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ORIGINAL ARTICLE

# Host response of five potato cultivars to *Meloidogyne* nematodes

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**Abstract**
Potato (*Solanum tuberosum* L.) is a well-known food crop that is regarded as an important component in the worldwide battle against hunger and malnutrition. Root-knot nematodes (RKN), *Meloidogyne* species, are a serious limitation in the potato industry. Potato, being a tuberous crop, yield reduction is mainly due to tuber quality and quantity. In order to evaluate the response of five commercial potato cultivars, viz 'Buffelspoort 1', 'Hertha', 'Larnoma', 'Mnandi' and 'Up-to-date' to two RKN species, viz *M. enterolobii* and *M. javanica*; pot experiments were conducted under net house conditions. Ten separate experiments, each with treatments: 0, 500, 1500, 2500 and 3500 eggs + second-stage juveniles (J2), were arranged in a randomized complete block design (RCBD) with five replicates. Fifty-six days after inoculation, nematode effect on plant yield was evaluated. Potato tubers were assessed for root galls, and nematodes reproductive factor (RF) was computed. There were significant differences amongst treatments on the following potato growth parameters: plant height, stem diameter, chlorophyll content, number of tubers and tuber weight in both *M. enterolobii* and *M. javanica* ($P \leq 0.05$). The RF was above unity (one) in all potato cultivars for both *M. enterolobii* and *M. javanica*; with *M. enterolobii* showing more aggressiveness compared to *M. javanica*. Further, cultivars 'Buffelspoort 1' and 'Hertha' showed the highest susceptibility, whilst cultivar 'Mnandi' showed the least susceptibility. Infection of potato cultivars by the nematodes had severe effects on growth parameters of all the cultivars. Results suggested that all five commercial potato cultivars were susceptible to *M. enterolobii* and *M. javanica*. Thus, there is an urgent need for RKN management intervention in the aforementioned cultivars.

**Keywords** Interaction · Reproductive factor · Root galls · Susceptible

## Introduction

Plant-parasitic nematodes (PPN) are a subject of extensive scientific research because they constitute a significant barrier to the world's food production by lowering crop quantity and quality (Gregory et al. 2017; Khan 2015). At least one PPN species is present in majority of agricultural areas, and annual global crop losses brought on by them are estimated to account for 8.8–14.6% (Baidya et al. 2017). *Meloidogyne* genus has several species that are highly aggressive and extensively dispersed across a variety of environmental conditions on a wide array of crops; making it the most economically significant (Jones et al. 2013; Yigezu Wendimu 2021).

Potato (*Solanum tuberosum* L.) is the world's third most significant food crop (Mickiewicz et al. 2022) and the first most important vegetable crop in South Africa (SA) (PSA 2021a). In SA, potato is grown in 16 different agro-ecological regions, in a variety of soils and climates; guaranteeing a year-round supply of fresh produce. Limpopo (19%), Western Free State (16%), Sandveld (15%) and Eastern Free State (11%) regions are the largest potato producing areas in SA (PSA 2021a). The SA potato industry is largely self-sufficient, and the country exports a significant amount of fresh and processed produce. South Africa is the fourth largest potato producer in Africa (NPCK 2022). In 2020, approximately 51,000 ha of potato were planted under irrigation, with year-around plantings and a total of 2.6 million tonnes harvest in SA (PSA 2021b).

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Potato yield and quality may be negatively impacted by *Meloidogyne* nematodes infection and feeding resulting in formation of galls and blemishes on the tubers. This is due to the fact that *Meloidogyne* species distort roots by forming galls, thereby restricting absorption of water and nutrients. *Meloidogyne* nematodes further deform tubers, resulting in unmarketable produce (Bali et al. 2021; Teklu et al. 2023). In SA, species including *M. enterolobii*, *M. javanica*, *M. arenaria* and *M. incognita* are the most prevalent pests that affect majority of crops, including potato (De Waele and Elsen 2007; Onkendi and Moleleki 2013). *Meloidogyne enterolobii* is the most aggressive compared to other RKN (Brito et al. 2004). This is owing mostly to the species capacity to overcome resistance genes, such as the tomato *Mi-1* gene (Kiewnick et al. 2009).

Additionally, these parasites interact with other plant pathogens to create disease complexes and overwhelm defences against other pathogenic infections (Begum et al. 2012). The severe losses brought on by RKN can be reduced by a number of different management practices. Nematode management generally involves utilizing synthetic nematicides, bio-control agents, resistant hosts and cultural techniques including crop rotation (Stirling 2018; Sasanelli et al. 2021; Poveda et al. 2020; Sivasubramaniam et al. 2020).

However, it is first necessary to ascertain how the crop and RKN interact prior to establishing a nematode management approach. In plant–nematode interactions, Seinhorst (1966) introduced two concepts to describe nematode response: (i) host-status and (ii) host-sensitivity. Host-status is described according to nematode reproductive function which estimates the maximum reproduction rate using initial nematode population (Pi) before planting and final nematode population (Pf) after harvesting (RF = Pf/Pi). Host-sensitivity, instead, refers to plant growth and development in response to nematode infection.

Better understanding of plant–nematode interactions led to classifying plants as being either susceptible, tolerant or resistant. Through intensive nematology research, several plants have been identified and characterized as either susceptible, tolerant or resistant (Audil et al. 2019; Daneel et al. 2018; Verdejo-Lucas and Talavera 2019). The objective of the study was to screen for response of five selected commercial potato cultivars to the aggressive and widespread *M. enterolobii* and *M. javanica*.

## Materials and methods

### Nematode inoculum

Isolates of *Meloidogyne* species were received from Agricultural Research Council-Tropical and Subtropical Crops (ARC-TSC), Mbombela, SA, and raised nematode susceptible tomato (*S. lycopersicum* cv. 'Hotstuff'). Eggs + second-stage juveniles (J2) of the two *Meloidogyne* species were extracted from galled tomato roots through root maceration method as described by Coyne et al. (2007). The roots were gently washed under tap water to remove soil debris and blotted dry using a paper towel. The roots were chopped into approximately 1.5-cm long pieces. Roots were weighed, and water added at a ratio of 1 g of fresh root to 20-mL water and 1% NaOCl solution into a blender and blended for 30 s at 30 000 rpm (Hooper et al. 2005). The resultant suspension was sieved using top–down 250-, 63- and 25-µm aperture sieves into a beaker and eggs enumerated using a dissecting microscope to estimate concentration per 5 ml. The number of eggs + J2 $mL^{-1}$ of suspension was determined using a counting dish under a compound microscope (Hussey and Barker 1973). The nematode inoculum was diluted to the appropriate concentration and kept in the refrigerator for later use.

### Pathogenicity tests

Ten parallel experiments, five of *M. enterolobii* with potato cultivars 'Buffelspoort 1', 'Hertha', 'Larnoma', 'Mnandi' and 'Up-to-date' and *M. javanica* with the same five potato cultivars, were conducted under a net house. In each experiment, five treatments: 0, 500, 1500, 2500 and 3500 numbers of *M. enterolobii* or *M. javanica* eggs + J2 per pot were laid out in a randomized complete block design (RCBD) with five replications. Thirty-centimetre (30 cm) diameter plastic pots were filled with a 1:1 ratio (v/v) mixture of steam pasteurized Hutton series with a red loam field soil + river sand (72% sand, 20% silt and 8% clay) with a pH ($H_2O$) 6.25 at 121 ℃ for an hour and were placed in the net house at 0.5-m inter-row and 0.5-m intra-row spacing. Potato seeds of each cultivar were sown in planting pots. At 7 days after seedling emergence, each pot was inoculated by dispensing appropriate eggs + J2 of *M. enterolobii* or *M. javanica*, i.e. according to treatments. Inoculum was prepared by extracting eggs and J2 from tomato roots in 1% NaOCl solution (Hussey and Barker 1973). Irrigation was applied in all trials by pouring 500-mL tap water every 2nd day into the tray of each pot from a watering-can. Plants in all trials were sprayed with mercaptothion (Malasol®/Malathion®) and tetradifon (Redspidercide®) alternatively every 2 weeks as preventative control of aphid and red spider mite, respectively. The trials were conducted twice, February–April and September–November for data validation.

### Data collection

Fifty-six (56) days after inoculation with nematodes, shoots were cut at the soil level, and root systems were removed from the pots, immersed in water to remove soil particles.

Fully developed root galls were assessed using the North Carolina Differential Scale: 0 = no galls, 1 = 1–2 galls, 2 = 3–10 galls, 3 = 11–30 galls, 4 = 31–100 galls and 5 > 100 and counted per root system (Taylor and Sasser 1978). Nematodes were extracted from total root system per plant by maceration and blending for 30 s in 1% water solution of sodium hypochlorite (Hussey and Barker 1973). The aliquot was passed through top–down nested 250-, 63- and 25-µm screen open sieves. Contents of the 25-µm screen sieve were poured into 100-mL plastic containers for counting under a stereo microscope.

Soil per pot was thoroughly mixed, and 200-mL soil sample was collected. Nematodes were extracted from soil samples using the modified sugar flotation and centrifugation method (Jenkins 1964). Nematode numbers were converted to 5-L soil per pot to estimate Pf. Reproductive factor (RF = Pf/Pi), which is a proportion of Pf and Pi, was computed for each inoculum level. At harvest, plant length was measured from the soil level to the tip of the flag leaf. Shoots were cut at the soil level, chlorophyll content was measured using a chlorophyll metre (MINOLTA, SPAD-502) and stem diameter measured 5 cm from the cut end of the stem using a digital Vernier calliper. Fresh shoots were oven-dried for 72 h at 52 ℃ for dry matter determination.

### Statistical analysis

The RF nematode data were subjected to analysis of variance (ANOVA) procedure using SAS software (9.4 version). Significant treatments were at the probability level of 5%. Mean separation was achieved using Tukey's Least Significant Difference (LSD) (Gomez and Gomez 1984).

## Results

### Host-status of *Meloidogyne* species on potato cultivars

Responses of RF values to increasing Pi levels were modelled by the regression curve estimations resulting to a quadratic equations (Fig. 1).

Data from the two planting seasons were not significantly different ($P \leq 0.01$); hence, data were pooled. The number of galls of *M. enterolobii* and *M. javanica* was significantly different ($P \leq 0.05$) in all five potato cultivars. Cultivar 'Hertha' supported the highest *Meloidogyne* reproduction and a subsequent higher galling severity (Fig. 2).

Cultivar 'Buffelspoort 1' had a higher gall number under *M. javanica* as compared to *M. enterolobii*. Likewise, cv. 'Up-to-date' had a higher gall number under *M. enterolobii* as compared to under *M. javanica*. For all screened cultivars, gall number showed a positive relationship with RF; as increase in galls exhibited an increase in RF. Cultivar 'Larnoma' had the lowest *M. enterolobii* galling severity, a factor of Pf and RF, per root system with all tested treatments (Table 1). Significant variables were analyzed at 5% probability level according to Tukey's LSD.

### Host-sensitivity of potato cultivars under *Meloidogyne* species infestation

Potato growth parameters were evaluated at 56 days after inoculation in order to determine each cultivar's susceptibility and allow for completion of the nematode life cycle. In contrast with the corresponding controls, yellowing signs of the leaves of nematode-infected plants were observed. Tested potato cultivars' growth parameters, viz plant height, stem diameter, chlorophyll content, fresh shoot weight, dry shoot weight, number of tubers and weight of tubers, varied amongst different cultivars (Table 2: Supplementary material). The lowest inoculum density resulted in the smallest decreases in these parameters, whereas the highest density resulted in the greatest reductions.

## Discussion

Galling severity scores for *M. enterolobii* were comparatively higher than *M. javanica*, with an average range of 21–30 and 1–20, respectively. Accordingly, even if *Meloidogyne* Pi did not reduce tuber number or size, it still showed potential to substantially impedes tuber quality. For this reason, both population densities from roots and soil were quantified to determine how susceptible the chosen potato cultivars were to nematode development and feeding. Following nematode extraction, a higher number of nematodes persisted inside the roots of all five cultivars.

A host's susceptibility is determined not only by its genotype but also by the number of nematodes that are affecting it, thus Pi. As such different Pi densities were administered. It has been demonstrated that plants suffer a significant decline in growth at high population densities (Kayani et al. 2017); however, plant susceptibility is also affected by environmental factors (Starr and Mercer 2009). This is not to suggest that lower Pi has no effect on plant development or production, quite the contrary.

For instance, other Solanaceae species, such as *S. quitoense*, can be severely affected by low *M. incognita* Pi (Revelo and Sandoval 2003). As current potato cultivars have been shown to be susceptible to *Meloidogyne* nematodes, all inoculated nematode stages had potential to damage tuber quality. The expanding potato root system was invaded by the initial generation (primary inoculum) in the soil, the J2 from the second-generation hatched from galls of inoculated initial J2 generation, which entered the roots at planting.

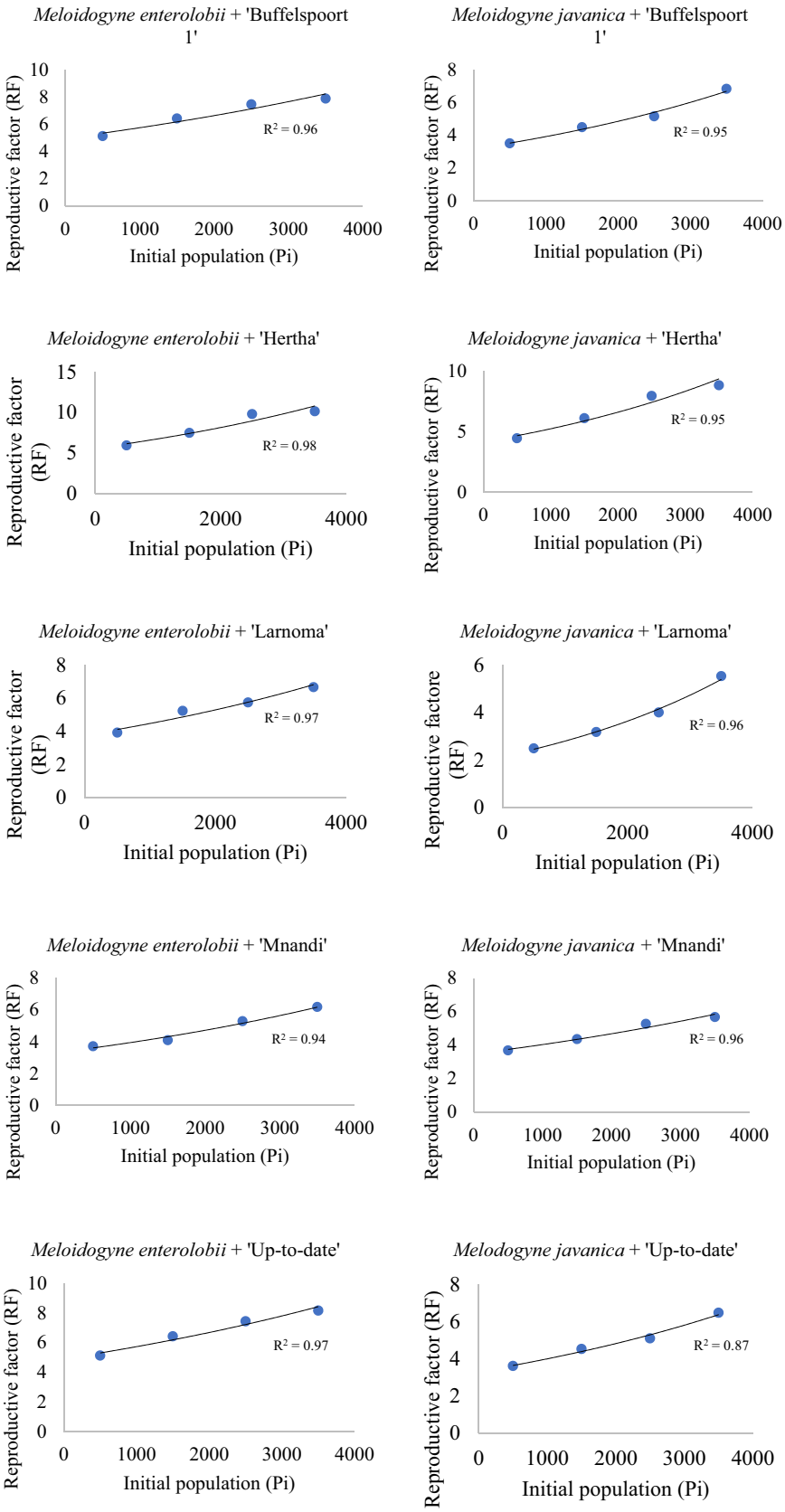


**Fig. 1** Relationship between reproductive factor (RF) values and initial population (Pi) of *Meloidogyne enterolobii* and *Meloidogyne javanica* on five potato cultivars under greenhouse and microplot conditions at 56 days after inoculation ($n = 10$)

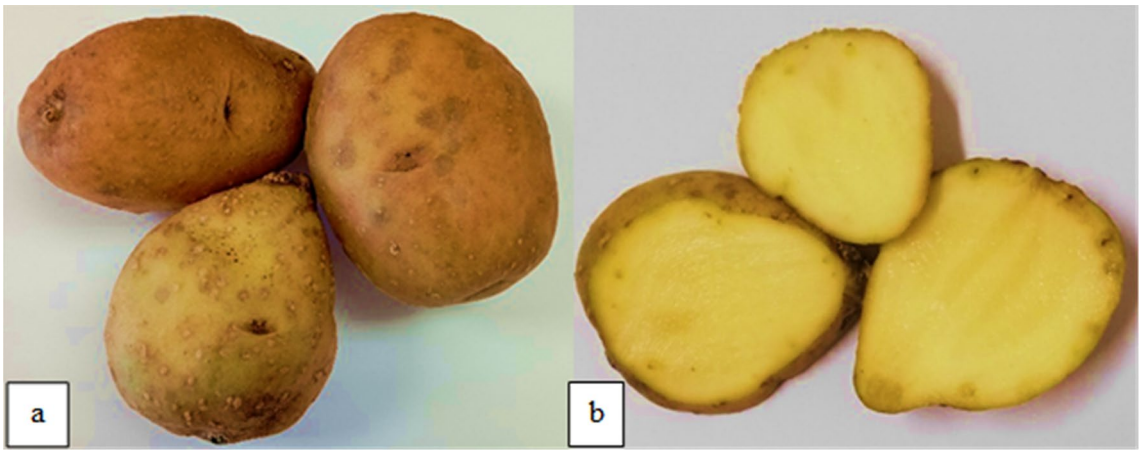


**Fig. 2** 'Hertha' potato tubers infected with *Meloidogyne enterolobii* with symptoms of **a** galling and **b** blemishes. Pictures taken by Mukondeleli Ndivhuwo Ramatsitsi

Even though results from this study demonstrated that there were no significant differences between tuber number and tuber mass at different Pi levels within the same cultivar, tuber quality damage is generally not correlated with Pi. Be that as it may, a susceptible host supports *Meloidogyne* populations that would increase to have high Pi for the following cropping season. In any case, Pi ends up playing a pivotal role in crop yield.

Potato crop optimum growing temperatures range between 17 and 26 ℃ (Kim and Lee 2016), the same temperatures that support *Meloidogyne* species growth and reproduction (Velloso et al. 2022). During the course of the current experiments, mean soil temperature at 20 cm (representing the root zone) was around 25–29 ℃ in March–April 2020 and 25–29 ℃ in August–September 2020. These conditions, thus, represent sufficient time for approximately three generations during the course of the experiments, likely reflected in the galling severities and nematode Pf observed. The average generation time for many *Meloidogyne* species is 28–35 days at optimal base temperatures of approximately 24–28 ℃ (Bridge and Starr 2007). At 25–30 ℃, *Meloidogyne* species had average of 15–33% infection rates on *S. lycopersicum* 'BHN 589', with J2 development relatively higher at 25 ℃ when compared to 30 ℃. The same nematode species completed one generation cycle in 29 days at 30 ℃ (Velloso et al. 2022).

Soil sampled in this study was a sandy loam texture, with sand contents ranging from 65 to 75% which may have facilitated migration of *M. enterolobii* and *M. javanica* through the soil profile. Soil texture has also been correlated with nematode movement in soil, with coarse textured soils facilitating increased migration of *Meloidogyne* species and crop damage (Al-Ghamdi 2021; Koenning et al. 1996). This behaviour was attributed to the nematodes' increased penetration rates, which offer enough aeration for the nematodes owing to coarse soil characteristics, resulting under improved mobility (Kim et al. 2017).

At all nematode inoculum levels, *M. enterolobii* showed severe symptoms as compared to *M. javanica*. This is most likely a result of *Meloidogyne* species varied genetic makeup (Rashidifard et al. 2018). In a study by Tuncsoy (2021), *M. javanica* induced more galling in *C. pepo* as compared to *M. incognita*. All nematode population densities for *M. enterolobii* and *M. javanica* inoculation on potato cultivars resulted in reduced plant development. By 30 days following inoculation with 1500 or more eggs + J2 of *M. enterolobii* or *M. javanica* per pot, plant stunting and yellowing as well as a decrease in plant shoot development were evident. All plants infected with more than 500 egg and J2 per pot displayed stunting and yellowing 45 days after inoculation, even though the plants were regularly irrigated.

Based on RF, potato cultivars' response to the two nematodes varied: Cultivar 'Hertha' was highly susceptible to *M. enterolobii*, whilst 'Buffelspoort 1' and 'Up-to-date' were moderately susceptible, and 'Larnoma' and 'Mnandi' were susceptible. On the other hand, 'Hertha' was highly susceptible to *M. javanica*, 'Buffelspoort 1' and 'Larnoma' were moderately susceptible, whilst 'Mnandi' and 'Up-to-date' were susceptible to *M. javanica*. Crops within the same genera can have different susceptibility levels to the same RKN. For example, there was a lower Pf/Pi ratio for *M. charantia* on pumpkins (*Cucurbita moschata*), followed by cucumber (*Cucumis sativus*) and bottle gourd (*Lagenaria siceraria*) (Chandra et al. 2010). The Pf/Pi for *M. incognita* was lower on zucchini (*Cucurbita pepo* 'Amalthee') than *C. sativus* 'Dasher II' (López-Gómez et al. 2015; Verdejo-Lucas and Talavera 2019).

According to Montasser et al. (2019), potato cultivars evaluated for *Meloidogyne* response varied and were classified as being either resistant, moderately susceptible or

**Table 1** Mean reproductive factor (RF) and gall numbers in five potato cultivars infected by *Meloidogyne enterolobii* and *Meloidogyne javanica* under net house conditions at 56 days after inoculation ($n = 10$)

| | | *Meloidogyne enterolobii* | | *Meloidogyne javanica* | |
|---|---|---|---|---|---|
| Genotype | Pi | Galls | RF | Galls | RF |
| | 500 | 4.40[a] | 5.12[d] | 3.80[a] | 3.51[d] |
| Buffelspoort 1 | 1500 | 3.00[b] | 6.42[c] | 3.20[a] | 4.49[c] |
| | 2500 | 4.20[ab] | 7.45[b] | 3.60[a] | 5.15[b] |
| | 3500 | 4.60[a] | 7.89[a] | 3.80[a] | 6.83[a] |
| $LSD_{0.05}$ | | 1.16 | 1.01 | n.s[2] | 1.00 |
| P | | < 0.01 | < 0.01 | 0.51 | < 0.01 |
| F | | 17.45 | 18.53 | 18.53 | 17.45 |
| | 500 | 3.00[ab] | 5.66[d] | 3.40[a] | 4.44[d] |
| Hertha | 1500 | 1.80[b] | 7.36[c] | 3.20[a] | 5.75[c] |
| | 2500 | 3.00[b] | 9.75[b] | 3.20[a] | 7.62[b] |
| | 3500 | 4.00[a] | 10.06[a] | 2.00[a] | 8.81[a] |
| $LSD_{0.05}$ | | 0.50 | 2.12 | n.s | 0.66 |
| P | | < 0.01 | < 0.01 | 0.34 | < 0.01 |
| F | | 14.40 | 7.07 | 17.23 | 17.23 |
| | 500 | 4.40[a] | 3.92[d] | 3.40[a] | 2.49[d] |
| Larnoma | 1500 | 3.00[a] | 5.23[c] | 3.80[a] | 3.18[c] |
| | 2500 | 3.20[a] | 5.75[b] | 3.80[a] | 4.00[b] |
| | 3500 | 4.00[a] | 6.66[a] | 3.40[a] | 5.53[a] |
| $LSD_{0.05}$ | | 2.38 | 0.22 | n.s | 0.11 |
| P | | 0.04 | 0.04 | 0.68 | < 0.01 |
| F | | 3.09 | 3.09 | 12.05 | 12.05 |
| | 500 | 3.60[a] | 3.71[d] | 2.75[a] | 3.68[d] |
| Mnandi | 1500 | 4.00[a] | 4.09[d] | 2.40[a] | 4.35[c] |
| | 2500 | 4.20[a] | 5.29[b] | 2.60[a] | 5.26[b] |
| | 3500 | 4.20[a] | 6.19[a] | 3.20[a] | 5.67[a] |
| $LSD_{0.05}$ | | n.s | 0.65 | n.s | 1.00 |
| P | | 0.90 | < 0.01 | 0.14 | < 0.01 |
| F | | 40.75 | 40.75 | 16.00 | 16.00 |
| | 500 | 2.20[a] | 5.14[d] | 2.60[ab] | 4.79[c] |
| Up-to-date | 1500 | 2.00[a] | 6.39[c] | 2.60[ab] | 5.00[c] |
| | 2500 | 2.40[a] | 7.64[b] | 3.00[a] | 6.19[b] |
| | 3500 | 2.60[a] | 8.31[a] | 3.20[a] | 6.98[a] |
| $LSD_{0.05}$ | | n.s | 0.03 | 0.22 | 0.11 |
| P | | 0.12 | 0.05 | 0.04 | 0.02 |
| F | | 10.76 | 10.76 | 2.17 | 2.17 |

zColumn means followed by the same letter were not different ($P \leq 0.05$) according to LSD

[2]n.s = not significant

Gall scale: 0 = no galls, 1 = 1–2 galls, 2 = 3–10 galls, 3 = 11–30 galls, 4 = 31–100 galls and 5 > 100

highly susceptible to nematode infection. These variations within the same plant genera and amongst the same and/or different *Meloidogyne* species can be attributed to genotype of specific host, making one cultivar more susceptible than the other; as well as nematode genotype, making one species more virulent than its counterpart. The substantial inter- and intra-specific diversity in *Meloidogyne* populations increases adaptation and provides stronger selection advantages over their hosts, which include various Solanaceae species (González et al. 2010), a trend that was established in this study.

The present study's observations of the two *Meloidogyne* species parasitic behaviour on potato tubers and feeder roots indicate that *Meloidogyne* infection has the potential to cause significant potato damage. The severity of the root galling on the feeder roots of cultivars 'Buffelspoort 1' and 'Hertha' and the significant impairment of plant growth caused by an increase in the initial inoculum density in the soil proved

that *Meloidogyne* has a high potential for reproduction and damage on potato. A similar pattern of potato response to *Meloidogyne* species was observed by Vovlas et al. (2005) and Melakeberhan et al. (2012).

The current results show that the tested commercial potato cultivars have a variety of capacities for supporting *Meloidogyne* reproduction, given that none of the cultivars was able to suppress nematode reproduction. The cultivars 'Hertha', 'Up-to-date' and 'Buffelspoort 1' sustained higher nematode densities. This study further demonstrates that comparatively, *M. enterolobii* is more virulent to potato than *M. javanica*; although *M. javanica* still significantly impedes potato quality. The screened cultivars are continuously grown in potato fields across SA, which may facilitate the spread of nematodes into un-infested areas whilst also allowing the preservation and growth of Pi already existing there. To enable efficient integrated control of these nematodes on potato, accurate diagnostic and estimation of soil population densities of *M. enterolobii* and *M. javanica* as well as other RKN should be performed prior to planting. There is a need for further studies on efficacy of sustainable management practices, such as application of indigenous nematophagous fungi. This is because indigenous nematophagous fungal isolates may have a greater potential of establishing themselves in the rhizosphere and subsequently suppressing target RKN than exotic/introduced isolates.

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**Author contributions** MNR and MCK helped in conceptualization; MNR and MCK helped in methodology; MNR and SN worked in formal analysis and investigation; MNR contributed to writing—original draft preparation; MNR, SN, KR and MCK contributed to writing—review and editing; MNR worked in funding acquisition; MNR and MCK worked in resources and KR and MCK worked in supervision.

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**Data availability** Data generated or analysed during this study are included in this published article [and its supplementary information files are available at Harvard Data verse https://doi.org/https://doi.org/10.6084/m9.figshare.24609147].

## Declarations

**Conflict of interest** The authors have no competing interests to declare that are relevant to the content of this article.



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