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Relationships between initial population densities of *Meloidogyne incognita* race 2 and nematode population development in terms of variable soybean resistance

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Abstract: The effect of increasing initial population density levels (Pi) of *Meloidogyne incognita* race 2 on nematode population development and yield of a susceptible (Prima2000) and resistant (LS5995) soybean cultivar was investigated. Two experiments, one in a hail net cage and one in microplots, were conducted one each during two consecutive growing seasons at Potchefstroom in the North West Province of South Africa. Nematode reproduction was assessed by determining the number of eggs and second-stage juveniles (J2) in the rhizosphere and roots, egg masses, egg-laying females (ELF) and reproduction factor (Rf) values per root system at harvesting 110 days after planting. Percentage yield reduction in the two cultivars was also calculated. Strong non-linear relationships existed between all nematode variables as well as between Pi and percentage yield loss in both cultivars for both experiments in this study. Significantly higher numbers of eggs and J2, egg masses and ELF were maintained in the roots of the nematode-susceptible Prima2000 than in the resistant LS5995 from Pi = 100 and higher in both experiments. Rf values were inversely related to Pi for both cultivars and were lowest on LS5995, with Prima2000 maintaining significantly higher Rf values in both experiments. Yield loss in LS5995 was at least six times higher than that of Prima2000. The difference in monetary terms is demonstrated, although it is suggested that host plant resistance to plant-parasitic nematodes may not be sufficient as the only management tool in highly infested soils or in rotation systems including nematode susceptible crops.

Key words: Initial population levels, *Glycine max*, host-parasitic relationship, *Meloidogyne incognita* race 2, resistance, soybean.

Quantitative research in Nematology aims to establish the relationship between detectable, pre-plant numbers of plant-parasitic nematodes and their effect on crop performance, which generally entails plant growth, yield and/or product quality (Barker and Olthof, 1976; Schomaker and Been, 2006). Optimal economic protection of crops against plant-parasitic nematodes, therefore, necessitates quantitative knowledge of the relationship between these organisms during planting as well as responses of host plants (Schomaker and Been, 2006). Knowledge of relevant principles and determination of damage functions under specific conditions for specific crops are prerequisites for the estimation of nematode economic threshold values (Ferris, 1978a; Schomaker and Been, 2006) and are essential for nematode pest management programs (Ferris, 1978b; Schomaker and Been, 2006).

The mere presence of plant-parasitic nematodes in soil does not guarantee crop damage or yield loss, since a nematode population may remain below the damage threshold level for a specific field (Brown, 1987; Schomaker and Been, 2006; Khan, 2008). Factors such as environmental conditions, soil type, previous cropping history, the specific nematode species and or race present, pathotype distribution, prevailing nematode distribution pattern, nematode multiplication rate, and plant cultivar that is grown will all have a bearing on whether crop damage and yield reduction will be inflicted (Brown, 1987; Schomaker and Been, 2006; Khan, 2008).

The relationship between soybean (*Glycine max* L.) Merr yield loss and initial *Meloidogyne incognita* (Kofoïd & White) Chitwood numbers has been illustrated in several studies with resistant as well as susceptible soybean cultivars (Kinloch, 1981; Barker, 1982; Appel and Lewis, 1984; Niblack et al., 1986a; Herman et al., 1990; Carpentieri-Pípolo, 2005, Bridge and Starr, 2007). According to Bridge and Starr (2007) initial population densities of 150 second-stage juveniles (J2) of *M. incognita* per 500cm^3 soil can result in yield suppression of 10%. Earlier it was reported that this parasite suppressed yields of resistant and susceptible soybean cultivars by more than 40% and 90% in the USA (Kinloch, 1974; Kinloch, 1982). In Brazil a 10% to 16% increase in yields was evident when resistant rather than susceptible soybean cultivars were grown (Carpentieri-Pípolo, 2005). Although damage to resistant cultivars may be relatively low, high residual *M. incognita* numbers present in a soil after a resistant cultivar was planted may pose a threat to subsequent, susceptible crops (Herman et al., 1990).

Information about nematode-crop relationships is also crucial for soybean producers to decide on economically viable management strategies within crop production systems (Schomaker and Been, 2006). The need, therefore, exists to quantify the relationship between *M. incognita* race 2 and local soybean cultivars, since the use of root-knot- nematode resistant cultivars is currently one of the few options available locally for managing these parasites. The objective of this study was to determine the relationships between pre-plant, initial (Pi) and final population densities (Pf) of *M. incognita* race 2 in plant roots and soil, as well as percentage yield loss for both a resistant and a susceptible soybean cultivar (LS5995 and Prima2000) under semi-controlled growing conditions.

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MATERIALS AND METHODS

A hail-net-cage experiment was followed by a microplot experiment during a consecutive growing season. The local *M. incognita* race 2-resistant soybean cv. LS5995 [maturity group VI (MG VI)] and susceptible cv. Prima2000 (MG V) were selected for this study because of their host status to the experimental nematode race was known (Fourie et al., 2005).

Hail-net-cage experiment: Black plastic bags (25,000 cm^3 capacity) were filled with a methyl bromide-fumigated and steam-pasteurized, sandy-loam soil (3.9% clay, 1.9% silt, 93.6% sand, 0.6% organic material); soil pH was 6.55. Plant nutrients were added according to a soil nutrient analysis. One seed was planted per bag. Inoculation was performed at planting by pippetting the desired nematode inoculum density on and around each seed. The range of Pi used for each cultivar was approximately 100, 500, 1 000, 5 000, 10 000 and 20 000 *M. incognita* race 2 eggs and J2 per seed. The untreated control treatment was not inoculated (Pi = 0).

Microplot experiment: Microplots used in this study consisted of round concrete tubes (1-m-diam. x 1.25 m high), partially buried vertically in an open field and filled with the same soil used for the hail-net-cage experiment. Twelve soybean seeds were planted per microplot and each seed was inoculated as described above. The range of Pi used in this experiment was approximately 100, 500, 1 000, 5 000, 10 000, 20 000 and 40 000 *M. incognita* race 2 eggs and J2 per seed. The untreated control treatment was not inoculated (Pi = 0).

Trial layouts: Layouts for both the hail-net-cage and microplot trials were randomized complete block designs with 12 replicates per treatment. Single plants were treated as replicates. Soybean seeds for both experiments were inoculated with *Bradyrhizobium japonicum* bacteria after inoculation to optimize nitrogen fixation. Plants in both trials were watered by means of micro-irrigation three times a week, except when rainfall occurred. In such cases irrigation was rescheduled to prevent water logging of bags or microplots.

Nematode reproduction assessment: The whole root system of each plant for each treatment as well as corresponding soil samples were taken 110 days after planting (DAP) and inoculation (DAI) in both experiments. Niblack et al. (1986) reported that population densities of *M. incognita* reach their maximum levels at ± 90 DAP on a susceptible cultivar but may still be increasing at ± 120 DAP on a resistant cultivar. Plant roots were rinsed free of adhering soil and debris under running tap water, blotted on towel paper, weighed and the number of egg-masses per root system was counted. Staining and counting of egg masses were performed and egg masses were rated according to the zero to 5 scale of Hussey and Boerma (1981), where 0 = no egg-masses; 1= 1 to 2 egg-masses; 2 = 3 to 10 egg-masses; 3 = 11 to 30 egg-masses; 4 = 31 to 100 egg-masses and 5 = more than 100 egg-masses per root system. Subsequently the eggs per root system were extracted using Riekert's (1995) NaOCl method and were counted using a dissection microscope (magnification: x100). The reproductive potential of the nematodes was determined using Oostenbrink's reproduction factor (Rf) (Windham and Williams, 1987), which was calculated as follows: Rf = final egg and J2 number (Pf)/ initial egg and J2 number (Pi). *Meloidogyne incognita* race 2 J2 was extracted from 200-ml-soil samples using the adapted decanting-and-sieving method (Hooper et al., 2005) and (Khan, 2008); the latter method was originally described by Cobb (1918). The decanting-and-sieving method was followed by the adapted sugar flotation method (Hooper et al., 2005) and was originally described by Caveness and Jensen (1955).

Yield loss assessment: Yield data were obtained 138 DAP for the hail-net-cage experiment and 154 DAP for the microplot experiment. The harvested soybean plants were air dried until the moisture content of the seeds was approximately 12%. Soybean pods were subsequently threshed and seed mass per plant determined for each of the treatments. Percentage yield loss was determined as follows: Pod mass (g) of soybean from untreated control (Pi = 0) / Pod mass (g) of soybean from the respective inoculated treatment (e.g., Pi = 100 to 20,000 for hail-net-cage experiment and Pi = 100 to 40,000 for microplot experiment) – 100.

Data analyses: Nematode data (Pf in soil and roots, number of egg masses and ELF per root system, Rf values (dependent variables) were regressed non-linearly on the various Pi levels (independent variable) using the rational, linear-divided-by-linear (ldl) model, $y = a + b/(1 + d * x)$, as well as the quadratic-divided-by-quadratic model (qdq), $y = a + (b + c * x)/(1 + d * + e^\wedge x)$ (Genstat for Windows). These rational functions are ratios of polynomials and are representative of the data ranges obtained in these experiments. Pf in soil was analyzed by means of the Behren-Fisher t-test (Statgraphics Plus 5 for Windows). Pf in each plant root system was $ln(x + 1)$ transformed for data analysis. The percentage yield loss (dependent variable) was also non-linearly regressed on the various Pi (independent variable) using the models as described above. Nematode and yield data were also subjected to a factorial analysis of variance, with the two cultivars as the main effects and Pi levels as the sub-factor. Means were separated by the Tukey test (Statgraphics Plus 5 for Windows).

RESULTS

The relationships between Pi and Pf in roots, number of egg masses and ELF, Rf values and percentage yield loss in the hail-net-cage (Fig. 1) and microplot (Fig. 2) experiment were strong and highly significant (Table 1). Except for Rf against Pi in the hail-net-cage experiment (Fig. 1) and percentage yield loss against Pi in the microplots (Fig. 2), the respective relationships were

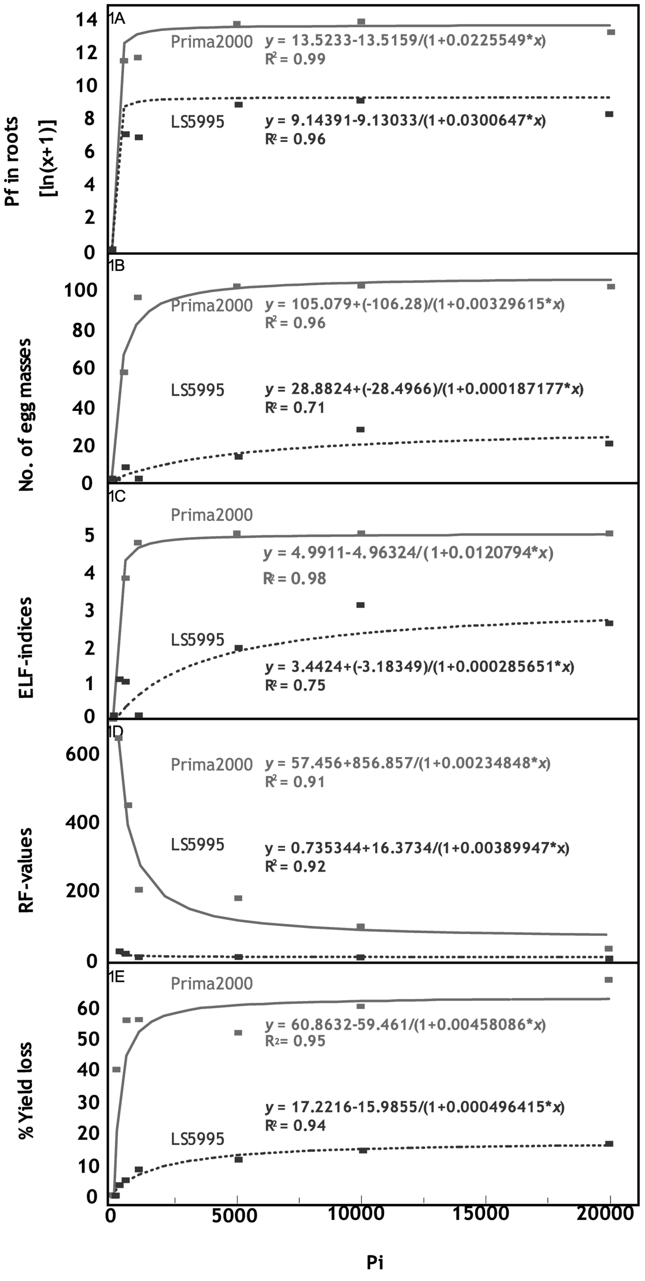

Fig. 1. Relationships between initial and final population densities (Pf and Pi) in roots, number of egg masses and egg-laying females (ELF) and reproduction factor (Rf) at 110 days after inoculation (DAI) of a susceptible cultivar Prima2000 and a resistant cultivar LS5995 with the root knot nematode *Meloidogyne incognita* race 2 in a hail-net-cage experiment.

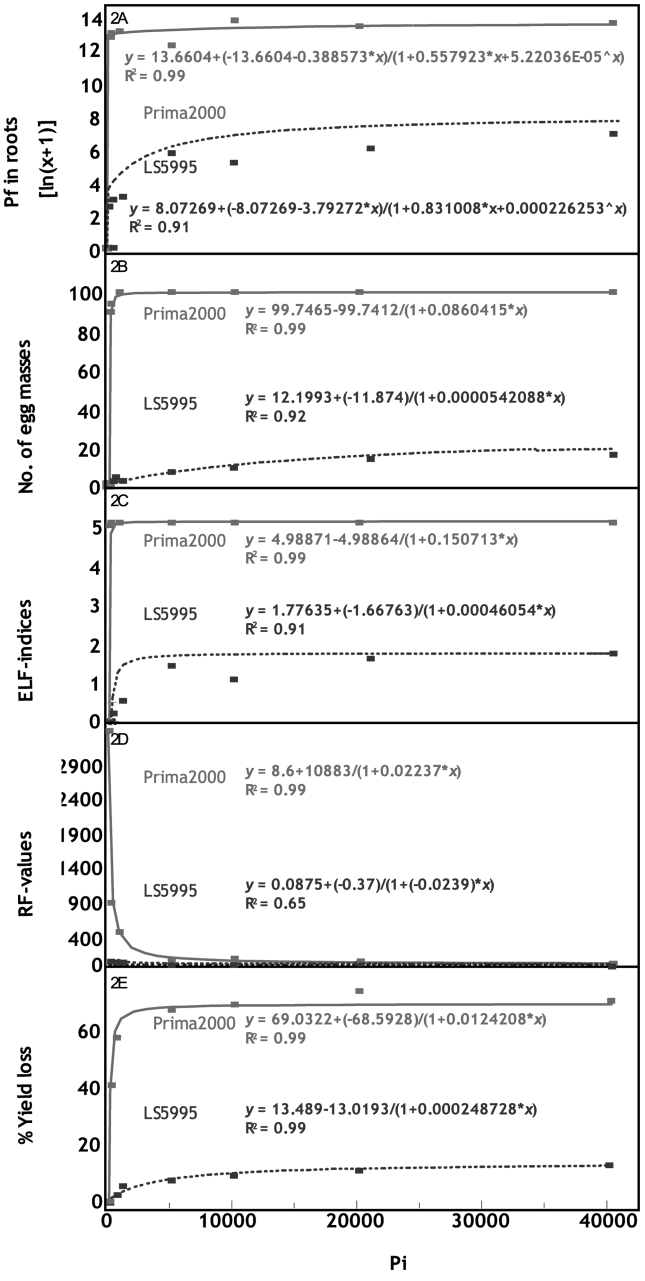

Fig. 2. Relationships between initial and final population densities (Pf and Pi) in roots, number of egg masses and egg-laying females (ELF) and reproduction factor (Rf) at 110 days after inoculation (DAI) of a susceptible cultivar Prima2000 and a resistant cultivar LS5995 with the root knot nematode *Meloidogyne incognita* race 2 in a microplot experiment.

stronger for Prima2000 than for LS5995, the resistant soybean cultivar (Figs. 1,2).

Pf in roots: Significantly ($P \leq 0.05$) higher numbers of *M. incognita* race 2 eggs and J2 were observed in the roots of Prima2000 than LS5995 from Pi = 100 and higher in both experiments (Tables 1,2).

The relationship between Pi and Pf in roots was best described as strong, non-linear equations in both experiments both for Prima2000 and LS5995 (Fig. 1A;2A). According to the regression lines of both cultivars in both experiments Pf started leveling off from Pi = 1,000, which indicated that Pf in the roots of both cultivars did not increase when more than 1,000 *M. incognita* eggs and J2 were inoculated per plant.

Pf in soil: M. incognita race 2 J2 numbers were significantly ($P \leq 0.05$) lower in soil samples taken from the rhizospere of LS5995 than those of Prima2000 both in the hail-net-cage and microplot experiments (Tables 1,2). Due to the low nematode numbers in the soil in both experiments no significant relationships were

TABLE 1. Final population density (Pf), number of egg masses, egg-laying females (ELF-indices), reproduction factor (Rf values) and percentage yield loss at 110 days after inoculation (DAI) of a susceptible (Prima2000) and resistant (LS5995) soybean cultivar in a hailnet cage experiment.

		Pf	Pf				
Pi	Cultivar	Soil (250 cm^3)	Roots (50 g)	Egg masses	ELF-indices	Rf values	Yield loss (%)
100	LS5995	0a	1 238a	0.9a	0.3a	12.4a	3
	Prima2000	95b	12 828b	24b	3b	742b	41
500	LS5995	35a	3 792a	7a	1.3a	8a	4
	Prima2000	783b	58 490b	56b	4b	517b	58
1 000	LS5995	3a	2 495a	0.42a	0.3a	2a	8
	Prima2000	346b	219 617b	94b	5b	219b	58
5 000	LS5995	26a	9 940a	11a	2a	2a	11
	Prima2000	2 234b	988 021b	100b	5b	197b	51
10 000	LS5995	42a	15 143a	26a	3a	2a	14
	Prima2000	1 474b	1 044 264b	100b	5b	104b	60
20 000	LS5995	124a	14 968a	19a	3a	1a	17
	Prima2000	2 112b	555 868b	100b	5b	27b	71

Means in the same column followed by the same letter do not differ significantly ($P \leq 0.05$) according to the Behren-Fisher t-test.

found between the various variable. A progressive increase in Pf along with increased Pi was evident in both cultivars in both experiments, however (Tables 1,2).

Number of egg masses: Significantly ($P \leq 0.05$) higher numbers of egg masses were maintained by Prima2000 compared to LS5995 at each corresponding Pi in both trials (Tables 1,2). The relationship between Pi and number of egg masses was best described in the hail-net-cage experiment for both cultivars by the relevant non-linear equations (Fig. 1B) with 96% of the variation explained for Prima2000 and 71% for LS5995. The regression line for Prima2000 leveled off from Pi = 1,000 and higher, while that of LS5995 leveled off from Pi = 5,000 and higher. This indicates that the number of egg masses did not increase in Prima2000 when more than 1,000 eggs and J2 were inoculated per plant, while nematode population growth in roots of LS5995 stabilized from Pi = 5,000 onwards.

Strong, non-linear relationships also occurred in the microplot experiment for both cultivars between Pi and number of egg masses per root system (Fig. 2B). The regression line for Prima2000 leveled off from Pi = 500 and higher, while the line of LS5995 leveled off only from Pi = 20,000 onwards. In this experiment the Pi threshold value was somewhat smaller for Prima2000 but much higher for LS5995 than in the hail-net-cage experiment.

Number of ELF: Numbers of ELF were significantly higher ($P \leq 0.05$) on Prima2000 than those in roots of LS5995 in both experiments (Tables 1,2; Figs. 1C;2C). The relationship between Pi and numbers of ELF was best described by a non-linear model in the hail-net-cage experiment for both cultivars. The regression line of Prima2000 leveled off from Pi = 1,000, while that for LS5995 still showed a slight increase at Pi = 20,000. Strong non-linear relationships also existed between Pi and number of ELF in the microplot experiment.

Rf values: Rf values were inversely related to Pi for both cultivars and were lowest for LS5995 in both experiments (Figs. 1D;2D). The Rf values for Prima2000 were significantly higher ($P \leq 0.05$) at all corresponding Pi

TABLE 2. Final population density (Pf), number of egg masses, egg-laying females (ELF-indices) reproduction factor (Rf values) and yield loss at 110 days after inoculation (DAI) of a susceptible (Prima2000) and resistant (LS5995) soybean cultivar in a microplot experiment.

		Pf	Pf				
Pi	Cultivar	Soil (250 cm^3)	Roots (50 g)	Egg masses	ELF-indices	Rf values	Yield loss (%)
100	LS5995	9a	35a	0a	0a	0.4a	1
	Prima2000	1 207b	337 094b	90b	5b	3 371b	41
500	LS5995	6a	63a	0.3a	0.3a	0.13a	1.9
	Prima2000	828b	449 167b	94b	5b	898b	58
1 000	LS5995	3a	67a	1a	0.5a	0.07a	4
	Prima2000	1 055b	486 354b	100b	5b	486b	58
5 000	LS5995	1a	1 022a	4a	1.5a	0.2a	7
	Prima2000	630b	317 233b	100b	5b	63b	66
10 000	LS5995	1a	398a	3a	1.2a	0.04a	9
	Prima2000	572b	953 021b	100b	5b	95b	67
20 000	LS5995	24a	1 328a	7a	1.6a	0.06a	11
	Prima2000	414b	668 575b	100b	5b	33b	74
40 000	LS5995	23a	3 232	9a	1.8a	0.08a	13
	Prima2000	1 068b	678 038	100b	5b	17b	66

Means in the same column followed by the same letter do not differ significantly ($P \leq 0.05$) according to the Behren-Fisher t-test.

than those for LS5995 in both experiments (Tables 1,2; Figs. 1D;2D). Higher Rf values were recorded in the hail-net-cage experiment for LS5995 than in the microplot experiment but at lower Pi (100 to 500) the Rf of Prima2000 was substantially higher in the microplot experiment (Tables 1,2). The non-linear models in both experiments (Figs. 1D;2D) indicate that optimum nematode population growth rate in roots of the susceptible cv. Prima2000 is reached at fairly low Pi (<2,500).

Percentage yield loss: Percentage yield loss was substantially higher for Prima2000 from Pi = 100 and higher in both experiments compared to those for LS5995 (Figs. 1E;2E) (Tables 1,2). Maximum yield losses were evident at the highest Pi's (20 000 and 40 000) in both experiments for both cultivars except for Prima2000 in the microplot experiment (Table 2), where percentage yield loss peaked at Pi = 20 000. The relationship between Pi and percentage yield loss was best described by non-linear regression equations for both cultivars in both experiments (Figs. 1E;2E). The percentage yield loss generally leveled off for Prima2000 from Pi = 500 to 2,500 in both experiments, while yield loss still seemed to increase for LS5995 at the highest inoculum level in both experiments (Figs. 1E;2E).

Prevailing temperature data were recorded from planting of both experiments until harvesting. An average temperature of 19.8°C and minimum and maximum temperatures of 12.4°C and 30.6°C, respectively, were recorded for the hail-net cage experiment. For the microplot experiment the average temperature was 20.5°C, while the minimum and maximum temperatures were 12.7°C and 28.2°C, respectively.

Discussion

The very high probability and significance values obtained between Pi of *M. incognita* race 2, number of egg masse, ELF indices, Rf and percentage yield loss in soybean in both experiments under semi-controlled conditions in the first instance indicated high repeatability of the results. The substantial differences between the two soybean cultivars in terms of all the variables measured reiterate previous findings (Fourie et al., 2006; 2008) of large differences in the host suitability of the two cultivars to this parasite. This is further substantiated by the significant differences between all corresponding variables that were compared during this study. The respective non-linear models for Pi against percentage yield loss in both experiments indicate a damage level difference of at least 6-fold between the two cultivars. However, according to the real values for yield loss the damage level difference could be more than 13-fold. In real terms this is of significant economic importance to producers. Should the two cultivars have a similar yield potential of 2.5 mt per ha under similar conditions a yield loss of 3% for LS5995 will imply a 75kg loss in grain per ha. A 41% yield loss for Prima2000 will mean a 1,025kg per ha loss. At a theoretical price for soybean of US$330 per mt the monetary value will translate into a $24-75 loss per ha for LS5995, while it would be $338 per ha for Prima2000. Should the difference be only six-fold as suggested by the regression models the loss for Prima2000 grown in a *M. incognita* race-2 infested field could still be in the region of $150 per ha. Similar results of differential yield loss in soybean cultivars grown in *M. incognita*-infested microplots have been reported by Apple and Lewis (1984) and Herman et al. (1990).

Damage threshold values, although valuable are evidently difficult to determine because they are highly variable as again demonstrated by results from this study. As our results also clearly indicate, damage-threshold values will also differ between cultivars, which would largely depend on the cultivar's susceptibility to a specific nematode species or race. This observation is further demonstrated by the findings of Niblack et al. (1986) that 31 *M. incognita* race 3 J2 per 100cm^3 of soil are already above the tolerance levels of susceptible soybean cultivars. Kinloch (1982) further predicted a yield loss of 5kg per ha when a single *M. incognita* J2 is present in 10cm^3 of soil where a particular susceptible soybean cultivar is grown.

Many controversial reports exist about the principle of damage-thresholds for plant-parasitic nematodes, whether it should be expressed in terms of Pi or Pf (Mc Donald et al., 2005). We, therefore, suggest that damage-threshold values for nematodes in agricultural crops should be considered circumspectively and at most be used as rough indicators, as Barker and Noe (1987) suggested with reference to hazard indices. A lot of field data of specific nature will be needed to construct models for threshold values (Barker and Noe, 1987; Schomaker and Been, 2006) and it is likely that those will still vary between conditions, crops, cultivars and nematode genera, species, races and even populations.

In addition to variation in damage-threshold nematode-population levels the absence of J2 in the rhizosphere of soybean at harvesting is not a given. Our results show that cultivar susceptibility to nematodes has an effect. Several investigations on *M. incognita* on resistant soybean cultivars in the USA (Minton et al., 1978; Kinloch, 1985; Niblack et al., 1986; Herman et al., 1990) indicated high nematode populations in the rhizosphere at the end of the growing season. This suggest that other factors may also have an effect on the presence or absence of nematodes in the soil at given times during the growing period of a crop. The potential risk this holds for successive crops warrants further investigation into the dynamics of plant-parasitic nematode populations, particularly when resistance as a nematode management tool is recommended.

Our results provide further proof that it is important to consider as many as possible nematode parameters when investigating aspects such as host plant resistance. Because plant resistance could represent one or more of several different mechanisms of resistance (Cook and Starr, 2006), it is important to establish whether there is a relationship between the number of ELF, egg masses and Pi and Pf. This trend has been indicated in other studies on soybean cultivars (Hussey and Boerma, 1981; Fourie et al., 2001, 2006) and on cotton (Shepherd, 1979). In some of these latter cases crop cultivars exhibited low gall ratings but high ELF indices and high numbers of eggs per plant. Gall ratings would, therefore, have lead to this interpretation of cultivar resistance.

High Rf for Prima2000 at low nematode rates in both experiments of our study suggest high susceptibility of this cultivar to *M. incognita* race 2, which agrees with results of a study by Nardacci and Barker (1979). However, intraspecies competition (Cook and Starr, 2006; Schomaker and Been, 2006; Seinhorst, 1965) comes into effect fairly early in our study since the regression lines for Prima2000 generally leveled off from as low as Pi = 500 for most of the parameters measured. This indicates the strong competition for sites between J2 of this root-knot nematode species feeding in the susceptible Prima2000. Conversely this was not the case with the resistant LS5995, which suggest that the use of host plant resistance in only one crop in rotation with other susceptible crops such as sunflower (Bolton et al. (1989), potato (Steyn, 1997; Fourie et al., 1998) or dry bean (Keetch and Buckley, 1984) may not be sufficient for keeping *M. incognita* race 2 population levels below damage-threshold levels in the medium to long term.

Soybean yield reduction increases in proportion with the Pi have also been demonstrated in other studies (Apple and Lewis, 1984; Herman et al., 1990). Although yield suppression in resistant cultivars may also be significant (Herman et al., 1990), the relative impact between susceptible and resistant cultivars is of significant economic importance, as illustrated above. However, as suggested in the case of plant-parasitic nematode populations remaining in soil after the crop has been harvested, this latter situation emphasizes that host-plant resistance alone may not be sufficient and that the careful construction of nematode management systems (Sikora et al., 2005; Cook and Starr, 2006; Khan, 2008) will need to be considered when producing nematode-susceptible crops in infested soils. The relative value of nematode resistance in susceptible field crops in the presence of variable nematode population levels, however, has been demonstrated clearly in this study.

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