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ORIGINAL ARTICLE

The host status of glyphosate-tolerant soybean genotypes to *Meloidogyne incognita* and *Pratylenchus* infection

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Abstract

The host status of South African adapted, genetically modified (GM) glyphosate-tolerant soybean genotypes to root-knot (field and glasshouse) and lesion (field) nematodes were assessed. Analyses of root and soil samples of 29 genotypes (collected from seven production areas during the 2014/15 season) enabled the identification of nine plant-parasitic nematode genera and 10 species. Predominant endoparasitic genera in root samples were *Meloidogyne* (*Meloidogyne incognita* and *M. javanica*) and *Pratylenchus* (*Pratylenchus brachyurus*, *P. zeae* and *P. teres*). *Rotylenchulus parvus* was the predominant semi-endoparasite in soil, followed by *Scutellonema brachyurus* and *Helicotylenchus* sp. Only 'PAN 1583 R' and 'PAN 1521 R' maintained less than 10% of the *Meloidogyne* spp. densities present in roots of the most susceptible genotype, while all genotypes were susceptible to the *Pratylenchus* spp. The host status of 36 soybean genotypes to *M. incognita* infection, evaluated in two follow-up glasshouse experiments terminated 56 days after inoculation of *ca.* 1000 *M. incognita* eggs and second-stage juveniles (J2) per seedling, varied substantially for final population density (Pf), reproduction factor (Rf) and relative percentage susceptibility (%S). Only 'PRF-GCI7' and the resistant reference 'LS 5995' had Rfs < 1 for both experiments, despite higher minimum and maximum temperatures recorded for the second experiment. Continuous evaluation of soybean genotypes for their host status to predominant nematode pests and their use to reduce densities of such species in producer's fields are crucial to enable sustainable crop production, and contribute towards food provision and security.

Keywords *Glycine max* · Resistance · Root-knot nematodes · Root-lesion nematodes

Introduction

Soybean (*Glycine max* L.) is an important oilseed and protein crop cultivated in South Africa (Dlamini et al. 2014; PRF 2020), with genetically modified (GM), glyphosate-tolerant soybean genotypes dominating local production. Pronounced changes have been experienced in terms of the implementation of advanced technology and cropping practices in soybean-based cropping systems since the first nematode survey was done in the mid-1990s (Fourie et al. 2001). These are for example represented by the commercialization of glyphosate-tolerant soybean genotypes (from the 2001/2002 growing season (Wolson 2007) and also increased conservation agriculture being practiced by local producers (Engelbrecht 2016). Factors like these undoubtedly contributed towards more than a tenfold increase in the soybean production area (± 730,500 ha) and quantity (± 1.1 million metric tons) being recorded during the 2018/19 growing season (Grain 2020) compared to such figures attained nearly two centuries ago.

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Plant-parasitic nematodes remain a major challenge in crop production, especially in sub-Saharan African countries such as South Africa (Fourie et al. 2017; Coyne et al. 2018). Nematodes are important pests of soybean worldwide (Jones et al. 2013). In South Africa, about 57 plant-parasitic nematode species have been listed on soybean (Marais et al. 2017a; Mbatyoti et al. 2020) with root-knot nematodes (*Meloidogyne* spp.) being predominant (Fourie et al. 2015). *Meloidogyne incognita* (Kofoid and White 1919) Chitwood, 1949, is the economically most important root-knot nematode species in South Africa, followed by *Meloidogyne javanica* (Trued 1885) Chitwood, 1949. Root-knot nematodes are also worldwide generally perceived as the most widespread and damaging nematode pests of soybean (Beneventi et al. 2013; Korayem and Mohamed 2018). Estimated soybean yield losses, mainly due to *Meloidogyne* spp. infection, ranging from 25 to 100% have been reported for South African production areas (Riekert and Henshaw 1998; Fourie et al. 2015).

Another economically important plant-parasitic nematode genus that causes considerable damage to soybean worldwide is *Pratylenchus* (root-lesion nematodes), with *Pratylenchus brachyurus* (Godfrey 1929) Filipjev and Schuurmans Stekhoven, 1941, generally being the most damaging (Bridge and Starr 2007; Lima et al. 2015). In the soybean production areas of South Africa, *Pratylenchus zeae* Graham, 1951, and *P. brachyurus* were reported as the predominant root-lesion nematode species (Fourie et al. 2001). Although yield losses ranging from 30 to 50% has been recorded from Brazilian production areas due to *P. brachyurus* infection (Ferraz 2006; Inomoto 2011; Lima et al. 2015), no yield loss data is available for damage caused by this root-lesion nematode species to soybean in South Africa.

In the past, the use of chemical nematicides was the most popular and effective strategy used to control plant-parasitic nematodes (Niblack et al. 2004; Nyczepir and Thomas 2009). However, during the past two decades, nematicides have been increasingly withdrawn from the world markets, or their use have been restricted, due to environmental concerns (Rich et al. 2004; Haydock et al. 2013). In South Africa, evaluation of various synthetically derived nematicides during the early 2000s to reduce the population density of root-knot nematodes (*M. incognita* and *M. javanica*) on soybean did not yield economically viable results (Fourie and Mc Donald 2001, 2007). To date no nematicide has been registered for use on soybean in the country.

An alternative management strategy that is being used with success to control plant-parasitic nematodes, in particular root-knot nematodes on soybean and follow-up crops, is genetic host plant resistance (Oyekanmi and Fawole 2010; Sharma et al. 2012). Since the 1970s, considerable progress has been made in identifying resistant genotypes and breeding for *M. incognita* resistance in soybean (Hussey and Boerma 1981; Luzzi et al. 1997; Fourie and De Waele 2020). Since the late 1990s, numerous soybean genotypes with resistance to root-knot nematodes, in particular *M. incognita*, have been reported in countries such as the USA (Wilkes and Kirkpatrick 2020), Brazil (De Oliveira et al. 2015), China (Jiao et al. 2015) and elsewhere in the world (Fourie and De Waele 2020), including South Africa (Fourie et al. 1999; Mienie et al. 2002; Van Biljon 2004; Fourie et al. 2008; Venter 2014). However, the situation in South Africa is bleak since only a few soybean genotypes with resistance to *M. incognita* are currently available (Fourie et al. 2015; Mbatyoti 2018) including, for example, the conventional genotype Egret (Fourie et al. 2013) and the genetically modified (GM) genotype DM 6.2i RR that is tolerant to glyphosate (Venter 2014; Mbatyoti 2018). Another highly resistant genotype (LS 5995), identified in the early 2000s, showed a 22% yield increase compared to a susceptible reference genotype when grown under *M. incognita*-infested field conditions (Fourie et al. 2013), but is no longer available for commercial production. Although *M. incognita* resistance has been introgressed from LS 5995 into seven conventional soybean genotypes that are adapted to local environmental conditions, this plant material is in the process of being commercialized by the owner institution (Agricultural Research Council-Grain Crops; ARC-GC) since the lines are not glyphosate tolerant (Fourie et al. 2015).

The objectives of this study were thus to examine the host status of (i) the commercially cultivated GM glyphosate-tolerant soybean genotypes in South Africa to the most common plant-parasitic nematodes present in the local soybean production areas where the National Soybean Cultivar Trials were conducted and (ii) 36 soybean genotypes (including 31 GM glyphosate-tolerant genotypes that are commercially available in South Africa) to *M. incognita* which is the predominant root-knot nematode species occurring in local soybean production areas.

Materials and methods

National Soybean Cultivar Trials field study

Seeds of all genotypes evaluated in this study were sourced from the ARC-GC located in Potchefstroom, North West province, South Africa. During the 2014/15 growing season (February–March), 29 GM glyphosate-tolerant soybean genotypes, included in the National Soybean Cultivar Trials conducted by the ARC-GC, were grown on seven localities representative of the major soybean production areas of South Africa. These localities were located in the Free State Province (Bethlehem, Hoopstad and Kroonstad), North West Province (Brits and Potchefstroom) and Mpumalanga Province (Groblersdal and Middelburg).

Physical and chemical soil properties, crop history, rainfall and irrigation of each locality are listed in Table 1.

The lay-outs of the experiments at each of the seven localities were randomized complete block design with three replicate plots for each soybean genotype. Each plot consisted of four rows (5 m long) planted with 170 soybean seeds per row with inter- and intra-row spacings of 90 and 3 cm, respectively. Seeds were inoculated with *Bradyrhizobium japonicum* strain WB74 (Soygro (Pty) Ltd., Potchefstroom) before planting at a dosage of 250 g/50 kg seed (www.soygro.co.za).

At each locality, rhizosphere samples (root and soil) were collected at flowering from six soybean plants, chosen at random, per genotype/plot (*i.e.* per 5-m-long row, per replicate plot). Of each sample, one sub-sample of 200 g soil, 5 g and 50 g roots was taken for nematode extraction. Root-knot nematode eggs and second-stage juveniles (J2) were extracted from the 50 g root sub-samples using the 1% NaOCl method (Riekert 1995), which was originally developed by Hussey and Barker (1973) for the optimal extraction of eggs of sedentary, endoparasitic egg-mass producing nematodes. Root-knot nematode J2 as well as the vermiform stages (juveniles and adults) of a wide range of migratory endoparasitic nematodes were extracted from the 5-g root sub-samples using the centrifugal-flotation method (Marais et al. 2017b). The decanting and sieving method (Marais et al. 2017b) was also used to extract juveniles and adult nematodes present in the soil from the 200 g soil sub-samples.

Nematodes extracted from the 5 and 50 g root sub-samples were transferred to a De Grisse counting dish (De Grisse 1963) and, using a stereomicroscope (× 60 magnification), identified to genus level and counted. Eggs and J2 of *Meloidogyne* spp. were counted in the 50-g root sub-samples. In the 5-g root sub-samples, only J2 of *Meloidogyne* spp. were counted and the vermiform stages of all other plant-parasitic nematode genera. No eggs were counted in either the 5-g root or 200-g rhizosphere soil sub-samples since eggs of nematodes cannot be identified to neither genus nor species level. Nematodes extracted from the 200-g rhizosphere soil sub-samples were transferred to a 1-ml Hawksley slide (Dickerson 1977) using a light microscope (× 1000 magnification), identified at genus level and counted. For identification at species level, at least 30 individuals of each genus were hand-picked from the counting dishes after counting, using a fine tip needle, killed and fixed in a heated formaldehyde-propionic-acid-water (FPG) solution (100 mL of a 40% formalin solution, 10-ml propionic acid and 890-ml distilled water; Marais et al. 2017b). The glass dish with the fixed nematodes was placed in an incubator at 40 °C for 72 h and the FPG solution stepwise replaced with glycerin (Marais et al. 2017b). The fixed nematodes were hand-picked from the glycerin and permanently mounted in glycerin on glass slides using the paraffin-ring method (Marais et al. 2017b). The nematode-taxonomists of the ARC-Plant Health and Protection, Roodeplaat, South Africa, identified the nematodes to species level.

Identification of the root-knot nematode species was based on morphological inspection of the shape of the perineal and oesophageal regions of mature females (Hartman and Sasser 1985; Kleynhans 1991; Marais et al. 2017b). Material for such identifications were obtained as follows: the eggs and J2 that had been extracted from the 50 g root sub-samples for each locality were pooled for all the samples counted and inoculating on roots of potted (10-L pots) seedlings of the root-knot nematode susceptible tomato genotype Floradade (Fourie et al. 2012). Thus, seven root-knot nematode populations were established from the seven localities sampled, maintained and mass reared *in vivo* in a greenhouse at an ambient temperature range of ± 20–26 °C and a 14:10 light:dark photoperiod. Forty days after nematode inoculation, 21 mature females of each of the seven *Meloidogyne* populations were hand-picked from the infected tomato roots and their perineal and oesophageal regions cut, and identified using light microscopy (× 1000 magnification) according to the method of Marais et al. (2017b).

Table 1 Soil physical and chemical properties, crop history, rainfall and irrigation figures for the seven localities where the study was conducted during the 2014/15 growing season

Locality	Soil physical properties (%)			Soil chemical properties	Crop history (2013/14)	Rainfall	Irrigation
	Sand	Silt	Clay	pH		(mm)	(mm)
Bethlehem	80	4	16	6.73	Soybean	639	0
Brits	66	8	26	7.53	Soybean	429	300
Groblersdal	71	17	12	6.59	Soybean	598	315
Hoopstad	95	0	5	7.35	Maize	403	0
Kroonstad	91	7	2	7.93	Soybean	608	0
Middelburg	81	10	9	6.58	Soybean	784	0
Potchefstroom	66	8	26	7.39	Maize	548	420

Glasshouse study

The soybean genotypes included in the glasshouse studies consisted of 31 commercially available GM glyphosate-tolerant soybean genotypes (of which 30 genotypes host response to root-knot nematode species infection was unknown) and four conventional soybean genotypes with varying levels of resistance to *M. incognita* infection (Fourie et al. 2015). The highly *M. incognita*-resistant 'LS 5995' (Fourie et al. 2006) and susceptible GM glyphosate-tolerant 'LS 6248 R' (Mbatyoti et al. 2013; Venter 2014) served as the reference genotypes.

Fifteen seeds of each soybean genotype inoculated with *Bradyrhizobium* strain WB74 were planted in 4-L plastic pots filled with a Telone II-fumigated (dosage rate of 150 L/ha; active substance 1,3 dichloropropene at 1110 g/L) sandy soil (5.3% clay, 93.6% sand, 1.1% silt and 0.47% organic matter; pH (H_2O) 7.5). Ten days after emergence, one seedling was transplanted to a 0.5-L plastic tube containing the same sandy loam soil. During transplanting, each tube was inoculated with approximately 1000 *M. incognita* eggs and J2 by pipetting 2 mL of a water suspension containing the eggs and J2 onto the exposed root system of each seedling after which the roots were covered with soil.

The eggs and J2 of the inoculum were obtained from a *M. incognita* population originally isolated from maize roots that were cultivated on a farm near Vryburg, Northern Cape Province, South Africa. A monoculture of this population was established from a single egg mass hand-picked from the maize roots on potted plants of the susceptible tomato genotype Rodade (Fourie et al. 2012) under glasshouse conditions at the premises of the North-West University, Potchefstroom, South Africa; ambient temperature range of 21–26 ± 1 °C and 14 L:10D photoperiod.

The experiment was repeated once. An ambient temperature range of 18–24 ± 1 °C and a 14:10 h light-dark photoperiod were maintained for the duration of the 1st experiment, while the ambient temperature range during the 2nd (repeat) experiment was higher, being 21–26 ± 1 °C. The lay-outs of both experiments were randomized complete block designs with six replicates (representing one plant per replicate) for each genotype. Plants were watered as needed, usually three times per week, and each tube weekly supplied with 250 mL of Hoagland's nutrient (Hoagland and Arnon 1950) solution throughout the duration of the experiments.

Both experiments were terminated 56 days after inoculation (DAI). Root systems of each of the genotypes were gently uprooted, rinsed under running tap water and weighed. Eggs and J2 were extracted from the complete root systems of each genotype using the 1% NaOCl method (Riekert 1995) and counted using a stereomicroscope (× 60 magnification).

Data analyses and statistics

For the field study, the nematode data for root and soil subsamples were pooled per locality and the frequency of occurrence (%F), mean population density (MPD) and prominence value (PV) of the predominant nematode taxa across localities and on each of the soybean genotypes calculated as follows (De Waele and Jordaan 1988):

$$PV = \text{Population density of each genus} \times \sqrt{\text{frequency of occurrence}}/10.$$

To evaluate the host response of each soybean genotype included in the National Soybean Cultivar Trials to the root-knot and root-lesion infections, the reduction in reproduction, referred to as the percentage susceptibility expressed (%S), was calculated as the reduction in Pf (eggs and J2 per 50 g roots) of a genotype compared to the Pf of the most susceptible genotype (Hussey and Janssen 2002). A genotype was regarded as highly resistant when it had a %S value < 10%.

For the glasshouse study, the reproductive potential of *M. incognita* in the roots of each soybean genotype was calculated using Oostenbrink's reproduction factor (Rf) according to the following equation: Rf (Pf/Pi) = final number of eggs and J2/inoculated number of eggs and J2 (Windham and Williams 1987), while the %S was also calculated for each genotype. Data for each experiment were subjected to Analysis of Variance (ANOVA) and finally to Factorial ANOVA when a significant interaction ($P < 0.05$) existed between the experiments using Statistica 12.2 (www.statsoft.com). Means of each nematode parameter were separated by the Tukey HSD Test (Statistica, 12.2). Nematode data were log(x + 1) transformed before statistical analysis to reduce variation (Ribeiro-Oliveira et al. 2018).

Results

National Soybean Cultivar Trials field study

Nine plant-parasitic nematode genera and 10 species were identified from the rhizospheres (roots and soil) of soybean plants sampled at the seven localities. The genera included are the following: *Criconema*, *Criconemoides*, *Helicotylenchus*, *Meloidogyne*, *Nanidorus*, *Pratylenchus*, *Rotylenchulus*, *Scutellonema* and *Tylenchorhynchus*. The species identified were *Criconemoides sphaerocephalus* Taylor, 1936, *M. incognita*, *M. javanica*, *Nanidorus minor* (Colbran 1956) Siddiqi, 1974, *P. brachyurus*, *Pratylenchus teres* Khan and Singh, 1975, *P. zeae*, *Rotylenchulus parvus* (Williams 1960) Sher, 1961, *Scutellonema brachyurus* (Steiner 1938) Andrássy, 1958, and *Tylenchorhynchus brevilineatus* Williams, 1960. Since only immature developmental stages

of *Helicotylenchus* were found, the species could not be identified.

Root-knot nematodes per 50 g roots Based on morphological and molecular identification, a single-species population of *M. incognita* was present at six of the seven localities (Bethlehem, Brits, Grobersdal, Hoopstad, Middelburg and Potchefstroom), while a single-species population of *M. javanica* was present at one locality (Kroonstad). *Meloidogyne incognita* was thus the predominant root-knot nematode species, with high MPD (252219) and PV (236680) per 50-g roots when data were pooled across localities and genotypes, compared to substantially lower MPD (69260) and PV (25915) for *M. javanica* when data of all genotypes were combined per locality (data not shown).

The frequency of occurrence of the root-knot nematode species was higher than 70% for all genotypes; the number of eggs and J2 per 50-g roots were also high with MPDs ranging from 1816 ('PAN 1583 R') to 29,052 ('PAN 1623 R'), and PV values ranging from 1684 ('PAN 1583 R') to 24,480 ('PAN 1623 R') (Table 2). The %S ranged from 6 ('PAN 1583 R') to 74% ('LS6164 R' and 'LS6261') when compared to the most susceptible genotype PAN 1623 R (MPD = 29,052). Only two genotypes, PAN 1583 R and PAN 1521 R, had a %S < 10%; 22 genotypes had %S ranging between 10 and 50%; and four genotypes had %S ranging between 50 and 100%.

Plant-parasitic nematodes per 5 g roots *Pratylenchus* was the predominant genus, with *P. brachyurus* being the predominant species being present in 14% of the localities with MPD and PV values of 2996 and 1198, respectively (Table 3). *Pratylenchus zeae* ranked second (MPD = 1983; PV = 992) in terms of predominance. Other plant-parasitic nematode genera/species found in the 5-g root samples were, in descending order of predominance, *P. teres*, *Rotylenchulus* sp., *S. brachyurus* and *Helicotylenchus* sp.

Data for the genotypes that were pooled for the localities showed that the PVs of root-lesion nematodes per 5-g roots ranged between 1367 ('PAN 1664 R') and 5315 ('DM 6.2i RR'), frequency of occurrence between 71 and 100% and MPDs between 1622 ('PAN 1664 R') and 5731 ('DM 6.2i RR') (Table 4). The population density of root-lesion nematodes were reduced between 26 and 86% compared to genotype DM 6.2i RR. which had the highest MPD.

Plant-parasitic nematode population density per 200 g soil *Rotylenchulus parvus* (PV = 2145 and MPD = 3271), followed by *S. brachyurus* (PV = 1217 and MPD = 2260), was the predominant plant-parasitic nematode species present in soil samples (Table 5). Other nematode genera/species in decreasing order of predominance were *Helicotylenchus* sp., *C. sphaerocephalus*, *P. teres*, *T. brevilineatus*, *P. zeae*, *Criconema* sp. and *N. minor*.

Glasshouse study

No interaction (F-ratio = 1.1; $P = 0.381$) was evident for the Pf of *M. incognita* per root system in terms of genotypes x experiments, while a significant interaction existed for Rf (F-ratio = 4.7; $P = 0.001$) (Table 6).

The Pfs of *M. incognita* differed significantly among the soybean genotypes for each of the two experiments. In the 1st experiment, egg and J2 numbers per root system ranged from 42 ('PRF-GCI7') to 7563 ('DM 5.1i RR') (Table 6) being substantially higher in the 2nd experiment: ranging from 566 ('PRF-GCI7') to 57,068 ('DM 5953 RSF'). Thirteen genotypes had significantly higher Pfs for the second compared to the 1st experiment: PRF-GCI7, DM 6.8i RR, LS 6466 R, S722/6/1E, PAN 1454 R, LS 6146 R, PAN 1521 R, NS 6448, PAN 1666 R, LS 6248 R, NS 5909 R, PAN 1513 and DM 5.1i RR.

The Rf values of the genotypes also differed significantly among each other for each of the two experiments. For the 1st experiment, Rf values ranged from 0.04 ('PRF-GCI7') to 7.6 ('DM 5.1i RR') (Table 6). The latter genotype and others, *viz.* DM 5953 RSF, LS 6164 R, LS 6240 R, LS 6248 R, NS 5009 R, NS 5909 R, NS 6448, PAN 1500 R, PAN 1513 R, PAN 1521 R, PAN 1583 R, PAN 1666 R and PAN 1729 R, had Rf values > 1 indicating susceptibility. Twenty-two genotypes had Rf values < 1 indicating resistance with PRF-GCI7 (Rf = 0.04), LS 6261 R (Rf = 0.1) and LS 5995 (Rf = 0.2) being the most resistant genotypes. For the 2nd experiment, the Rf values of all the genotypes were in general substantially higher compared to the 1st experiment and ranged from 0.6 ('PRF-GCI7') to 57.1 ('DM 5953 RSF') (Table 6). Only two genotypes (PRF-GCI7 and LS 5995) showed resistance to *M. incognita* with Rf values < 1, while all other genotypes were susceptible (Rf > 1). Nine genotypes had significantly higher Rfs for the second compared to the 1st experiment: PAN 1664 R, SC SOCERER, PHB 94Y80 R, PAN 1623 R, DM 5953 RSF, LS 6248 R, PAN 1729 R, PAN 1513 R and DM 5.1i RR.

In the 1st experiment, the root systems of genotypes DM 6.8i RR, LS 5995, LS 6161 R, LS 6261 R, LS 6444 R, LS 6453 R, NS 7211 R, PAN 1614 R, PAN 1623 R, PHB 94 Y 80 R, PRF-GCI4, PRF-GCI6, PRF-GCI7 and SC SORCERER maintained less than 10% of the *M. incognita* population density of the most susceptible genotype DM 5.1i RR (Table 6).

In the 2nd experiment, DM 6.2i RR, DM 6.8i RR, LS 5995, LS 6146 R, LS 6240 R, LS 6444 R, LS 6453 R, NS 7211 R, PAN 1500 R, PAN 1583 R, PAN 1614 R, PHB 95 Y 20, PRF-GCI4, PRF-GCI5, PRF-GCI6 and PRF-GCI7 maintained less than 10% of the *M. incognita* population density of the most susceptible genotype DM 5953 RSF (Table 6).

Table 2 Data on prominence value, frequency of occurrence, mean population density and percentage reproduction reduction of mixed *Meloidogyne* spp. (*M. incognita* and *M. javanica*) in 50-g root samples of 29 soybean genotypes grown at seven localities in South Africa during the 2014/15 growing season

Cultivar	Prominence value (PV)[1]	Frequency of occurrence	Mean population density (MPD)	Percentage relative susceptibility (%S)[2]
PAN 1623 R[3]	24,480	71	29,052	100
LS 6164 R	19,912	86	21,472	74
LS 6261 R	19,837	86	21,391	74
NS 5009 R	17,309	86	18,665	64
LS 6146 R	15,081	71	17,898	62
PAN 1729 R	13,696	100	13,696	47
LS 6161 R	12,692	100	12,692	44
DM 5.1i RR	11,868	86	12,797	44
NS 7211 R	11,644	100	11,644	40
LS 6248 R	11,622	100	11,622	40
PHB 95 Y 20	11,609	100	11,609	40
LS 6466 R	10,994	86	11,855	41
LS 6240 R	10,913	100	10,913	38
LS 6444 R	10,644	86	11,478	40
LS 6453 R	9192	100	9192	32
PHB 94 Y 80 R	8602	100	8602	30
PAN 1664 R	7930	86	8551	29
PAN 1513 R	7348	86	7924	27
NS 5909 R	6940	86	7484	26
PAN 1500 R	6937	86	7480	26
PAN 1454 R	6394	71	7588	26
DM 6.2i RR	6031	86	6503	22
PAN 1614 R	5667	86	6111	21
DM 6.8i RR	5420	100	5420	19
DM 5953 RSF	5003	100	5003	17
NS 6448	4706	86	5075	18
PAN 1666 R	2900	86	3128	11
PAN 1521 R	2462	100	2462	9
PAN 1583 R	1684	86	1816	6

[1] *PV*, final population density (Pf) of each species × $\sqrt{\text{frequency of occurrence}}$ /10; [2] %S, final population density (Pf) of individual genotype/Pf of genotype that is most susceptible × 100

Table 3 Data on prominence value, frequency of occurrence and mean population density of plant-parasitic nematodes in 5 g root samples of 29 soybean genotypes grown at seven localities in South Africa during the 2014/15 growing season

Nematode	Prominence value (PV)[1]	Frequency of occurrence	Mean population density (MPD)
Pratylenchus brachyurus	1198	14	2996
Pratylenchus zeae	992	29	1983
Pratylenchus teres	503	43	718
Rotylenchulus sp.	436	29	809
Scutellonema brachyurus	153	14	382
Helicotylenchus sp.	115	14	2 87

[1] *PV* final population density (Pf) of each species × $\sqrt{\text{frequency of occurrence}}$ 10

Table 4 Data on prominence value, frequency of occurrence and mean population density of *Pratylenchus* spp. in 5 g root sub-samples of 29 soybean genotypes grown at seven localities in South Africa during the 2014/15 growing season

Cultivar	Prominence value (PV)[1]	Frequency of occurrence	Mean population density (MPD)	Percentage relative susceptibility (%S)[2]
DM 6.2i RR[3]	5315	86	5731	100
PAN 1666 R	4571	86	4929	86
PAN 1513 R	4132	86	4456	78
PAN 1623 R	3944	100	3944	69
LS 6444 R	3853	86	4155	73
LS 6240 R	3768	71	4472	78
LS 6146 R	3725	86	4017	70
DM 5.1i RR	3594	100	3594	63
LS 6261 R	3466	86	3738	65
PAN 1729 R	3379	71	4010	70
PAN 1454 R	3375	86	3639	64
PAN 1614 R	3331	86	3592	63
NS 7211 R	3115	86	3359	59
LS 6466 R	3071	86	3312	58
DM 6.8i RR	2978	71	3534	62
NS 5009 R	2908	71	3451	60
LS 6164 R	2891	86	3118	54
PHB 94 Y 80 R	2822	86	3043	53
PAN 1521 R	2817	86	3038	53
LS 6453 R	2772	86	2989	52
PHB 95 Y 20	2631	71	3122	55
LS 6248 R	2610	71	3098	54
NS 5909 R	2567	86	2768	48
PAN 1500 R	2542	86	2741	48
PAN 1583 R	2503	71	2971	52
DM 5953 RSF	2036	71	2416	42
NS 6448	1550	86	1671	29
LS 6161 R	1398	86	1508	26
PAN 1664 R	1367	71	1622	28

[1] *PV* final population density (Pf) of each species × $\sqrt{\text{frequency of occurrence}}$ /10; [2] %S, final population density (Pf) of individual genotype/Pf of genotype that is most susceptible × 100

Table 5 Data on prominence value, frequency of occurrence and mean population density of plant-parasitic nematodes in 200 g rhizosphere soil samples of 29 soybean genotypes grown at seven localities in South Africa during the 2014/15 growing season

Nematode	Prominence value (PV)[1]	Frequency of occurrence	Mean population density (MPD)
Rotylenchulus parvus	2145	43	3271
Scutellonema brachyurus	1217	29	2260
Helicotylenchus sp.	765	29	1421
Criconemoides sphaerocephalus	18	14	49
Pratylenchus teres	17	29	31
Tylenchorhynchus brevilineatus	8	29	15
Pratylenchus zeae	7	43	10
Criconema sp.	5	29	9
Nanidorus minor	2	14	4

[1] *PV* final population density (Pf) of each genus × $\sqrt{\text{frequency of occurrence}}$ /10

Table 6 Glasshouse reproduction data for *Meloidogyne incognita* in roots of 36 soybean genotypes 56 days after inoculation (DAI) with 1000 (Pi) eggs and J2 per root system: experiment 1 (2014) and experiment 2 (2015)

Genotype	Final population density (Pf)		Reproduction factor (Rf)		Percentage relative susceptibility (%S[3])	
	Exp. 1	Exp. 2	Exp. 1	Exp. 2	Exp. 1	Exp. 2
PRF-GCI7	42 abcdefghi**	566 abcd	0.04 a	0.6 abcde	1	1
PAN 1664 R	95 bcdefg	6670 abcd	0.1 abcdefg**	6.7 hijklmnop	13	12
LS 6261 R	126 abcd**	5425 abc	0.1ab	5.4 efghijklmnop	2	10
LS 5995[1]	167 abc	718 abcd	0.2 ab	0.7 abcdefg	2	1
NS 7211 R	213 ab	1456 ab	0.2ab	1.5 abcdefghi	3	3
PRF-GCI4	221 abcd	1205 abcd	0.22 abc	1.2 abcdefgh	3	2
LS 6444 R	280 abcdefg	3098 abcd	0.3 abc	3.1 abcdefghijklmn	4	5
PRF-GCI6	330 abcd	3007 abcd	0.3 abc	3.0 abcdefghijk	4	5
SC SORCERER	379 bcdefghi	6738 abcd	0.4 abcd**	6.7 ghijklmnop	5	12
PAN 1614 R	410 bcdefg	2555 abcd	0.4 abcd	2.6 abcdefghijkl	5	6
DM 6.8i RR	427 abcd**	3675 abcd	0.4 abc	3.7 bcdefghijklmno	6	10
DM 6.2i RR	458 abcd	995 abcd	0.5 abcd	1.0 abcdefgh	4	2
PHB 94 Y 80 R	515 cdefghi	10,225 abcd	0.5 abcde**	10.2 klmnopq	16	18
PAN 1623 R	645 defghi	12,075 abcd	0.7 abcdefg**	12.1 lmnopq	9	21
LS 6453 R	683 bcdefg	4918 abcd	0.7 abcdef	4.9 defghijklmnop	9	9
LS 6161 R	703 bcdefghi	5641 abcd	0.7 abcde	5.6 efghijklmnop	9	10
PHB 95 Y 20	774abcd	1097 abcd	0.8 abcde	1.1 abcdefgh	10	2
LS 6466 R	871 defghi**	13,195 abcd	0.8 abcdefg	13.2 nopqr	11	23
S 722/6/1E	890 defghi**	14,502 bcd	0.9 abcdefgh	14.5 mnopqr	12	25
PRF-GCI5	900 abcdefg	2475 abcd	0.9 abcde	2.5 abcdefghijkl	12	4
PAN 1454 R	905 defghi**	11,480 abcd	1.0 abcdefgh	12.0 klmnopq	13	20
LS 6146 R	983 bcdefg**	7648 abcd	1.0 abcdefgh	2.4 abcdefghijkl	13	4
PAN 1521 R	1050 defghi**	8820 bcd	1.1 abcdefgh	8.8 jklmnopq	14	15
PAN 1500 R	1358 abcdefg	2450 abcd	1.4 abcdefgh	2.5 abcdefghijkl	18	4
LS 6164 R	1424 defghi	2372 abcd	1.4 abcdefgh	7.7 ijklmnopq	19	13
NS 5009 R	1675 efghij	12,513 bcd	1.7 abcdefghij	12.5 mnopq	22	22
NS 6448	1817 defghi**	16,503 abcd	1.8 abcdefghij	17 qprs	24	29
DM 5953 RSF[2]	2486 j**	57,068 d	2.0 abcdefghijkl**	57.1 s	27	100
LS 6240 R	2538 bcdefgh	3288 bcd	2.5 abcdefghijkl	3.3 abcdefghijklmno	34	6
PAN 1583 R	2748 bcdefghi	4480 abcd	2.8 abcdefghijkl	4.5 cdefghijklmnop	36	8
PAN 1666 R	2784 defghi**	6335 bcd	2.8 abcdefghijkl	6.34 ghijklmnop	48	55
LS 6248 R	3643 fghij**	31,238 bcd	3.6 abcdefghijklm**	31.2 qrs	12	4
NS 5909 R	4238 efghij**	18,305 cd	4.2 abcdefghijklmn	18.3 qprs	56	32
PAN 1729 R	4372 ij	55,802 cd	4.4 abcdefghijklmn**	55.8 rs	58	98
PAN 1513 R	7158 hij**	28,998 d	7.2 fghijklmnop**	28.0 qrs	95	49
DM 5.1i RR	7563 ij**	54,543 cd	7.6 cdefghijklmnop**	54.5 t	100	96
Interactions: Genotypes x Experiments						
P value	*0.381*		*0.001*			
F ratio	*1.1*		*4.7*			

[1] Resistant standard; [2] Susceptible standard; [3] %S, final population density (Pf) of individual genotype/Pf of genotype that is most susceptible × 100; *Lower case letters that are different for Pf and Rf indicate significant differences (in the respective columns) among genotypes for each experiment; **Indicates significant differences (across rows) for each genotype between the two experiments; Tukey's HSD ($P < 0.05$) (Statistica for Windows, Version 13.3) was used

Discussion

Meloidogyne and *Pratylenchus* were identified as the predominant nematode taxa in soybean roots obtained from the field study, agreeing with reports by Fourie et al. (2001) and Mbatyoti et al. (2020). For the field study, only genotypes PAN 1583 R and PAN 1521 R had substantially lower %S for root-knot nematodes compared to the most susceptible genotype PAN 1623 R (data pooled across the seven localities). For root-lesion nematodes, however, all genotypes had high %S (> 10%), with 'PAN 6161 R' having the lowest (26%) and therefore will be the most suitable genotype to plant to limit an increase in the population density of this genus.

Glasshouse host status evaluations showed that genotypes LS 5995 and PRF-GCI7 consistently showed resistance to *M. incognita* with Rf < 1 and %S < 10, confirming results by Fourie et al. (2006) and Venter (2014). This trend was evident despite differences in temperature regimes recorded for the two experiments suggesting that increased temperature did not affect the high level of resistance expression by these genotypes.

The predominance of *M. incognita*, followed by *M. javanica*, and that of *P. brachyurus* followed by *P. zeae*, in local soybean fields resulting from this present study is similar to results by Fourie et al. (2001). These authors listed the same taxa as the predominant in local soybean production areas during the mid-1990s. The presence of the said nematode species commonly occurs in either single or mixed populations in the traditional maize production areas (De Waele and Jordaan 1988; Riekert 1996; Riekert and Henshaw 1998) to where soybean production has been expanding during the last two decades. Rotation crops used in these areas, *viz.* groundnut, dry bean, sunflower, potato and maize in particular, are highly susceptible to *M. incognita* and *M. javanica* and also *P. brachyurus* and *P. zeae* (De Waele and Jordaan 1988; Fourie et al. 2017; Jones et al. 2017; Mc Donald et al. 2017). Both root-knot and root-lesion nematode problems in grain production areas are hence aggravated by such crop rotation systems and ultimately limit sustainable crop production.

The MPD and PV of the plant-parasitic nematode taxa recorded during this present study were similar to those reported by Mbatyoti et al. (2020), but substantially higher compared to those reported for the mid-1990s (Fourie et al. 2001). For root-knot nematodes, the values of these two parameters were up to > 200 times higher compared to those recorded by Fourie et al. (2001). The differences between the studies could be partially explained by the poor-host genotypes (*viz.* LS5995, Egret PAN812, A7119 and Gazelle) (Fourie et al. 1999, 2006; Mienie et al. 2002) being commonly grown at commercial level during the mid-1990s (Fourie et al. 2001); unlike in the present study and that of Mbatyoti et al. (2020) where only 'DM 6.2i RR' (having some level of resistance according to Venter 2014) was cultivated.

The substantially higher abundance of the predominant lesion nematode species (*P. brachyurus*, followed by *P. zeae*) in soybean roots in the present study compared to that reported by Fourie et al. (2001) is also interesting, although the opposite order in terms of dominance was recorded by the latter authors, namely, *P. zeae* followed by *P. brachyurus*. Explanations for the higher densities of root-knot and root-lesion nematode densities are elusive, but since the same extraction techniques were used for the former (Fourie et al. 2001; Mbatyoti et al. 2020) studies and the present study, it can be disregarded as a possible contributing factor regarding these differences. Other possible factors that could have impacted on increased densities of these two taxa are temperature and/or other abiotic or biotic factors.

Except for *P. brachyurus* and *P. zeae*, *P. teres* were also identified in the present study, but not *P. crenatus* Loof, 1960, *P. flakkensis* Seinhorst, 1968, *P. neglectus* (Rensch, 1924), Filipjev and Schuurmans Stekhoven, 1941, *P. penetrans* (Cobb 1917) Filipjev and Schuurmans-Stekhovens,1941, *P. scribneri* Steiner, 1943, *P. thornei* Sher and Allen, 1953, and *P. vulnus* Allen and Jensen, 1951 (Fourie et al. 2015; Mbatyoti et al. 2020). Root-lesion nematodes were previously regarded of lesser importance to global soybean production (Bridge and Starr 2007) and a secondary nematode pest of the crop in Brazil (Machado 2014), but their high abundance in the present study and that of Mbatyoti et al. (2020) suggests that it should now be considered a major pest of local soybean. Interestingly, PV for *P. brachyurus* and *P. zeae*, respectively, were 18 and 9 times higher than those reported for the mid-1990s survey (Fourie et al. 2001). This finding complements reports that *P. brachyurus* is increasingly considered an economically important nematode pest of soybean, for example, in Brazil (Machado 2014; Lima et al. 2015) where severe yield losses have been experienced (Lima et al. 2015). The mean population density of *P. brachyurus* (2996/5 g roots) recorded in the present study was well within the range as reported for Brazilian soybean fields (24–5482/10 g roots) where this species has become a major pest in especially the Cerrado region (Lima et al. 2015; Bellé et al. 2017). Lima et al. (2015) furthermore showed that rotation of soybean with maize or sorghum in Brazilian production areas as well as inclusion of *Crotalaria juncea* in a cropping system (Braz et al. 2016) favoured reproduction of *P. brachyurus*. Similarly, *P. brachyurus* and also *P. zeae* reproduce well on crops that are commonly used in rotation with local soybean crops including maize (Mc Donald et al. 2017) and grain legumes (*viz.* groundnut and sunflower) (Fourie et al. 2017). Densities of *P. teres* in soybean roots, 126 times higher than that recorded for the species in the mid-1990s survey (Fourie et al. 2001), also occurred in high densities in cotton-based rotations in the

Vaalharts area (Northern Cape Province, South Africa) (Van Biljon et al. 2015) where soybean is also grown. Its damage potential to soybean is, however, unknown. The high abundance, wide host range and distribution of lesion nematodes in local grain crop production areas (Fourie et al. 2017; Mc Donald et al. 2017; Van den Berg et al. 2017) at all localities sampled during the present study suggest that more research should be aimed at studying the impact of this genus on soybean growth and yield.

The predominant ectoparasitic species identified in the soil, *viz. S. brachyurus* and *Helicotylenchus* sp., also agreed with former South African studies (Fourie et al. 2001; Mbatyoti et al. 2020). Their PV and MPD were also substantially higher (48 and 16 times respectively) compared to those reported by Fourie et al. (2001). Higher PV, MPD and frequency of occurrence values recorded in the present study for *R. parvus* are another interesting phenomena which may be attributed to the constant expansion of soybean production into maize production areas. Recently, Bekker et al. (2016) reported that *R. parvus* has been frequently encountered at a high population density in local maize production areas since 2011. This species has in the past been listed to commonly occur, but generally in low abundance, in local soils where cereal crops (Jordaan et al. 1992), groundnuts (Venter et al. 1992) and sunflower (Bolton et al. 1989) were produced, with its impact on such crops being unknown (Bekker et al. 2016). *Scutellonema brachyurus* followed as the second predominant semi-endoparasitic species in soil samples. This is in contrast to results from the mid-1990s survey (Fourie et al. 2001) and most recent survey (Mbatyoti et al. 2020) where *S. brachyurus* followed *H. dihystera* in terms of dominance. *Scutellonema brachyurus* occurred at nearly 63% of the localities and was nearly 10 times more abundant (MPD), with a six times higher PV in present study than recorded for the mid-1990s survey (Fourie et al. 2001). In Brazil, *H. dihystera* and *S. brachyurus* are listed as emerging species with the potential to become major pests of soybean due their increased occurrence and higher population density in soybean growing areas (Lima et al. 2009; Machado et al. 2019).

The occurrence of other nematode pest species of *Criconema*, *Criconemoides*, *Nanidorus* and *Tylenchorhynchus* is generally not considered to be important on soybean locally since they generally only occur sporadically in high densities (Fourie et al. 2015). Results from the present study, however, reconfirmed that soybean is a host to these species and therefore they can potentially become major pests of the crop as has been found with *H. dihystera* and *S. brachyurus* in Brazil (Lima et al. 2009; Machado et al. 2019). The present field study did not yield new genera and species other than the ones reported by Fourie et al. (2015), Mbatyoti et al. (2020) and those listed in the South African Plant-Parasitic Nematode Database (SAPPNS) (Marais et al. 2017a).

Valuable information about the host status of soybean genotypes to *Meloidogyne* spp. (field and glasshouse) and *Pratylenchus* spp. (only field study) has also been generated from the present study. Pooled data for *Pratylenchus* spp. root densities were high for all genotypes, but varied substantially among them. 'PAN 1664 R' maintained the lowest lesion nematode densities, although not < 10% of the most susceptible genotype, and will be the best choice to plant to limit increased lesion nematode infections. The opposite is applicable for genotype DM 6.2i RR, resistant to *M. incognita* (Venter 2014), which was the most susceptible and will generally support high lesion nematode densities. In Brazil where *P. brachyurus* is also widespread in soybean fields, no resistant genotype has also been identified to this species (Rios et al. 2016).

Under field conditions, all genotypes had high susceptibility levels for *Meloidogyne* spp. (data pooled across the seven localities), except for PAN 1583 R and PAN 1521 R. These genotypes maintained < 10% of the population density recorded for the most susceptible 'PAN 1623 R' and could therefore be regarded as being resistant according to the host status protocol of Hussey and Janssen (2002). The majority of genotypes sampled in the present field study were thus susceptible to the two *Meloidogyne* spp. identified coinciding with results of the 2nd *M. incognita* glasshouse experiment that was conducted at a higher temperature range compared to the 1st experiment. Field results for 'DM 6.2i RR', classified as a poor host of *M. incognita* and *M. javanica*, respectively (Fourie et al. 2015); however, only partly corresponded with glasshouse evaluations. These genotypes hosted intermediate root-knot nematode population densities (MPD = 6503; data pooled over the seven localities), but maintained < 10% of the *Meloidogyne* spp. densities at four of the seven localities: being 1% each of the *M. incognita* populations at Groblersdal and Potchefstroom and zero at Hoopstad; and 7% of the *M. javanica* densities at Kroonstad (data not shown) rendering it as resistant. These field reports hence agree with glasshouse screenings that listed 'DM 6.2i RR' as resistant to *M. incognita* supporting the recommendation that its use will reduce *M. incognita* densities substantially compared to a highly susceptible genotype. Inconsistent findings for glasshouse and field experiments, however, included that 'DM 6.2i RR' was susceptible to field populations of *M. incognita* at Bethlehem, Brits and Middelburg. This is not unexpected since such anomalies have been reported from other studies for *M. incognita*- and/or *M. javanica*-resistant genotypes (Fourie et al. 2006; Sharma et al. 2006). Also, the Brazilian 'BRSGO Raissa' was classified as susceptible to *M. javanica* (Embrapa 2011), while Teixeira et al. (2017) reported it as resistant. Such contrasting results may be due to the occurrence of different races or pathotypes or virulent populations of the

target root-knot nematode species, as well as abiotic or biotic factors that occur in different climatic zones (Hussey and Janssen 2002) where soybean is grown.

The host response of the soybean genotypes to *M. incognita* infection included in the glasshouse study varied from resistant to highly susceptible. Genotypes LS 5995 and PRF-GCI7 consistently had low Rf and %S values for both experiments despite the difference in temperature ranges between the experiments confirming their superior resistance reported earlier (Fourie et al. 2006; Venter 2014). Various other genotypes, *viz.* LS 6146 R, DM 6.2i RR, PAN 1583 R, PHB 95 Y 20 and the PRF-GCI entries, had low to moderate nematode population levels in both experiments with their Rf being substantially lower than those of the two highly susceptible genotypes (DM 5.1i RR and DM 5953 RSF); classifying them as moderately resistant to *M. incognita*.

Despite the uniformity of the experimental conditions, the Pf and Rf of 13 and 9 of the genotypes, respectively, differed significantly from each other for the two experiments. Nematode-host plant reactions are known to be influenced by several environmental conditions such as temperature and moisture, for example (Ferris et al. 2013; Vandegehuchte et al. 2015). The higher mean temperature (range of 2.5 °C) recorded for the 2nd experiment (compared to that of the 1st experiment) was the only difference observed between the two experiments since the seedlings were grown in similar containers in soil obtained from the same source and inoculated with the same *M. incognita* population at the same Pi. Also, the water regime (schedule, volume and source) was similar for both experiments. Nardacci and Barker (1979) reported that the Rf of *M. incognita* in soybean roots was profoundly influenced by temperature and that it was lowest at temperatures ranging from 16 to 20 °C and highest at 30 °C. Results of this study agree with those of the latter authors and that of Thomason and Lear (1961) who reported that the reproduction factors of four different *M. incognita* populations were higher at 25–32 °C compared to lower temperature ranges. Noting that the optimal temperature range for *M. incognita* development is 22–30 °C (Diez and Dusenbery 1989), the results of the 2nd experiment of the present glasshouse study are considered to be more accurate.

Although 21 genotypes had Rfs < 1 in the 1st experiment, none of them except PRF-GCI7 and DM 6.2i RR could maintain the resistance trait (Rf < 1) under the higher temperature regime of the 2nd experiment. The present results hence coincide with those of Teixeira et al. (2017) who showed that only the *M. javanica* resistance trait could be verified for two of the 14 soybean genotypes that were classified as resistant in an initial glasshouse experiment.

The Rf, considered a quantitative parameter that could be compared across studies (Niblack et al. 1986; Moura and Régis 1987; Windham and Williams 1988; Sharma et al. 2006; Bruinsma and Antoniolli 2015), however, was insufficient on its own to describe the resistance of root-knot nematodes. Windham and Williams (1988) also suggested that using Rf values alone may be misleading at times. Therefore, Rf was supplemented by the %S of each soybean genotype (Hussey and Janssen 2002) in our study; with a %S value of < 10% indicating resistance. Consequently, nine genotypes that were susceptible based on their Rf were resistant to *M. incognita* infection based on their %S. This discrepancy in terms of Rf and %S was reported by Venter (2014) who examined the host response of 31 soybean genotypes to *M. incognita* infection. Nine of these genotypes had a %S < 1%, while their Rf were > 1. Fourie et al. (2012) reported a similar tendency when screening tomato genotypes for resistance against *M. javanica*. In the current study, 'LS 6444 R', for example, had an Rf = 3 for the 2nd experiment, indicating susceptibility, but a %S = of 3 indicating resistance. The use of more than one parameter to evaluate the host response of genotypes to root-knot nematode infection is thus crucial to make more accurate and informed decisions, and recommendations to producers.

Resultantly, a genotype such as DM 6.2i RR that is classified as moderately resistant to *M. incognita* based on its Rf (1) and %S (2) should be the first choice for producers that experience problems with this root-knot nematode species. This genotype also showed a high yield potential when evaluated in soybean production areas with moderate temperatures and areas with warm temperatures (De Beer 2015). Regrettably, resistant genotype PRF-GCI7 is not commercially available and cannot be recommended to producers as a management strategy to reduce the population density of *M. incognita*. Other genotypes identified in Experiment 2 with low Rf (≤ 5) and %S (≤ 10) such as PHB 95 Y 20 (1.1 and 2, respectively) and NS 7211 R (1.5 and 3, respectively) can be the second choice (to DM 6.2i RR) for cultivation; particularly for areas where the latter genotype is not well adapted. Cultivation of genotypes that had high susceptibility levels (Rf > 5) (Windham and Williams 1988) LS 6161 R, LS6164 R, LS 6261 R, LS 6444 R, LS 6466 R, NS 5009 R, NS 5909 R, NS 6448, PAN 1454 R, PAN 1513 R, PAN 1521 R, PAN 1623 R, PAN 1664 R, PAN 1666 R, PAN 1729 R, PHB 94 Y 80 R, S 722/6/1E and SC SORCERER should, however, be avoided in *M. incognita* infested fields.

The importance of determining the host response of soybean genotypes to root-knot and lesion nematodes cannot be over emphasized. Soybean genotypes must be evaluated not only for their yield potential but also for their susceptibility and sensitivity to diseases and pests, including the economically important nematode pest species. Although the results of several glasshouse studies in South Africa regarding the host response of soybean genotypes to root-knot nematodes have been reported (Fourie et al. 1999, 2006, 2015; Mbatyoti et al. 2013; Venter 2014), this is the first study that gives an

indication of the host status of soybean genotypes to lesion nematodes. The higher abundance of root-knot and lesion nematode species recorded for the present field study compared with those reported 19 years ago (Fourie et al. 2001) when the first official nematode-soybean survey was undertaken is concerning. It underlines that host status assessments of genotypes (GM glyphosate-tolerant-dominated) to economically important nematode pests should be done continuously to minimize the damage caused by these pests and ultimately enable the sustainable production of crops in nematode-infested soils.

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Authors' contributions HF and AM designed the study. ADB supplied seeds for the glasshouse study and identified fields for the surveys. AM performed the glasshouse and field work to obtain the data. HF, MSD and AM performed the statistical analysis. AS and MM identified the nematodes to species level. DDW and AM prepared the first draft of the manuscript. All authors reviewed the manuscript and gave final approval for publication.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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