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Insights into the life-cycle development of *Meloidogyne enterolobii, M. incognita* and *M. javanica* on tomato, soybean and maize

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Abstract *Meloidogyne enterolobii* is a highly pathogenic nematode species that renders host plant resistance ineffective that exists for other species. The life-cycle development and duration of three *Meloidogyne* species, viz. *M. enterolobii, M. incognita* and *M. javanica* was determined in roots of three crops: tomato ('Moneymaker'), soybean ('DM-5953-RSF') and maize ('P-2432-R') under glasshouse conditions. At different time intervals, 3-, 5-, 10-, 15-, 20-, and 25-days after inoculation (DAI), 20 randomly selected individuals, representing different life-stages of each species, were isolated from roots. *Meloidogyne enterolobii* had a quicker life cycle development compared to the other two species. Mature females were observed 15 DAI for all three species, but single eggs of *M. enterolobii* were present at 15 DAI opposed to egg masses only found 20 and 25 DAI for the other two species. Second generation motile J2 were observed for *M. enterolobii* and *M. javanica* from 20 DAI and at 25 DAI for *M. incognita*. Substantially less degree days (DD) were recorded for *M. enterolobii* being 216 for tomato, 195 for soybean and 232 for maize; for *M. incognita* it was 292 for tomato, 264 for soybean and 314 for maize; and for *M. javanica* it was 276 for tomato, 248 for soybean and 298 for maize. The use of genotypes with shorter growing periods is suggested to reduce the number of generations of *M. enterolobii* which is foreseen to potentially result in lower population densities and less crop damage.

Keywords Day degrees · Life cycle · Maize · Root-knot nematodes · Soybean · Tomato

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Introduction

Root-knot nematodes (RKN) are among the most damaging plant-parasitic nematode genera infecting a wide range of agricultural and ornamental crops as well as weeds (Jones et al., 2013). The reduced ability of RKN-infected roots of host plants to assimilate and translocate nutrients and water from their roots to their aerial parts have been reported and contributes towards non-optimal crop development and low yields

(Abad et al., 2009). The life cycle of RKN starts with the egg which is followed by three juvenile stages (infective second/J2, third/J3 and fourth/J4) that ultimately develop into sexually dimorphic mature males or females (Moens et al., 2009). The duration of the life cycle of the economically most important thermophilic RKN species have been noted as 19 days for *M. arenaria*, 15 days for *M. incognita* and 17 days for *M. javanica* at 30 ˚C (Dávila-Negrón & Dickson, 2013). According to literature *M. enterolobii* advances to maturity in 24–28 days in guava (*Psidium guajava*) roots, while in green pepper (*Capsicum* spp.) roots the species' life cycle duration is indicated as 28 days (Ashokkumar et al., 2019; Marques et al., 2020).

An important factor that should be taken into consideration when determining the life cycle duration of organisms is the calculation of the degree-days (DD). It is described by Arnold (1960) as the thermal constant used to record the physiological time required for the completion of a biological process. It hence represents the heat units required for the development of a motile J2 to a mature life stage (egg-laying female or a male). The calculation of DD requires the inclusion of the base temperature (Tb) of the species under investigation. The Tb is the temperature at which the lowest rate of development occurs for such a species (Negron, 2006). Although the required DD for the development of an egg-laying female is recorded as 317 for *M. arenaria*, 300 for *M. incognita* and 334 for *M. javanica* (Dávila-Negrón & Dickson, 2013), this reported to be as short as 273 for *M. enterolobii* on tomato (Velloso et al., 2022).

The duration of the life cycle of most RKN species has been documented and contains crucial information regarding their life stage development over time, which is critical for the management of these pests (Curto et al., 2005; Khan et al., 2006; Wesemael et al., 2014). However, for the highly pathogenic species, *M. enterolobii,* parasitizing and causing severe damage to agri-and horticultural crops globally (Brito et al., 2004) limited and fragmented information is available regarding this crucial aspect of its biology (Ashokkumar et al., 2019). By contrast, insightful reviews on the geographic distribution, identification and management of this species are available (Castagnone-Sereno, 2012; Collett et al., 2021; Philbrick et al., 2020). However, the reports focusing on the life cycle of *M. enterolobii* have been done only for vegetable and fruit crops: tomato (Velloso et al., 2022), green pepper (Marques et al., 2020) and guava (Ashokkumar et al., 2019). Except for DD requirements, no information could be found about the life-cycle duration of *M. enterolobii* for grain crops, which this species also infects and damages in South African production areas (Pretorius, 2018; Visagie et al., 2018). In sub-Saharan Africa, for example, grain crops constitute a major part of the diet of the human population while it is also used as fodder for animals (GrainSA, 2022a, b). Production of these crops is threatened due to infection by, and resultant damage caused by RKN species, including *M. enterolobii*. This species was identified from a major maize and soybean production area of South Africa (Pretorius, 2018), and is routinely identified from samples received from producers by personnel of the Nematology Laboratory of the North-West University (H. Fourie, North-West University Potchefstroom), and therefore it became urgent to elucidate its biology and life cycle in roots of grain crops.

Although it is known that *M. enterolobii* counteracts genetic host plant resistance that is effective against its thermophilic counterpart species (*M. arenaria*, *M. incognita* and *M. javanica*) in various crop genotypes (Brito et al., 2007), no study to date aimed to investigate the comparative nature of the life cycles of these three thermophilic species in roots of grain crops. Since the life cycle duration of *M. enterolobii* might be a critical aspect that can shed light on understanding why this species is difficult to control, this study thus was conducted to determine its life-cycle duration, life-stage development and reproduction potential compared to that of *M. incognita* and *M. javanica* in glasshouse experiments in roots of a RKN susceptible tomato cultivar (*Lycopersicon esculentum*) that served as the model plant species, and in roots of genotypes of grain crops soybean (*Glycine max*) and maize (*Zea mays*) that served as the experimental crop species.

Materials and methods

In vivo rearing and verification of the identity of *Meloidogyne* species

The three RKN species used in this study were collected from various localities (Table 1) and reared as single-egg mass populations in roots of the susceptible tomato cultivar ('Floradade') (Fourie et al., 2012) in a glasshouse as described by Rashidifard et al.

Table 1 Locality and hosts of the three South African *Meloidogyne* species populations used in the study

Species	Area and province in South Africa	Host
Meloidogyne enterolobii	Mbombela, Mpumalanga Province	Guava (*Psidium guajava*)
Meloidogyne incognita	Sandveld, Western Cape Province	Potato (*Solanum tuberosum*)
Meloidogyne javanica	Sandveld, Western Cape Province	Potato (*Solanum tuberosum*)

(2018). The identities of the three RKN species, were verified using the morphological approaches (Kleynhans, 1991; Marais et al., 2017; Rashidifard et al., 2019a).

For molecular identification, the sequence characterized amplified region – polymerase chain reaction (SCAR-PCR) was used. The PCR performed using species-specific primers indicated in Table 2 based on the amplification process reported by Rashidifard et al. (2019b). Finally, the PCR product was loaded on 1.5% agarose gel and stained using GelRed and inspected under an ultraviolet transilluminator to determine the size of the DNA fragments present.

Meloidogyne species inoculum

Tomato roots infected with *in vivo* reared populations of *M. enterolobii*, *M. incognita*, and *M. javanica* (Table 1) were separated from the aerial plant parts 30–40 days after the rearing processes commenced. The roots of the respective tomato plants were washed under running tap water to remove excess soil and decomposed plant material. The roots were then subjected to the adapted NaOCl method (Riekert, 1995) for the extraction of eggs. The eggs obtained this way were counted in a de Grisse counting dish (De Grisse, 1963) using a stereomicroscope (60 × magnification).

The extracted eggs of each species were next placed onto a 25-µm mesh aperture sieve that was submerged in a 2-L capacity plastic container, filled halfway with tap water, that was placed into a temperature-regulated growth chamber at an ambient temperature of 28 °C. The J2 that hatched from the eggs was collected by decanting them onto a 20-µm aperture mesh sieve. The collected J2 were counted under a stereomicroscope (60 × magnification) before they were used as inoculum..

Inoculation of crop seedlings with *Meloidogyne* J2

Maize and soybean seeds were obtained from the respective suppliers, namely Monsanto South Africa (Pty) Ltd (now known as Bayer (Pty) Ltd) and Agricol. The seeds were not treated with any fungi-, herbi- or pesticides since it was requested to be used in nematode experiments. Two-leaf stage tomato seedlings were obtained from Ezigro seedlings (White River, Mpumalanga Province, South Africa) and were not treated with any nematicide product.

Maize and soybean were obtained by growing it from the respective seeds in 4-L capacity pots within a glasshouse under the same controlled conditions as indicated earlier for the *in vivo* rearing of the RKN species. During sowing of soybean, each seed was inoculated with 5 mg of the nitrogen-fixing bacteria (*Bradyrhizobium japonicum*), which was obtained from Soygro (Pty) Ltd (Potchefstroom, North West Province; http://www.soygro.co.za/rhizobium/), to stimulate and promote seed germination and nitrogen fixation. After sowing of

Table 2 Identification of South African populations of *Meloidogyne enterolobii*, *M. incognita* and *M. javanica* using the sequence characterised amplified region – polymerase chain reaction (SCAR-PCR)

Primer code	Primer sequence (5' → 3')	Specificity	Reference	Origin of standard populations used
Me-F	AACTTTTGTGAAAGTGCCGCTG	*M. enterolobii*	Long et al. (2006)	Guava (*Psidium guajava*); Mpumalanga
Me-R	TCAGTTCAGGCAGGATCAACC			
F-inc	CTCTGCCCAATGAGCTGTCC	*M. incognita*	Zijlstra et al. (2000)	Maize (*Zea mays*); Northern Cape
R-inc	CTCTGCCCTCACATTAGG			
Fjav	GGTGCGCGATTGAACTGAGC	*M. javanica*	Zijlstra et al. (2000)	Pumpkin (*Curcurbita pepo*); Northern Cape
Rjav	CAGGCCCTTCAGTGGAACTATAC			

the seeds (maize and soybean) and setting seedlings (tomato), 250 ml tap water was added to each pot. The seedlings were watered every 2nd day for 10 days or as needed. The following nutrient solution, Ca = 7,0%; K = 13,0%; Mg = 2,2%; N = 6,5%; P = 2,7%; S = 7,5%; < 0,1% micro-elements (B, Cu, Fe, Mn, Mo, and Zn), was applied to the pots (according to soil analysis) in which the seedlings were transplanted. At the second-leaf stage the seedlings were uprooted from the pots and one seedling of each crop transplanted into 400 ml plastic PVC tubes filled with fumigated soil (Telone® II @ 150 L/ha; a.i. 1,3 dichloropropene). Each tube had two holes (each 0.5 cm in diameter) at the bottom to enable sufficient drainage of water. The roots of each crop seedling were inoculated with the 2000 and 950 motile J2 for initial and repeat experiments, respectively, due to difficulty in obtaining the same number of hatched J2 for all three RKN species (Table 3). The initial experiment for each crop was conducted at different times due to limited space available in the greenhouse, subsequently the ambient temperature for each crop slightly fluctuated (Table 3). Three DAI, the seedlings (of each crop) were removed from the soil, carefully rinsed with tap water, and transplanted into fumigated soil in another set of 400-ml capacity PVC tubes. These plants were kept until termination of each experiment. This was done to ensure that only the J2 that penetrated the roots of the three crops' seedlings, during the 3-day exposure period, were present in the roots and developed to the subsequent life stages. The six sampling intervals used were 3, 5, 10, 15, 20 and 25 DAI for each of the crops and for each of the three RKN species, with five replicates per sampling interval.

Table 3 Information about the three crops used for life-stage developments, duration and reproduction of three *Meloidogyne* species as well as information about conditions of the experiments

Crop	Mean Min temp (°C)	Mean Max temp (°C)	Number of J2 inoculated per pot
Tomato cultivar Moneymaker			
Initial experiment	21.7	32.2	2 000
Repeat experiment	16.0	32.0	950
Soybean genotype DM-5953-RSF			
Initial experiment	13.0	31.0	2 000
Repeat experiment	16.0	32.0	950
Maize genotype P-2432-R			
Initial experiment	18.5	32.0	2 000
Repeat experiment	16.0	32.0	950

Staining of *Meloidogyne* species life stages

The acid-fuchsin method (Byrd et al., 1983) was used to stain RKN specimens present in the roots of each plant for each of the sampling intervals. This procedure enabled the isolation of 20 stained individuals per crop root system of the inoculated species for determining their life stages (Fig. 1) using the protocol of Triantaphyllou and Hirschmann (1960).

Calculation of degree-days (DD) to determine the *Meloidogyne* species' life-cycle durations

Developmental DD required for J2 to reach the egg-laying female stage was calculated for each species. The Tb values (also listed in Table 4) recorded in the literature for the three RKN species were used in this study in calculations to determine their DDs: 10.0 °C for *M. enterolobii* (Jacobs et al., 2011) and 9.8 °C and 10.6 °C for *M. incognita,* and *M. javanica* (Negron, 2006), respectively. The DD for each species was hence calculated for each experiment using the following equation: $DD = [(Tmax + Tmin)/2 - Tb] \times$ number of days required to complete; Tmax = maximum temperature for the period of development; Tmin = minimum temperature for the period of development; and Tb = base temperature of the RKN species in question.

Data analyses

For data analyses the J2 life stages including the motile and swollen individuals were grouped together and indicated as J2. Similarly, the J3 and J4 life stages were grouped together and indicated as J3 & J4. The females are represented by immature and mature individuals.

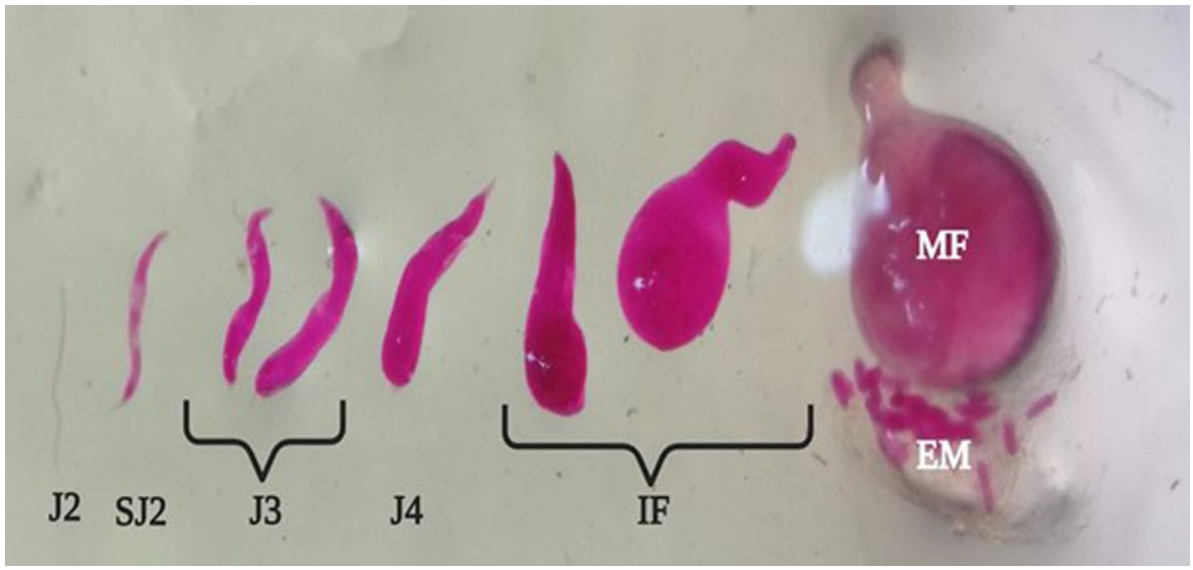

Fig. 1 Different life stages of *M. enterolobii* ranging from motile second stage juveniles (J2), swollen second stage juveniles (SJ2), third stage juveniles (J3), fourth stage juveniles (J4), immature females (IF), and a mature female (MF) with an egg-mass (EM) as determined using the protocol of Triantaphyllou and Hirschmann (1960) (Photo: Raymond, Collett, North-West University, South Africa)

Data of life stages were subjected to ANOVA. After such analyses, factorial ANOVAs were done (Statistica, Version 13.3; www.statsoft.com) with RKN species as the main factor, sampling intervals (3, 5, 10, 15, 20 and 25 DAI) as sub-factor 1 and crops as sub-factor 2. Since initial and repeat experiments showed no interactions for Species*Sampling Intervals, the data for the experiments were pooled, subjected to ANOVA and discussed.

Results

Identification of *Meloidogyne* species

The identities of the three RKN species used were verified using both SCAR-PCR and morphology (perineal patterns of females) and were confirmed to be single species populations of *M. enterolobii*, *M. incognita* and *M. javanica*.

Table 4 Degree-day data required to develop egg-laying female for *Meloidogyne enterolobii*, *M. incognita* and *M. javanica* in roots of tomato cultivar Moneymaker, soybean genotype DM-5953-RSF and maize genotype P-2432-R under glasshouse conditions

Species	Min temp (°C)	Max temp (°C)	Base temp (Tb; °C)	Time interval (DAI)	Degree Days (DD)
Tomato cultivar Moneymaker					
M. enterolobii	17.3	31.5	10	15	216
M. incognita	17.3	31.5	9.8	20	292
M. javanica	17.3	31.5	10.6	20	276
Soybean genotype DM-5953-RSF					
M. enterolobii	14.5	31.5	10	15	195
M. incognita	14.5	31.5	9.8	20	264
M. javanica	14.5	31.5	10.6	20	248
Maize genotype P-2432-R					
M. enterolobii	18.9	32.1	10	15	232
M. incognita	18.9	32.1	9.8	20	314
M. javanica	18.9	32.1	10.6	20	298

Life stage development of *Meloidogyne* species

No significant interactions ($P \leq 0.05$) existed for each of the life stage groups (J2 and J3 and J4,) and females (immature and mature) for the initial and repeat experiments of the three crops for Species×Time Interval (DAI); therefore, the data was pooled.

For all three species and crops, the J2 number was significantly higher 3 and 5 DAI compared to the other sampling intervals (Fig. 2A, D, G), with no significant difference being evident among the three species. For tomato and soybean, 10 DAI, significant differences ($P \leq 0.05$) were observed between the three species with *M. enterolobii* having significantly lower J2 number (Fig. 2A, G). For maize, 20 and 25 DAI, *M. enterolobii* had significantly higher J2 number compared to the other two species (Fig. 2D).

Third- and fourth stage juvenile numbers for all three species generally peaked 15 DAI in the roots of all three crops, except for *M. incognita* in maize which peaked at 10 DAI and *M. enterolobii* in tomato roots where they peaked 10 DAI with significantly higher numbers than the two other species (Fig. 2B, E). For soybean, *M. enterolobii* showed significantly higher numbers of J3 and J4 10 DAI compared to the other two species, although it peaked only 15 DAI. The number of *M. enterolobii* J3 and J4 was however significantly lower than that of *M. javanica* 15 DAI (Fig. 2H). For maize, the number of J3 and J4 for *M. incognita* and *M. javanica* peaks 10 DAI, while *M. enterolobii* peaked 15 DAI. Significant differences between *M. enterolobii* and the two other species were observed 15 DAI and between *M. incognita* and *M. javanica* 10 DAI with *M. incognita* having the highest numbers (Fig. 2E).

Females (immature and mature stages) were recorded from 15 DAI in roots of all three crops for all three species (Fig. 2C, F, I). *Meloidogyne incognita* had significant less females than the other two species 15 DAI for tomato, while no significant differences were observed for the other sampling intervals for tomato and soybean between the three species (Fig. 2C, I). For maize, *M. incognita* and *M. javanica* had significantly higher female numbers 15, 20 and 25 DAI compared to those for *M. enterolobii* (Fig. 2F).

Life cycle durations of *Meloidogyne* species

Single eggs were recorded for *M. enterolobii* 15 DAI and therefore this sampling interval was used for calculating the DD needed to develop to an egg-laying female. For *M. incognita* and *M. javanica,* eggs were only recorded as part of egg mass production by females from 20 DAI and therefore their DD calculated using the latter sampling interval (Table 4).

The development of each of the three RKN species according to DD calculations, proposed that *M. enterolobii*'s were substantially shorter in the roots of all three crops, and it generally having the shortest DD for soybean (Table 4). For tomato, *M. enterolobii* needed 216 DD to reach egg-laying female stage, this was 76 and 60 DD less compared to those of *M. incognita* (292) and *M. javanica* (276), respectively. For soybean, *M. enterolobii* (195) required 69 and 53 less DD than that of *M. incognita* (264) and *M. javanica* (248), respectively. For maize *M. enterolobii* (232) had 82 and 66 shorter DD compared to those of *M. incognita* (314) and *M. javanica* (298), respectively.

Discussion

The comparative glasshouse study enabled the generation of novel and valuable information about the life-stage development and life-cycle duration of three economically important RKN species (Fourie et al., 2017; Jones et al., 2017), *M. enterolobii*, *M. incognita* and *M. javanica*, for three economically important food crops (maize, soybean, and tomato). Since *M. enterolobii* is referred to as a threat species worldwide and its wider distribution in South Africa has been recorded during the past decade (Marais, 2014; Onkendi & Moleleki, 2013; Rashidifard et al., 2019b; Visagie et al., 2018), this study was crucial.

The most interesting and important findings of our study were the that the egg production of *M. enterolobii* was recorded 15 DAI which was shorter compared to that of its counterpart species for which eggs were recorded 20 DAI. This implies that more generations of *M. enterolobii* can potentially be produced per growing season resulting in higher population densities that can cause more severe damage in a shorter period. Furthermore, recording shorter DD required by *M. enterolobii* for all three crops and earlier production of single eggs 15 DAI, which was not the case for the other two species, further accentuates the risk posed by this species to potentially build up to higher population densities and inflict higher levels of

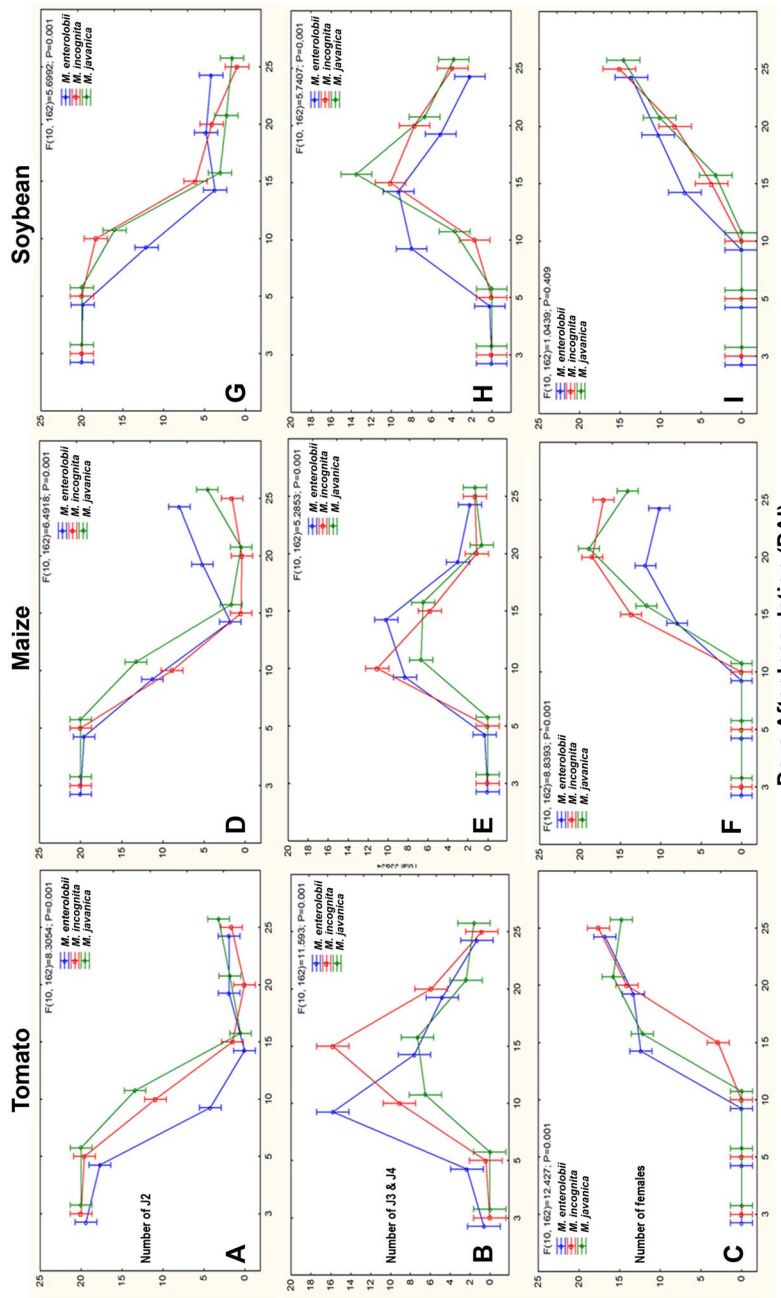

Fig. 2 The development of motile and swollen second-stage juveniles (J2), third (J3) and fourth (J4)-stage juveniles and females of *M. enterolobii* (red line), *M. incognita* (green line) and *M. javanica* (blue line) in roots (**A-C**) of tomato ('Moneymaker), (**D-F**) maize ('P-2432-R') and (**G-I**) soybean ('DM-5953-RSF') maize from 3 to 25 days after inoculation (DAI) during a glasshouse experiment. The X axis shows DAI and Y axis shows the number of individuals at respective life stage of *Meloidogyne* species. The data is presented in format of Mean; Whisker: Mean ± SE

damage in fields where it occurs. It should, however, be noted that egg production by *M. incognita* and *M. javanica* recorded on 20 DAI might not be precise due to 5-day intervals used in this study. Hence, the production of eggs by *M. incognita* and *M. javanica* females could have taken place anytime between 16 to 20 DAI. To precisely record the life-cycle duration, shorter time intervals should be used.

Dávila-Negrón and Dickson (2013) reported an average 303 DD, at a constant temperature range of 24–35 °C, required for *M. incognita* and 334 DD for *M. javanica* to reach the egg-laying female in roots of okra (*Abelmoschus esculentus*). The DD reported for *M. incognita* by the latter authors was in a similar range to our results, with 292 DD for tomato and 314 DD for maize, but longer than the 264 DD for soybean. Likewise, results from our study showed that *M. javanica* had shorter DD for the three crops (276 for tomato, 248 for soybean and 298 for maize, respectively) than the 334 reported by Dávila-Negrón and Dickson (2013). These differences in DD can be ascribed to various factors, one being the RKN populations used in our study originating from different hosts (guava and potato *vs* tomato) and geographical regions (South Africa *vs* US) than those for the study of Dávila-Negrón and Dickson (2013). Also the different host crops used in the two studies could offer a partial explanation for the differences in required DD for the two RKN species since the anatomy and morphology of root tissues of the crops (maize, okra, soybean and tomato) differ substantially (Hochholdinger, 2009; Terekhova & Konstantinovich, 2021; Thomas et al., 2007) and may have had an influence on the penetration, feeding and resultant life-cycle development and -duration observed. Further, the 273 DD reported by Velloso et al. (2022) at the temperature range of 25–30 °C for *M. incognita* to develop to egg-laying females on tomato is in same range to our finding (295), however, our recorded DD for *M. enterolobii* (216) on tomato was substantially less than the recorded value (273) by these authors for this species.

In terms of life-stage development, data generated during our study differ from that of Marques et al. (2020) who recorded J2 of *M. enterolobii* in roots of *Capsicum baccatum* (susceptible genotype Cambuci) 7 DAI compared to 3 DAI as was found in our study. Velloso et al. (2022) recorded J2 of *M. enterolobii* 5 DAI in roots of tomato (cv. BHN 589). The study of Marques et al. (2020) furthermore showed that J3, J4 and egg laying females of *M. enterolobii* were recorded 14, 21 and 28 DAI, respectively, while our study revealed that J3 was present already from 5 DAI in all three crops (data not shown). Velloso et al. (2022) recorded J3 and J4 of *M. enterolobii* 7 and 11 DAI, respectively, in tomato roots. However, our study did show that J4 were present for *Meloidogyne enterolobii* at 5 DAI in tomato and 10 DAI for maize and soybean (data not shown). *Meloidogyne enterolobii* egg-laying females were recorded from 15 DAI in roots of all three crops, which was later than the 13 DAI reported by Velloso et al. (2022); this was pronouncedly earlier compared to 28 DAI for *M. enterolobii* in the roots of *C. baccatum* (Marques et al., 2020); 17 DAI and 21 DAI for USA populations of *M. incognita* and *M. javanica*, respectively, in okra roots (Dávila-Negrón & Dickson, 2013); and 21–24 DAI for non-egg producing females of an Indian population of *M. enterolobii* in guava roots (Ashokkumar et al., 2019). Although *M. enterolobii* had lower numbers of females 20 DAI for maize and tomato compared to *M. incognita and M. javanica*, this was accompanied by considerably higher numbers of a second generation of *M. enterolobii* J2 in the roots of maize 20 DAI compared to the other two species.

The fundamental knowledge generated in the current study on life stage development and life cycle duration of three RKN species is of both scientific and practical importance. The data suggest, for example, that during a 60-day period under environmental conditions like those existing in the glasshouse study (favorable for both the development and growth of the crop and development and reproduction of RKN species), *M. enterolobii* is likely to complete up to four. *Meloidogyne enterolobii* thus has the potential to proceed through more life cycles in a given time and reach higher population densities which is known to cause more damage to crops; this phenomenon is likely to result in higher yield losses as was reported for soybean infected with different population densities of *M. incognita* (Fourie et al., 2010).

To assist farmers and mitigate the adverse effect of RKN species, especially for *M. enterolobii*, the generation of applicable, fundamental research-based information is crucial. Since this species is one of the most damaging nematode pests of a wide range of crops, data obtained about its life-cycle duration, as well as that of the other two important RKN species, now provides scientists and crop producers with an additional tool to better understand its damage potential and most importantly that damage to crops can be minimized by using short-growing genotypes.

Author contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Raymond Lesley Collett and Hendrika Fourie. The first draft of the manuscript was written by Milad Rashidifard, Raymond Lesley Collett and Hendrika Fourie. All authors reviewed and approved the final manuscript.

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Declarations

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

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