley, 1984; Kleynhans, 1991; Riekert, 1996). In addition, some populations of *M. incognita*, *M. javanica* and *M. arenaria* have been reported as virulent to this gene (Jacquet et al., 2005; Williamson and Kumar, 2006). Some of the genotypes screened in this study, therefore, might contain the *Mi*-1 gene but it was also demonstrated that claims by owners about varieties might not hold true for all root-knot nematode populations or conditions. Therefore, it would be important to investigate the sources of resistance indentified in this study to see whether they are mono- or polygenic. Different sources of resistance could be present, which could be exploited in future tomato breeding programmes. This study did not allow for further, more extended and frequent screening of tomato varieties, including segregating material which is often grown in the resource-poor sector. However, it was suggested that screening of tomato varieties that are available to growers for nematode-host suitability would contribute greatly to more sustainable and profitable yield of this crop.

The latter particularly applies to those growers that cannot afford or do not have access to additional nematode management technology.

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Abbreviations: A.R.C., Agricultural Research Council; **a.s.**, active substance; **D.A.I.,** days after inoculation; **E.L.F.,** egg-laying females; **G.C.I.**, grain crops institute; **J2,** second-stage juvenile; **Pi,** initial egg and J2 numbers; **Pf,** final egg and J2 numbers; **Rf,** reproduction factor.

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