



Efficacy of pre- and post-infectional nematode-resistant crops in managing root-knot (*Meloidogyne* species) nematodes in potatoes under field conditions

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Abstract

Potato (*Solanum tuberosum* L.) does not have genotypes with resistance to root-knot (*Meloidogyne* species) nematodes. Thus, its sustainable production depends on intermittent inclusion of root-knot nematode-resistant crops in sequential cropping systems. The objective of this study was to investigate the efficacy of pre- and post-infectional nematode-resistant crops on managing population densities of *Meloidogyne* species in potato-based cropping sequences. Cropping sequences under field conditions comprised sweet stem sorghum (*Sorghum bicolor* L.) cv. 'Ndendane-X1', wild cucumber (*Cucumis africanus* L.F), potato cv. 'Mondial G3' and potato 'Mondial G3'-velum (control), which were randomly assigned to 2 m × 2 m sub-plots in Sequence 1. The treatments were laid out in a randomised complete block design, replicated six times at two different locations. Sole potato cultivation was done in Sequence 2. In Sequences 3 and 4, crop arrangement was as in Sequences 1 and 2, respectively. At 56 days after potato emergence, nematodes were sampled and extracted from roots and soil. Results from both locations showed an increase in final soil nematode population density in sorghum-potato (23% and 47%) and a decrease in *C. africanus*-potato (22% and 32%) cropping system. As such, post-infectional nematode resistance in the sequence *C. africanus*-potato was more effective in managing population densities of the test nematode species in the soil at both locations than the sorghum-potato sequence with pre-infectional resistance or the monoculture cropping.

Keywords Management · *Meloidogyne* species · Resistance mechanisms

Introduction

Globally, approximately 100 root-knot (*Meloidogyne* species) nematodes (RKN) have been identified (Elling 2013) on over 3000 host plants (Perry and Moens 2011; Belle et al. 2019). At least 22% identified *Meloidogyne* species occur in Africa in different vegetable and field crops (Karuri et al. 2017; Belle et al. 2019). In crops such as potato (*Solanum tuberosum* L.), where all genotypes are susceptible to *Meloidogyne* species (Silva et al. 2013; Fourie et al. 2017; Macharia et al. 2019), marketable tuber yield can decline by 50%, with incidents of complete crop failure in severely infested fields (Lima et al. 2018). Moreover, the predicted

increase in soil temperature due to climate change makes management of *Meloidogyne* species very difficult. The latter is because as temperature increases nematode ontogenies become shorter (Van der Waals et al. 2013), as observed on *M. enterolobii* Yang and Eisenback (1983) with a life cycle of 15 days (Collet 2020).

Previously, synthetic chemical nematicides were widely used to manage soil nematode population densities (SNPD) but have since 2005 been withdrawn from the agrochemical markets due to environmental concerns (Silva et al. 2013; Mashela and Pofu 2016; Fourie et al. 2017). The withdrawal increased research focus on developing alternative and environment-friendly nematode management strategies. Therefore, the inclusion of nematode-resistant crops in potato-based cropping sequences could serve as an environment-friendly strategy for managing population densities of RKN to below economic damage threshold levels (Mashela and Pofu 2016).

Generally, plants can possess two mechanisms of nematode resistance, namely pre- and post-infectional nematode

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resistance (Huang 1985; Shigueoka et al. 2019). In pre-infectious nematode resistance, the second-stage juveniles (J2) are prohibited from penetrating the root system of the resistant plant because of either (a) heavily suberized and lignified root structures (Underwood 2012; Mashela et al. 2017), (b) copious concentration of allelochemicals that are exuded within the rhizosphere which either kill, repel or reduce mobility of nematodes (Sikder and Vestergard 2019) or (c) failure of the non-host plant to produce attractive chemical cues required for J2 penetration to occur (Sikder and Vestergard 2019). In some cases, various early developmental stages (egg or J1) eventually enter cryptobiosis due to adverse conditions of allelochemicals (McSorley 2003; Mashela and Pofu 2016). Under such conditions, when a suitable host is introduced, the affected stages exit cryptobiosis and serve as a reservoir for crop infection. For example, sweet stem sorghum (*Sorghum bicolor* (L.) Moench) exhibits pre-infectious nematode-resistance mechanism against RKN by producing nematocidal root exudates collectively referred to as allelochemicals (Czarnota et al. 2003). However, its inclusion in nematode management cropping systems involving potato production has not been well documented despite its great adaptability to temperate, tropical and subtropical climates (Mangena et al. 2018).

In contrast, post-infectious nematode-resistance mechanism is triggered when J2 penetrate the root system (Bent 1996). Upon penetration, the resistant plant produces the plant genes that are incompatible to J2 gene products produced by either the ventral or dorsal glands of nematodes (Mashela et al. 2017). The interaction of plant genes and gene products can either promote or demote the establishment of the host status (Huang 1985; Mashela et al. 2017). *Cucumis africanus* (L.F.) is a post-infectious RKN resistant plant that is indigenous to South Africa (Ramatsitsi 2018). This plant inhibits the establishment of the feeding site and traps J2 within the root system until they die of starvation (Ramatsitsi 2018). Previous studies also showed that *C. africanus* produces cucurbitacin B ($C_{32}H_{46}O_8$), a carbon-rich tetracyclic triterpenoid with nematocidal properties (Pelinganga 2013). However, the inclusion of *C. africanus* plants in nematode management cropping systems has not been well documented.

In most studies related to the use of non-host plants in managing nematode population densities, the mechanism of nematode resistance is hardly mentioned. Similarly, the efficacy of the two known nematode-resistant mechanisms has hardly been compared. However, it had been shown that results of crops such as sorghum were highly inconsistent in nematode suppression (Dover et al. 2004). Ideally, a good nematode management strategy should reduce the carry-over nematode population density, as shown by consistent results in nematode suppression. Therefore, the objective of this study was to determine whether (1) potato monoculture

sequences, (2) sequencing potato with a post-infectious nematode-resistant *C. africanus* crop and (3) sequencing potato with a pre-infectious nematode-resistant sweet stem sorghum crop would have any effects on soil population densities of *Meloidogyne* species.

Materials and methods

Study area

Two field studies were conducted simultaneously from August 2017 to May 2019 at the University of Limpopo (UL), South Africa (23° 53'10"S, 29° 44'15"E), and the Agricultural Research Council Vegetable, Industrial and Medicinal Plants (ARC-VIMP), Roodeplaat, South Africa (25° 61'44"S, 28° 35'45"E). The soil at UL is predominantly Hutton sandy loam (65% sand, 16% clay, 19% silt), whereas ARC-VIMP soil is sandy loam (8% clay, 60% sand, 32% silt). The differences in soil texture and composition influence moisture retention, aeration, and the movement of nematodes within the soil profile (Elling 2013; Perry and Moens 2011). The fields at UL and ARC-VIMP were prior to the study under tomato (*Solanum lycopersicum* L.) and Swiss chard (*Beta vulgaris* subsp. *Vulgaris*) production, respectively. Both locations were historically infested with mixed populations of *M. incognita* Kofoid and White (1919) and *M. javanica* Treub (1885) nematodes. Prior to establishing the experiment, the fields were sampled for the initial nematode population densities (P_i) by randomly collecting 10 soil samples from each field and extracted from 250 ml soil using sugar centrifugal flotation method (Marais et al. 2017). Prior to the experiment, initial nematode population densities (P_i) at UL were 943 J2 per 250 ml of soil, whereas at ARC-VIMP, P_i was 578 J2 per 250 ml of soil. The higher initial population at UL could be attributed to differences in soil structure, which may have facilitated nematode movement and reproduction (Macharia et al. 2019).

Experimental design

In each location, the study area was divided into six major blocks, measuring 11 m × 2 m. Each block was sub-divided into four 2 m × 2 m sub-plots, separated by a 1 m pathway. In Sequence 1, the treatment crops, namely potato (cv. 'Mondial G3'), *C. africanus*, potato (Velum) and sweet stem sorghum cv. 'Ndendane-X1' were planted in sub-plots arranged in a randomised complete block design, replicated six times. In Sequence 2, the successor crop (potato) was cultivated on all sub-plots. The treatment randomisation established in Sequence 1 was maintained in Sequence 3. In Sequence 4, the main potato crop was sown on all

plots as in Sequence 2. Overall, four cropping sequences, namely (i) potato monoculture, (ii) sorghum-potato (iii) *C. africanus*-potato and (iv) potato (Velum)- potato (control) were assessed. Sequences 1 and 3 were established in spring (2017 and 2018) whereas Sequences 2 and 4 were established in autumn (2018 and 2019). The recommended commercial farming methods and cultural practices for each crop were carefully followed (DAFF 2010a, 2010b; Pofu 2012). However, the intra-row and inter-row spacing were standardised to 0.3 and 0.5 m, respectively.

Data collection

At 56 days after emergency, roots from each sub-plot were collected and combined to provide a composite sample of approximately 10 g fresh root for extraction of eggs and J2 using the blending and sieving method, followed by the sugar centrifugal flotation method (Marais et al. 2017). The reproductive potential (RP) of nematodes was calculated as $RP = J2 + \text{eggs/g fresh roots}$.

Soil samples were collected from the rhizosphere (25 cm deep) of every plant in each sub-plot and composited. The composite sample was mixed using a 120 L concrete mixer (Turner Morris, Pretoria, South Africa). Thereafter, a 250 ml soil subsample was used for nematode extraction using the sugar centrifugal flotation method (Marais et al. 2017). Nematodes from roots (eggs + J2) and soil were identified and quantified using a Leica Zoom 2000 stereomicroscope at $\times 45$ magnification.

Data analysis

The Shapiro–Wilk test was performed to determine the normality of distribution of the data (Shapiro and Wilk 1965). Since data were not normally distributed, data were subjected to nonparametric Friedman test using the XLSTAT 2019 software. The treatment means were compared at the probability level of 5% using the Nemenyi test (Nemenyi 1963; Pohlert 2014). Data from each location were analysed separately.

Results

Reproductive potential

At UL location, RP values of *Meloidogyne* species were significantly higher in potato, but lower in *C. africanus* and potato (Velum) in Sequence 1 (Table 1). However, RP values in sorghum were not significantly different from either the highest or lowest RP values (Table 1). In Sequence 2,

Table 1 Reproductive potential [J2+eggs/g(root)] of *Meloidogyne* species in four cropping sequences at the University of Limpopo, during spring (Sequence 1 and 3) and autumn (Sequence 2 and 4)

Cropping sequence	Sequence 1	Sequence 2	Sequence 3	Sequence 4
P–P	592 ^a ± 52	6028 ^a ± 192	3662 ^a ± 226	10463 ^a ± 1321
S–P	343 ^{ab} ± 15	5692 ^a ± 328	77 ^c ± 5	8975 ^{ab} ± 1422
C–P	210 ^b ± 21	3931 ^a ± 261	466 ^{bc} ± 28	5746 ^b ± 1008
PV–P	181 ^b ± 3	3739 ^a ± 220	1433 ^{ab} ± 117	5287 ^b ± 429

The four cropping systems were potato monoculture (P–P), sweet stem sorghum-potato (S–P), *Cucumis africanus*-potato (C–P) and potato (Velum)-potato (PV–P) control. ^xMeans ± standard errors sharing the same letter within a sequence (column) were not significantly different at $p \leq 0.05$ level of significance according to the Friedman's rank test followed by the Nemenyi's post hoc test. Nonparametric test was used because data were not normally distributed according to Shapiro–Wilk test

Table 2 Reproductive potential [J2+eggs/g(root)] of *Meloidogyne* species in four cropping sequences at the Agricultural Research Council-Vegetable and Ornamental Plants, during spring (Sequences 1 and 3) and autumn (Sequences 2 and 4)

Cropping sequence	Sequence 1	Sequence 2	Sequence 3	Sequence 4
P–P	1411 ^a ± 67	5646 ^a ± 166	767 ^a ± 31	9796 ^a ± 962
S–P	715 ^{ab} ± 12	4768 ^a ± 222	30 ^c ± 9	5147 ^{ab} ± 1272
C–P	2624 ^a ± 165	4171 ^a ± 182	291 ^{ab} ± 27	3027 ^b ± 522
PV–P	333 ^b ± 44	3978 ^a ± 153	149 ^{bc} ± 12	2221 ^b ± 365

The four cropping systems were potato monoculture (P–P), sweet stem sorghum-potato (S–P), *Cucumis africanus*-potato (C–P) and potato (Velum)-potato (PV–P) control. ^x Means ± standard errors sharing the same letter within a sequence (column) were not significantly different at $p \leq 0.05$ level of significance according to the Friedman's rank test followed by the Nemenyi's post hoc test. Nonparametric test was used because data were not normally distributed according to Shapiro–Wilk test

RP values in all investigated cropping sequences were not significantly different (Table 1).

In Sequence 3, sorghum and *C. africanus* had the lowest RP values, whereas potato monoculture had significantly the highest RP values. However, RP values in potato (Velum) were not significantly different from those in *C. africanus* or potato monoculture (Table 1). In Sequence 4, RP values trends were like those observed in Sequence 1.

At ARC-VIMP, *C. africanus* and potato had significantly higher RP values, whereas potato (Velum) had lower RP values in Sequence 1 (Table 2). In Sequence 1, RP values of sorghum were not significantly different from either the highest or the lowest values. In Sequence 2, RP values in all cropping sequences were not significantly different (Table 2). However, in Sequence 3 potato monoculture and sorghum had significantly higher and lower RP values,

respectively. Sorghum RP values did not significantly differ from potato (Velum), but the latter did not significantly differ from RP values on *C. africanus*.

In Sequence 4, RP values on the successor potato crop were significantly higher in potato monoculture, but lower in *C. africanus* and potato (Velum) cropping systems. However, RP values of potato in sorghum-potato were not significantly different from the lowest RP value on potato (Velum) (Table 2).

Soil nematode population densities

Soil nematode population densities of *Meloidogyne* species in potato monoculture and sorghum-potato plots were significantly higher than on potato (Velum)-potato plots in Sequence 1 at UL location (Table 3).

However, SNPD in *C. africanus*-potato plots were not significantly different from either the highest or the lowest recorded value. Potato monoculture maintained a significantly higher SNPD compared to those in *C. africanus*-potato and potato (Velum)-potato plots, whereas that in sorghum-potato plots were not significantly different from the highest or the lowest SNPD in Sequence 2, 3 and 4 (Table 3).

At ARC-VIMP, SNPD in potato monoculture and sorghum-potato plots were significantly higher than in potato (Velum)-potato in Sequence 1 (Table 4). However, SNPD on *C. africanus*-potato plots were not significantly different from the highest or the lowest values. In Sequence 2, the SNPD in all plots were not significantly different (Table 4).

In Sequence 3, sorghum-potato had the lowest SNPD which did not differ from that on *C. africanus*-potato and potato (Velum)-potato plots. Potato monoculture plots recorded significantly high SNPD (Table 4). In Sequence 4, SNPD trend was like that observed in Sequence 1.

Table 3 Nematode population densities per 250 ml of soil collected four cropping sequences at the University of Limpopo, during spring (Sequence 1 and 3) and autumn (Sequence 2 and 4)

Cropping sequence	Sequence 1	Sequence 2	Sequence 3	Sequence 4
P–P	310 ^a ± 61	290 ^a ± 25	196 ^a ± 24	2646 ^a ± 186
S–P	370 ^a ± 112	183 ^{ab} ± 20	80 ^{ab} ± 10	1390 ^{ab} ± 94
C–P	175 ^{ab} ± 32	176 ^{ab} ± 21	20 ^b ± 4	550 ^b ± 61
PV–P	120 ^b ± 44	106 ^b ± 21	60 ^{ab} ± 10	643 ^b ± 61

The four cropping systems were potato monoculture (P–P), sweet stem sorghum-potato (S–P), *Cucumis africanus*-potato (C–P) and potato (Velum)-potato (PV–P) control. ^aMeans ± standard errors sharing the same letter within a sequence (column) were not significantly different at $p \leq 0.05$ level of significance according to the Friedman's rank test followed by the Nemenyi's post hoc test. Nonparametric test was used because data were not normally distributed according to Shapiro–Wilk test

Table 4 Nematode population densities per 250 ml of soil collected from four cropping sequences at the Agricultural Research Council-Vegetable and Ornamental Plants, during spring (Sequence 1 and 3) and autumn (Sequence 2 and 4)

Cropping sequence	Sequence 1	Sequence 2	Sequence 3	Sequence 4
P–P	826 ^a ± 277	300 ^a ± 22	66 ^a ± 3	910 ^a ± 54
S–P	696 ^a ± 246	226 ^a ± 21	20 ^b ± 2	713 ^a ± 69
C–P	383 ^{ab} ± 30	240 ^a ± 11	30 ^{ab} ± 4	450 ^{ab} ± 21
PV–P	156 ^b ± 32	183 ^a ± 27	23 ^b ± 3	173 ^b ± 32

The four cropping systems were potato monoculture (P–P), sweet stem sorghum-potato (S–P), *Cucumis africanus*-potato (C–P) and potato (Velum)-potato (PV–P) control. ^aMeans ± standard errors sharing the same letter within a sequence (column) were not significantly different at $p \leq 0.05$ level of significance according to the Friedman's rank test followed by the Nemenyi's post hoc test. Nonparametric test was used because data were not normally distributed according to Shapiro–Wilk test

Discussion

Reproductive potential

The initial application of treatment crops at UL resulted in significantly higher *Meloidogyne* species RP values in potato monoculture and sorghum than in *C. africanus* and potato (Velum). Although Velum is a fungicide, it has been reported as an effective nematicide against RKN in potato fields (Korayem et al. 2012). The post-infectious nematode-resistant *C. africanus* plants (Ramatsitsi 2018) and potato (Velum) control treatment resulted in similar RP values. Similarly, other researchers reported low RP value on *C. africanus* plants (Pofu et al. 2010, 2012; Liu et al. 2015).

Post-infectious nematode-resistance mechanism exhibited in *C. africanus* plant is mainly associated with the hypersensitive response, which is clearly explained by the gene-for-gene model (Bent 1996; Mashela et al. 2017). Generally, in active hypersensitive resistance, J2 are trapped and starved to death during movement from the penetration to the feeding sites before reaching maturity and reproducing (Huang 1985). A previous study demonstrated how *C. africanus* plants inhibited the establishment of the feeding sites causing necrotic spots to form (Ramatsitsi 2018).

In contrast, *C. africanus* and potato monoculture had significantly high RP values compared to potato (Velum) and sorghum at ARC-VIMP, in Sequence 1. Thus, RKN were able to successfully infest and reproduce within the root system of *C. africanus* plants, which contradicted observations made at UL. The failure to display post-infectious nematode-resistant can be attributed to delayed hypersensitive response as observed on other post-infectious resistant crops (Das et al. 2008; Silva et al. 2013). The factors responsible for triggering delayed hypersensitive response are not fully

understood (Mashela et al. 2017), but have interactions with a wide range of abiotic and biotic stress factors such as pest, salinity, and heat stress (Mashela and Nthangeni 2002; Pofu et al. 2011; Silva et al. 2013; de Carvalho et al. 2015; Maleka 2021). Generally, in cases where the response is delayed, the defence mechanism becomes weak and vice versa (Mashela et al. 2017). However, in the current study, *C. africanus* plants were not exposed to any known abiotic or biotic stress factors, suggesting that the causes for delayed hypersensitive response could be purely chemical. The latter requires the plant to release the plant genes, with nematodes releasing the gene products, with both chemicals moving from high concentration to low concentration prior to meeting to produce a delayed response.

At both locations, *Meloidogyne* species RP on sorghum sequence was intermediate in Sequence 1. Thus, the root exudates produced by the pre-infectional nematode-resistant sorghum cultivar partially repelled or killed the target nematodes, with some of the nematodes managing to penetrate and reproducing within the root system. Similar observations were reported under field conditions when pre-infectional nematode-resistant crops were cultivated in different cropping systems (McSorley and Gallaher 1993; Djian-Caporalino et al. 2019).

In Sequence 2, *Meloidogyne* species managed to reproduce similarly on all cropping sequences when the successor potato crop was sown at both locations. Therefore, the successor crop had stimulatory effect on RP of the test nematode and subsequently nullified the treatment effect of the preceding crop. Similar findings were reported when different crops exhibiting different mechanisms of resistance were used to manage root-lesion (*Pratylenchus penetrans* Cobb 1917) nematodes in potato fields (Belair et al. 2006) and reniform (*Rotylenchulus reniformis* Linford and Oliveira 1940) nematodes in cotton (*Gossypium hirsutum* L.) fields (Stetina et al. 2007). Additionally, these results corroborate with those in other studies, which showed that short cropping sequences were at times not effective in managing population densities of plant nematodes under field conditions where multiple nematode species naturally occur (Miller et al. 2006; Westphal 2011).

The second application of treatment crops in Sequence 3 at both locations resulted in significantly higher and lower RP values on potato monoculture and sorghum-potato cropping systems, respectively. High RP value on nematode susceptible potato monoculture was expected, and similar observations were reported when susceptible wheat (*Triticum aestivum* L.) (Williamson et al. 2013) and cotton (Davis et al. 2003) cultivars were monocultured. The low RP of the test nematode observed on sorghum in the sorghum-potato sequence authenticates the non-host status of sorghum as reported in another study (Mashela and Pofu 2016). The low RP observed could be attributed

to sorgoleone ($C_{22}H_{29}O_4$), a root exudate released by most sorghum varieties with nematicidal properties (Czarnota et al. 2003; Sikora et al. 2005; Weston et al. 2013; Tibugari et al. 2019). Sorgoleone can either kill or repel RKN prior to penetration in the root system of sorghum. In one study, sorgoleone reduced mobility and increased mortality of *M. javanica* J2, which subsequently reduced RP values on sorghum (Campos et al. 2006).

Remarkably, RP of the test nematode on sorghum in the sorghum-potato sequence outperformed the potato (Velum) control. Similarly, cotton-aldicarb exhibited high RP values of the reniform nematode when compared to the inclusion of resistant soybean (*Glycine max* L.) and maize (*Zea mays* L.) varieties in the cotton-based cropping sequence (Davis et al. 2003). The inefficacy of synthetic chemical nematicides depends on several edaphic factors, chemical application method or rate, degradation of the chemicals by soil micro-organism, leaching beyond the root-zone and rate of volatilisation (Giannakou et al. 2005). However, *C. africanus* plants were just as effective as potato (Velum) in not supporting the test nematode population.

In Sequence 4, RP of *Meloidogyne* species on the successor potato crop was significantly higher in potato monoculture and sorghum-potato than in the *C. africanus*-potato and potato (Velum)-potato cropping sequence at both locations. The low RP on *C. africanus*-potato sequence, suggest that the successor potato crop might have been exposed to low infection levels. In contrast, high RP in the sorghum-potato sequence suggested that sorghum plants were self-protecting and less effective in reducing the carry-over nematode population densities. The observation corresponded with findings previously reported when sorghum-potato sequences were used to manage population densities of the test nematode (Mashela and Pofu 2016).

Soil nematode population densities

At both locations, *C. africanus* plants were more effective than sorghum and potato monoculture in reducing SNPD in Sequence 1. According to Huang (1985), J2 that penetrate the root system of post-infectional nematode-resistant plants become trapped and die of starvation after failing to establish feeding sites. Similarly, post-infectional nematode-resistant pepper (*Capsicum annuum* L.) crop reduced the RKN carry-over population densities by 10% (Navarrete et al. 2016). Kimpinski et al. (2000) and Wang et al. (2007) demonstrated that the inclusion of a post-infectional nematode-resistant marigold (*Tagetes* species) cultivar in potato-based cropping system significantly reduced SNPD by 14%, probably due to its trapping ability.

The ineffectiveness of sorghum in comparison with *C. africanus* in managing SNPD to can be attributed to the fact that the nematicidal root exudate, sorgoleone that is

released into the rhizosphere could cause the various stages of nematodes to enter survival stages (McSorley 2003; Perry and Moens 2011). In such cases, the pre-infectious nematode-resistant crop is protected from nematode damage since the root exudates renders the plant-parasitic nematodes inactive. However, once the environmental conditions become favourable and a susceptible crop such as potato is cultivated, the J1 dauers in eggs develop through moulting into J2, which hatch, causing the nematode populations to resurge prodigiously in successor crops (McSorley 2003).

Furthermore, sorgoleone usually persists in the soil for seven weeks or less before it is mineralised by soil micro-organisms (Weston and Czarnota 2001; Dayan et al. 2010). Thus, the effects of the sorghum crop in crop rotation can quickly diminish before the main crop is sown. The latter explains why high nematode resurgence was observed on potato following sorghum crop. Therefore, to improve the effectiveness of sorghum in managing RKN in cropping sequences the successor crop should be sown within the 7-week period after harvesting the non-host sorghum crop (Hooks et al. 2010).

In Sequence 2, *C. africanus*-potato and sorghum-potato had similar effects on SNPD when potato was sown at UL whereas all investigated treatment crops showed similar effects on SNPD when potato was sown at ARC-VIMP. The latter observation showed that the successor crop nullified the treatment effects of the preceding crop and promoted similar RKN stimulatory effect. The nullification of treatment effects was also reported on potato and cotton fields infested by root-lesion and reniform nematodes, respectively (Belair et al. 2006; Stetina et al. 2007). The observation suggested that a significant change in SNPD was not easily noticed upon initial introduction of the non- or poor-host crop in different cropping sequences (Brodie 1996; Reddy 2017; Lima et al. 2018). According to Davis et al. (2003), such observations normally occur where a mixture of plant-parasitic nematodes affect the treatment crop e.g. under field conditions.

In Sequence 3, the second cultivation of *C. africanus* was more effective in managing RKN than the cultivation of other treatment crops at UL. In contrast, sorghum was more effective in managing RKN than the cultivation of other treatment crops at ARC-VIMP. Similarly, SNPD was reduced by 21% after harvesting the non-host sorghum cultivar in okra (*Abelmoschus esculentus* L.)-based cropping systems (Mweke et al. 2008). The suppressive effect of sorghum can be attributed to delayed nematode egg hatch caused by the root exudates released in the rhizosphere which might have promoted entry of dauer survival phase (McSorley 2003).

Generally, the highest SNPD were observed on potato monoculture plots in all sequences at both locations. However, in some studies, significantly high SNPD under potato monoculture were only reported after at least two

years of monoculture (Crow et al. 2000; Eberlein et al. 2016). Such differences could be due to the differences in initial nematode population densities, the susceptibility of the cultivar to the test nematode, timing in sowing after harvesting the non-host or many other environmental factors that affect the host $\times$ nematode interaction.

In Sequence 4, SNPD trend was like that observed in Sequence 1 at both locations. Based on the results, *C. africanus*-potato cropping sequence was as effective as the potato (Velum)-potato control in reducing the carry-over nematode population densities. In contrast, the pre-infectious nematode-resistant sorghum crop protected it 'self against nematode damage but not the subsequent potato crops. The ineffectiveness of sorghum was attributed to the fact that, sorgoleone might have either (a) quickly mineralised into non-toxic substances upon removal of the non-host crop or (b) that the plant-parasitic nematodes entered chemobiosis when sorgoleone was released within the rhizosphere or (c) the quantity and quality of the root exudate might not have been adequate to effectively control the targeted RKN due to unidentified factors (Weston and Czarnota 2001; McSorley 2003; Dayan et al. 2010).

This study showed that the inclusion of post-infectious nematode-resistant crops such as *C. africanus* in potato production was a good option for managing RKN damage under field conditions. Although post-infectious nematode-resistance mechanism was more effective than pre-infectious nematode-resistance mechanism in managing RKN in potato-based cropping system, integrated nematode management strategies are always highly recommended for the effective control of the targeted plant-parasitic nematode pest.

Limitations of the study

Efficacy of using pre- and/or post-infection nematode-resistant crops in managing nematode population density of the test species depends much on edaphic and climatic factors prevailing in the area. This is due to the complex interaction between plant-parasitic nematodes and the environment. For example, soil properties such as texture, pH, salinity, organic matter content, nutrient availability, microbial diversity including others (Al-Ghamdi 2021; do Rêgo Barros et al. 2023) could influence the suitability of soils of the two studied locations (UL and ARC-VIMP) as habitats for *Meloidogyne* species in potato-based cropping systems. On the other hand, climatic conditions such as the heat stress and drought can significantly reduce nematode population density by affecting nematode survival (Khanal and Land 2023) and mobility (Bristol et al. 2023), respectively. As such, rigorous testing should be conducted in different environments before adoption of a cropping

system. However, the successful management of plant-parasitic nematodes requires an integrated approach.

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Data availability Data used in this project are available, upon reasonable request from the corresponding author.

Declarations

Conflict of interest The authors have no competing interests to declare.

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