Plant Soil
https://doi.org/10.1007/s11104-023-06194-1

RESEARCH ARTICLE

Attractive response of *Meloidogyne javanica* varies among non-host plants, while all of them reduce the nematode population when intercropped with host plants

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Received: 30 November 2022 / Accepted: 26 July 2023

Abstract
Background and aims Intercropping non-host plants is usually a feasible practice to reduce root-knot nematodes (RKN) in agricultural soils. Here, the chemotaxis of non-host roots for *Meloidogyne javanica*, its development in the roots and the possibility to intercrop non-host plants with tomato or lettuce to control RKN were estimated.
Methods Garlic (*Allium sativum*), Madagascar periwinkle (*Catharanthus roseus*) and yarrow (*Achillea millefolium*) were used as intercrops. Marigold (*Tagetes patula*) and tomato were used as positive and negative controls, respectively. Root attractiveness was evaluated for RKN by growing seedlings or using extracted exudates of each plant root on Petri dishes. The effects of lettuce or tomato intercropped with non-host plants on *M. javanica* were investigated by growing two plants side by side in a pot and later estimating the RKN egg formation.
Results There was high attraction of second-stage juvenile (J2) by tomato and marigold roots, whereas J2 penetration was higher in roots of tomato than Madagascar periwinkle and marigold. The most attractive exudates were secreted from tomato and marigold followed by lettuce and Madagascar periwinkle. Most J2 in Madagascar periwinkle and marigold roots did not develop to adults. The number of eggs was reduced by intercropping tomato or lettuce with any of the tested non-hosts. The shoot growth of both crops improved when intercropped with Madagascar periwinkle, yarrow, or garlic.
Conclusion Madagascar periwinkle, yarrow and garlic are novel model system plants to be used in the management of *M. javanica*, reducing RKN population and improving tomato and lettuce growth when intercropped.

Keywords Root-knot nematode · Antagonistic plants · Chemotaxis · Management · Root exudates · Tomato · Lettuce

Responsible Editor: Hans Lambers.

Supplementary information The online version contains supplementary material available at https://doi.org/10.1007/s11104-023-06194-1.

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Published online: 03 August 2023

Introduction

Root-knot nematodes (RKN) of the genus *Meloidogyne* are microscopic organisms that highly damage major crops over the world (Singh et al. 2015; Ralmi et al. 2016). The species *M. javanica* infects a wide range of crops, such as tomato (*Solanum lycopersicum* L.) and lettuce (*Lactuca sativa* L.) (Sikora and Fernandez 2005). The control of RKN using chemical nematicides is costly, which constantly demand other practices to reduce their population, as the use of resistant cultivars, biological control, crop rotation and intercropping with non-host or antagonistic plants (Collange et al. 2011; Sivasubramaniam et al. 2020; Mendoza-De Gives 2022).

The intercropping system aiming to control RKN is based on cropping non-host plants side by side with RKN hosts, requiring non-hosts with longer cycles than the hosts to efficiently reduce the pathogen population (Rodríguez-kábana and Canullo 1992; Torto et al. 2018b; Homulle et al. 2022). Different crops in the system would lead to novel plant-enemy interactions and consequently affect pathogenic invasions by changing the chemistry involved in the interaction (Verhoeven et al. 2009). The infective stage of RKN, the second-stage juveniles (J2), is equipped with sensorial organs that rapidly respond to root exudates and can promptly migrate and penetrate the host roots. In this scenario, root exudation is the first and the major player to mediate the host-attraction-repellence process for RKNs, which will determine the success or failure of increasing the population (Wilschut et al. 2017; Murungi et al. 2018).

The complexity of compounds from non-host plants may have nematicidal activity (Desmedt et al. 2020; Silva et al. 2020) or interfere with nematode migration (Ali et al. 2011; Filgueiras et al. 2016; Torto et al. 2018a). One of such crops is garlic (*Allium sativum*) which has nematicidal compounds effective against *M. incognita* in its essential oil or extracts (Jardim et al. 2020; Eder et al. 2021; Kouamé 2021). Similarly, marigold (*Tagetes* spp.) also produces nematicidal compounds (Xie et al. 2016; Long et al. 2019). On the other hand, Madagascar periwinkle (*Catharanthus roseus*) and yarrow (*Achillea millefolium*) are non-host plants for *Meloidogyne* spp. (Maciel and Ferraz 1996; de Mendonça et al. 2017),). Therefore, those plants can be extensively used in crop rotation or intercropping systems to manage RKN.

Actually, the intercropping affects the susceptible host infestation by RKN, due to the lower level of attraction or host suitability (Marques et al. 2012). The non-host may act against the RKN producing toxic compounds, repelling the second-stage J2 or even attracting the J2 and somehow stopping its development (Anwar and Mckenry 2000; Wang et al. 2018). Additionally, the intercrops could directly affect the growth of the neighboring crops (Zhou et al. 2011; Tringovska et al. 2015).

Understanding the interactions of intercropped non-hosts with the RKN and its hosts is crucial to recommend a correct intercropping system in infested areas. Based on that information, this study aimed to evaluate the *M. javanica* attraction by non-host roots and the J2's ability to penetrate and complete its life cycle. Subsequently, the RKN population behavior was investigated in intercropped systems of lettuce or tomato with the non-host plants by pot experiments.

Materials and methods

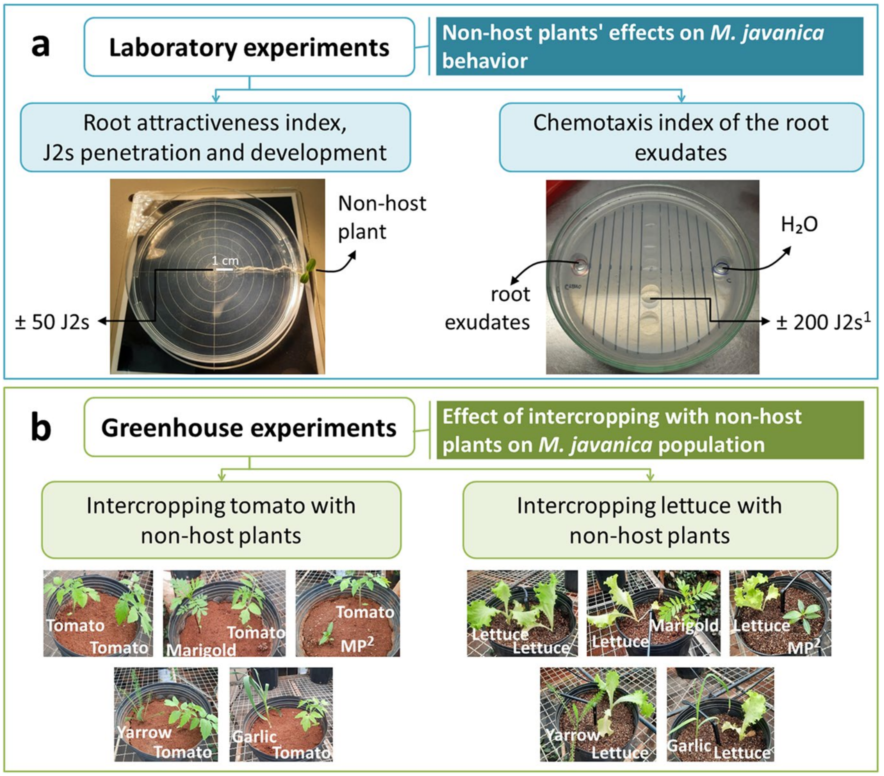
Laboratory and greenhouse experiments were conducted to evaluate effects of non-host plants on *M. javanica* directly and the intercropping of tomato and lettuce with the selected non-host plants in the management of *M. javanica* (Fig. 1).

Obtaining *Meloidogyne javanica* population

The RKN *M. javanica* (Treub) Chitwood was selected due to its large number of host plants and worldwide distribution (Sikora and Fernandez 2005; Pinheiro et al. 2014). All the *M. javanica* used in the experiments were obtained from a pure population established in tomato plants (*Solanum lycopersicum* L. cultivar 'Santa Clara') kept in a greenhouse at the Federal University of Lavras (UFLA), Brazil and identifieid by perineal morphology and esterase patterns (Carneiro et al. 2005).

Eggs were extracted by cutting roots into small pieces and stirring in a blender with 0.5% sodium hypochlorite (NaOCl) for 40 s. The grind root suspension was passed through a 0.075 mm (200 mesh) sieve coupled to a 0.025 mm opening (500 mesh), in which the eggs were collected and rinsed under

Fig. 1 Scheme of Laboratory (**a**) and greenhouse (**b**) experiments to evaluate the non-host plants' effects on *M. javanica* behavior confronting root exudates and non-host roots directly. [1] s-stage juveniles. [2]Madagascar periwinkle. Laboratory experiments were adapted from Dong et al. (2014), Wilschut et al. (2017) and Wang et al. (2019)



running water (Hussey and Barker 1973). To obtain second-stage juveniles (J2), the eggs were placed in hatching chambers by Baermann funnels, and only freshly collected J2 was used in the experiments.

Choice and acquisition of non-host plants

The non-host plants were selected based on studies regarding the potential species for nematode control. Garlic (*Allium sativum* L.) was selected due to the presence of nematicidal compounds effective against *Meloidogyne* spp. in its essential oil or extracts (Jardim et al. 2020; Eder et al. 2021; Kouamé 2021). Madagascar periwinkle (*Catharanthus roseus* (L.) G. Don.) was selected since it is a non-host plant to *Meloidogyne* spp., affecting nematode reproduction despite being a host plant (de Mendonça et al. 2017), suggesting the *Meloidogyne* attraction to the roots. Yarrow (*Achillea millefolium* L.) was selected because of its nature as a non-host to *M. javanica* (Maciel and Ferraz 1996). Marigold (*Tagetes patula* L.) was chosen as the positive control because it is widely used in the management of RKN by producing nematicidal compounds in its root exudation (Salem and Osman 1988; Verma 2006; Xie et al. 2016; Wang et al. 2018).

Marigold and Madagascar periwinkle were obtained from commercial seeds. Garlic and yarrow were obtained through vegetative propagation. The garlic bulbs were obtained from the horticulture branch of the Crop Science Department of UFLA, and the yarrow seedlings were grown in the Medicinal Plants Garden of UFLA.

Laboratory experiments

Roots attractiveness index, penetration and development of Meloidogyne javanica

The experiment was performed according to Dong et al. (2014) and Wilschut et al. (2017) with minor adaptations. Garlic bulbs and seeds of susceptible tomato cultivar 'Santa Clara', Madagascar periwinkle and marigold were disinfected for one minute in a water solution of 70% ethanol and 10 min in a water solution of 0.75% hypochlorite, followed by triple washing in distilled water. Then, they were planted in autoclaved vermiculite. Ten days after germination, the roots were washed in distilled water and placed on the surface of sterile agar–water medium (0.5%, 5 g L^{-1}) in Petri dishes (9 cm), leaving the shoots standing outside. The dishes were kept in a growth chamber at 25 °C with a 12-hour photoperiod. After five days, approximately 50 J2 of *M. javanica* were applied on the surface of the medium 1 cm away from the roots (Fig. 1a), and the dishes were kept at room temperature in the dark. After 4 h, the number of J2s inside the 0.5 cm area around the roots was quantified using a stereoscopic microscope. The number of nematodes inside the 0.5 cm area around the roots divided by the total number of J2s per dish was used as an attractiveness index; values ranged between 0 and 1, and the more attractive the root was, the closer the index value was to 1. Each plant species corresponded to a treatment. Tomato was used as a plant host control in this study.

Approximately 17 days after adding the J2s to the dishes, the nematodes inside the roots of the plants were stained following a methodology using food dye (Rocha et al. 2005). Then, the number of J2 that penetrated the roots was quantified, and the nematode development stages inside the roots were observed. Images were captured using Motic Images Plus software version 2.0 and an optical microscope (Motic BA310 Series, Schertz, TX, United States) coupled to a Moticam 3.0 MP camera (Motic, Schertz, TX, United States).

Obtention of root exudates

The root exudates were obtained based on the methodology described by Čepulyteet al. (2018) and Liu et al. (2019). Tomato (*S. lycopersicum* cultivar 'Santa Clara'), lettuce (*L. sativa* cultivar 'Solaris'), marigold (*T. patula*), Madagascar periwinkle (*C. roseus*), yarrow (*A. millefolium*) and garlic (*A. sativum*) plants with approximately five weeks of growth were used. The roots were washed and placed in glass flasks dipped in 40 mL of sterile distilled water, leaving the shoots outside the flask. The roots of 10 plants (tomato, Madagascar periwinkle, and marigold) or five plants (lettuce, yarrow, and garlic) were placed in each flask. The number of plants was defined according to their root systems volumes, which were submerged in 40 mL of water. The plants were kept under these conditions for 24 h at room temperature. Then, the water containing the root exudates was collected, filtered through filter paper and stored in conical tubes (15 mL). The tubes were stored in a refrigerator at 4 °C for approximately 24 h until the samples were used.

Chemotaxis index

To observe the effect of exudates released by the roots of non-host plants on the movement of *M. javanica*, a chemotaxis assay was performed based on the method described by Wang et al. (2019). The treatments corresponded to root exudates obtained (according to item 2.3.2) from each of the following plant species: tomato (*S. lycopersicum* cultivar 'Santa Clara'), lettuce (*L. sativa* cultivar 'Solaris'), marigold (*T. patula*), Madagascar periwinkle (*C. roseus*), yarrow (*A. millefolium*), garlic (*A. sativum*), and a control (distilled water). Petri dishes (9 cm) with 20 mL of agar–water medium (2%, 2 g L^{-1}) were used to observe the movement of *M. javanica* J2s (Fig. 1a). On both sides of the dish (test area and control area, Supplementary Fig. S1), holes were made in the agar–water medium using straws of 1 cm diameter. The holes were made approximately 2.5 cm from the neutral area where the J2 were added. A total of 100 µL of root exudates was added to the hole in the test area (+), and 100 µL of distilled water was added to the hole in the control area (-). The negative control consisted in adding only water on both holes (test area and control area, Supplementary Fig. S1). Approximately 200 J2 were placed in the center of the Petri dish (neutral area, Supplementary Fig. S1). Then, the dishes were kept at room temperature in the dark. After 16 h, the number of J2s in the test and control areas was quantified. The chemotaxis index (CI) was calculated using the equation below:

$$CI = \frac{(\text{number of J2s in the test area} - \text{number of J2s in the control area})}{\text{total number of J2s in the dish}}$$

According to Wang et al. (2019), CI values > 0.2 are considered highly attractive; CI > 0.1 but < 0.2, slightly attractive; and CI > -0.1 but < 0.1, a random response (not conclusive).

Greenhouse experiments

Intercropping tomato with non-host plants

Seedlings of tomato (*S. lycopersicum* cultivar 'Santa Clara'), marigold (*T. patula*), Madagascar periwinkle (*C. roseus*), yarrow (*A. millefolium*) and garlic (*A. sativum*), with approximately five weeks of growth, were grown under different treatments in 11 L pots filled with 10 L of soil mixed with sand, sterilized by solarization for five weeks and then sieved. The treatments consisted of one non-host species (Madagascar periwinkle, yarrow or garlic) intercropped with one tomato plant, resulting in two plants grown per pot (Fig. 1b). In the negative control, two tomato plants were planted per pot. Tomato cultivar susceptible to *M. javanica* 'Santa Clara' was used (Seid et al. 2015). Marigold was used as a positive control. The experimental design was completely randomized (DIC), consisting of five treatments.

Before transplanting the seedlings, soil samples were collected, and the presence of RKN was not detected. The chemical characterization of the soil was determined: pH = 4.84 ($CaCl_2$) and pH = 5.44 (H_2O); P = 1.19 mg dm^{-3}; K = 94.00 mg dm^{-3}; S = 0.87 mg dm^{-3}; Na = 0.00 mg dm^{-3}; Ca = 2.60 cmolc dm^{-3}; Mg = 0.73 cmolc dm^{-3}; Al = 0.04 cmolc dm^{-3}; t = 3.61 cmolc dm^{-3}; T = 7.67 cmolc dm^{-3}; aluminum saturation = 1.1%; base saturation = 46.54%; organic matter = 4.37%; Cu = 8.00 mg dm^{-3}; Fe = 43.40 mg dm^{-3}; Mn = 91.10 mg dm^{-3}; and Zn = 3.90 mg dm^{-3}. Two months before setting up the experiment, the soil pH was corrected to 6.00 with limestone. The soil was mixed with sterilized sand (2:1) to reduce the clay percentage from 53.5 to 17.8% and increase the sand percentage from 19.9 to 73.3%, since the reduction of clay and increasing sand are more favorable to the development of *M. javanica* (Rinaldi et al. 2014).

Approximately one week after transplanting the seedlings, approximately 5,000 eggs were added to small holes made in the soil around each plant, totaling 10,000 eggs per pot. The plants were kept in a greenhouse covered with transparent polyethylene film (150 μm) and 70% shade cloth. Irrigation was performed by drip irrigation to 60% field capacity.

The pots were fertilized before planting with simple superphosphate following technical recommendations (Ribeiro et al. 1999). During the experiment, topdressing fertilizers were applied in a mixture with potassium nitrate and calcium nitrate or with monoammonium phosphate and magnesium sulfate, applying each mixture twice a week. Foliar fertilization was also sprayed with potassium nitrate and amino acids, monoammonium phosphate and magnesium sulfate, or micronutrients (Supa trace 10 - Agrichem™, Ribeirão Preto, SP, Brazil).

Approximately 70 days after adding the eggs, plant height, fresh root mass and total number of eggs were evaluated. The eggs were extracted as previously described by Hussey and Barker technique. The total eggs were counted under an optical microscope using a nematode counting slide (Peters' slide), and three counts were performed per sample.

Intercropping lettuce with non-host plants

Lettuce (*L. sativa* cultivar 'Solaris'), marigold (*T. patula*), Madagascar periwinkle (*C. roseus*), yarrow (*A. millefolium*) and garlic (*A. sativum*) seedlings, with approximately five weeks of growth, were grown under different treatments in five-liter pots filled with a commercial substrate composed of peat, vermiculite, class A agro-industrial organic waste and limestone (Carolina Soil™, Santa Cruz do Sul, RS, Brazil). The treatments consisted of one non-host species (Madagascar periwinkle, yarrow and garlic) intercropped with one lettuce plant, resulting in two plants grown per pot (Fig. 1b). Two lettuce plants per pot were planted in the negative control. Lettuce susceptible to *M. javanica*, cultivar 'Solaris' was used (Sgorlon et al. 2018). Marigold was used as a positive control, being intercropped with lettuce as well as the other non-host plants. The experimental design was completely randomized (DIC), consisting of five treatments.

Approximately one week after planting, approximately 1,000 J2 were added to small holes made in the substrate around each plant, totaling 2,000 J2 per pot. The plants were kept in a greenhouse covered with transparent polyethylene film (150 microns) and 70% shade cloth. Irrigation was performed by drip irrigation according to the plant's needs. The plants were foliar fertilized with NIPHOKAM 108 (Fênix Agro, Tietê, SP, Brazil) following the manufacturer's recommendations.

Approximately 60 days after the introduction of the J2s to the substrate, the fresh mass of the aerial parts of the plants, the fresh root mass and the number of eggs were evaluated. The eggs were extracted as previously described by Hussey and Barker technique. The total eggs were counted as previously described, and three counts per replicate of each treatment were performed.

Statistical analyses

The normality of data and the homogeneity of the variances were evaluated by the Shapiro–Wilk test

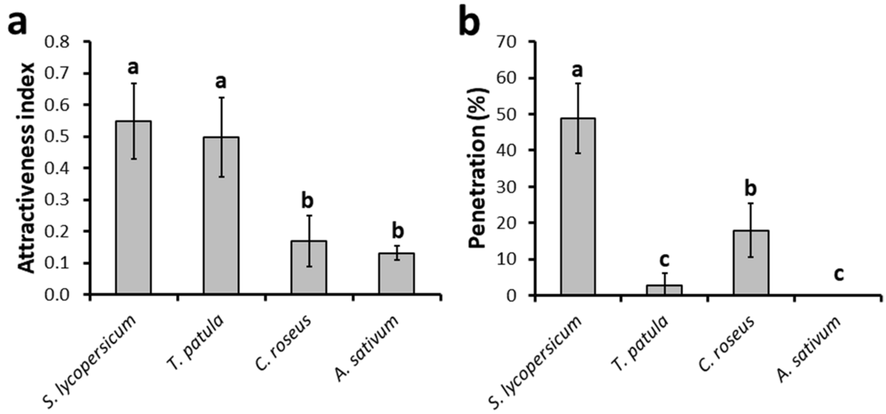


Fig. 2 Attractiveness index (**a**) and penetration percentage (**b**) of J2s of *Meloidogyne javanica* in the roots of tomato (*S. lycopersicum*), marigold (*T. patula*), Madagascar periwinkle (*C. roseus*) and garlic (*A. sativum*). Bars with the same letters do not differ significantly by Tukey's test at 5% of significance. Results represent a joint analysis of two experiments

and Levene test, respectively. All the experiments had five replicates. All the laboratory experiments were performed twice and the data from both experiments were combined when there was no significant difference effect of the repetition by analysis of variance (ANOVA) (Experiment 1 vs. Experiment 2). Then, the data were subjected to ANOVA. The chemotaxis index was grouped by the Scott–Knott's test at 5% significance, while the means of attractiveness index, penetration, root and shoot growth parameters, and number of eggs were compared by the Tukey's test at 5% significance. Statistical analyses were performed using R software (R Core Team 2019).Data of fresh root mass from lettuce plants did not show homogeneity and it was transformed by log(x) before analysis.

Results

Non-host plant roots attractiveness and *Meloidogyne javanica* penetration in the roots

M. javanica was attracted to tomato (*S. lycopersicum*), marigold (*T. patula*), Madagascar periwinkle (*C. roseus*) and garlic (*A. sativum*) roots with

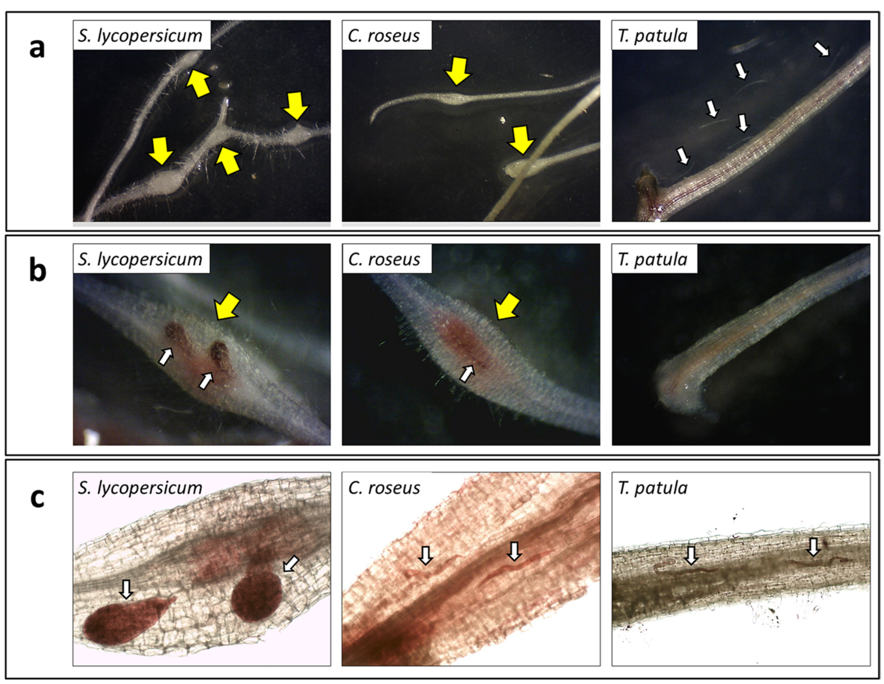


Fig. 3 Penetration of *Meloidogyne javanica* in tomato (*S. lycopersicum*), Madagascar periwinkle (*C. roseus*) and marigold (*T. patula*) roots. **a** Roots on agar–water medium 17 days after the introduction of J2s. **b** Roots after staining the nematodes. **c** Root blades with stained nematodes. The yellow arrows indicate galls, and the white arrows indicate nematodes

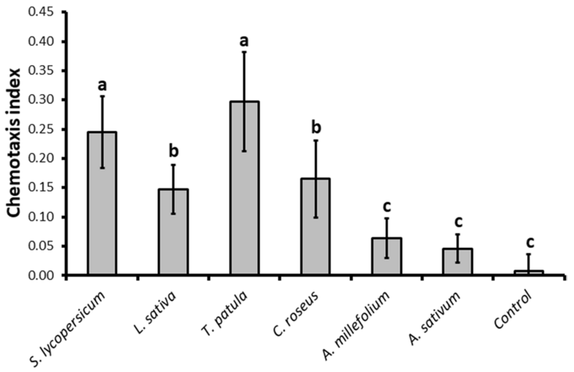


Fig. 4 Chemotactic response of *M. javanica* second-stage juveniles (J2) to tomato (*S. lycopersicum*), lettuce (*L. sativa*), marigold (*T. patula*), Madagascar periwinkle (*C. roseus*), yarrow (*A. millefolium*) and garlic (*A. sativum*) root exudates. The control was distilled water. Bars with the same letters were grouped by the Scott–Knott test at 5% of significance. Results represent a joint analysis of two experiments

different levels of attractiveness (Fig. 2a). The *M. javanica* J2 could be observed around the root system of these plants in the Supplementary Fig. S2. Marigold and tomato roots similarly attracted *M. javanica*. The attractiveness index of the Madagascar periwinkle and garlic roots differed significantly ($p < 0.001$) from the index observed for the tomato root (Fig. 2a). The J2s penetrated the roots of tomato, Madagascar periwinkle and marigold, with significant differences ($p < 0.001$). The highest percentage of J2 penetration was observed in the tomato roots. The penetration of the J2s in Madagascar periwinkle roots was 30% lower than in tomato, while only 2.86% penetrated the marigold roots. None of the J2 was found in the garlic roots (Fig. 2b).

The development of J2 that penetrated the Madagascar periwinkle and marigold roots was affected and they did not reach the adult stage in the evaluated period, while in the tomato roots, the J2 normally developed until reaching the adult stage (Fig. 3).

Chemotactic responses of *Meloidogyne javanica* to root exudates of non-host plants

The root exudates of marigold and tomato were highly attractive to *M. javanica* since chemotaxis index (CI) values were greater than 0.2 (Wang et al. 2019). Lettuce and Madagascar periwinkle had CI values between 0.2−0.1 which are considered slightly attractive. The root exudates of garlic and yarrow did not attract the J2s by presenting CI values below 0.1 (Fig. 4).

Pot intercropping of tomato with non-host plants in *Meloidogyne javanica* infested substrate

There was a significant reduction ($p < 0.001$) in the total number of *M. javanica* eggs by intercropping the tomato with non-host plants compared to the control (two tomato plants per pot) (Table 1).

Only the garlic promoted fresh root mass higher than the control for the tomato plant ($p = 0.0308$). In the treatments in which tomato plants were intercropped with Madagascar periwinkle, yarrow and garlic, stem diameters and heights were higher ($p < 0.001$) compared to the control (Table 2).

Pot intercropping of lettuce with non-host plants in *Meloidogyne javanica* infested substrate

There was a significant reduction ($p < 0.001$) in the total number of *M. javanica* eggs per pot in the treatments cultivating lettuce in an intercropped system with non-host plants when compared to the control (two lettuce plants per pot) (Table 3).

Table 1 Number of *Meloidogyne javanica* eggs on pots with the intercropping system

Intercropping system	Total number of eggs per pot (±SE[1])
Tomato + tomato (control)	239,867.00 (±11,416.10) a[2]
Marigold + tomato	123,015.50 (±19,976.13) b
Madagascar periwinkle + tomato	154,982.65 (±16,025.64) b
Yarrow + tomato	132,884.20 (±12,795.45) b
Garlic + tomato	166,750.00 (±10,359.17) b

[1]Standard error. [2]Means with the same letters in the columns do not differ significantly by Tukey's test at 5% of significance

Table 2 Tomato growth under the intercropping system with non-host plants

Intercrops[1]	Tomato plants		
	Fresh root mass (g) (±SE[2])	Stem diameter (cm) (±SE)	Height (cm) (±SE)
Control with tomato	19.30 (±2.15) b[3]	1.00 (±0.04) c	149.85 (±3.80) c
Marigold	23.40 (±3.63) ab	1.06 (±0.03) bc	153.10 (±7.17) bc
Madagascar periwinkle	33.20 (±3.06) ab	1.24 (±0.01) a	183.70 (±1.69) a
Yarrow	29.40 (±1.82) ab	1.22 (±0.02) a	172.40 (±4.68) ab
Garlic	36.00 (±5.16) a	1.18 (±0.03) ab	182.70 (±2.58) a

[1]Plant intercropped with tomato, where the control consists of two tomato plants per pot, instead of tomato with the non-host plant. [2]Standard error. [3]Means with the same letters in the columns do not differ significantly by Tukey's test at 5% of significance

Regarding the effects of the treatments on the growth of lettuce plants, only in intercropping systems of lettuce with Madagascar periwinkle or garlic was observed significant ($p < 0.001$) higher lettuce fresh root mass compared to the control (two lettuce plants per pot). In the intercropping system of lettuce with Madagascar periwinkle, yarrow or garlic, lettuce fresh shoot mass was significant higher ($p < 0.001$) when compared to control with two lettuce plants (Table 4).

Discussion

Root exudates play major roles in the interaction of plants with the rhizosphere microbiota and plant defense (Dennis et al. 2010; Baetz and Martinoia 2014; Homulle et al. 2022). Plant-parasitic nematodes are typically part of the soil ecosystem and highly exhibit chemotactic responses to host or non-host roots (Haichar et al. 2014; Wang et al. 2021). In this study, the J2 of *M. javanica* responded differently to the root exudates of the evaluated plants. The J2 were attracted by root exudates of tomato and lettuce, which are hosts of *M. javanica*. The J2 were also attracted by root exudates of the non-host marigold (*Tagetes patula*) and Madagascar periwinkle (*Catharanthus roseus*), while they were neither attracted nor repelled when subjected to root exudates of the non-hosts garlic (*Allium sativum*) and yarrow (*Achillea millefolium*) (Fig. 4). These results support that a plant being host or non-host of *M. javanica* is not only determined by the response of J2 attraction (Linsell et al. 2014). Non-host plants release root exudates containing toxic substances that differently act against RKN, blocking the J2 attraction in the soil when looking for a host, affecting the development of juveniles and suppressing egg hatching (Torto et al.

Table 3 Number of *Meloidogyne javanica* eggs on pots with the intercropping system

Intercropping system	Total number of eggs per pot (±SE[1])
Lettuce + lettuce (control)	5,576.67 (±290.92) a[2]
Marigold + lettuce	1,883.33 (±346.70) b
Madagascar periwinkle + lettuce	2,076.67 (±287.58) b
Yarrow + lettuce	2,920.00 (±497.31) b
Garlic + lettuce	2,696.67 (±453.12) b

[1]Standard error. [2]Means with the same letters in the columns do not differ significantly by Tukey's test at 5% of significance

Table 4 Lettuce growth under the intercropping system with non-host plants

Intercrops[1]	Lettuce plants	
	Fresh root mass (g) (±SE[2])	Fresh shoot mass (g) (±SE)
Control with lettuce	47.40 (±2.74) b[3]	298.80 (±18.07) b
Marigold	45.00 (±1.36) b	294.60 (±25.96) b
Madagascar periwinkle	95.20 (±9.47) a	585.00 (±8.23) a
Yarrow	71.20 (±8.58) ab	568.20 (±17.26) a
Garlic	73.00 (±4.50) a	538.20 (±15.42) a

[1]Plant intercropped with lettuce, where the control encompassed two lettuce plants per pot, instead of lettuce with the non-host plant. [2]Standard error. [3]Means with the same letters in the columns do not differ significantly by Tukey's test at 5% of significance. The fresh root mass from lettuce plants was transformed by log(x) before analysis

2018a; Sikder and Vestergård 2020). In this work, both attraction response and development of J2 inside the non-host roots were verified.

Root exudates of marigold (*T. patula*) are reported to repel J2 of *M. incognita* (Wang et al. 2018), while in the present study, marigold (*T. patula*) was highly attractive to *M. javanica* (Fig. 4). Different species of RKN may respond differently to the same plant root exudates, which supports the importance to verify each situation to avoid misguided recommendations (Sikder and Vestergård 2020). Marigold species *T. patula*, *T. erecta*, *T. signata*, and *T. minuta* have distinct host suitability to *Meloidogyne* spp., and it can lead to variations in their attraction or repellence (Hooks et al. 2010; Ploeg 1999; Shivakumara et al. 2018). These divergent results could also be associated with the concentration levels of marigold root exudates among the species, which may have interfered in the observed response of J2s (Kirwa et al. 2018; Shivakumara et al. 2018; Zhai et al. 2018). Further studies are necessary to investigate these aspects of exudates composition and concentrationin particular situations of host-RKN interactions.

Despite the *M. javanica* J2 were attracted to marigold and Madagascar periwinkle roots, it was observed a reduction in the penetration of J2s into their roots and a disturbance in J2s development inside the roots, interfering with the adult formation and reproduction. This behavior had been previously reported in different crops considered resistant to *Meloidogyne* spp. (Herman et al. 1991; Khan and Khan 1991; Windham and Williams 1994; Anwar and Mckenry 2000; Linsell et al. 2014). Marigold roots have been reported as attractive to other RKN species (Nježić et al. 2014; Oliveira et al. 2020). However, to the best of our knowledge, no studies have investigated the penetration and development of *Meloidogyne* spp. in Madagascar periwinkle roots. A previous study verified the host suitability of *M. paranaensis* in Madagascar periwinkle, indicating a high formation of galls and low reproductivity; thus, Madagascar periwinkle was considered a non-host plant for the RKN (de Mendonça et al. 2017). The results obtained in this study confirm the attractiveness of Madagascar periwinkle (Fig. 4) and demonstrated its negative effects on the development of *M. javanica* inside the roots (Fig. 3). These are relevant aspects in the management of *Meloidogyne* spp. to be explored in intercropping systems with non-host plants. Note worthy, intercropping in pot experiments obligates the RKNs to interact with tested plants and forces them into contact with non-host plants' nematicidal compounds.

Marigold has been widely applied in the management of RKN by intercropping with different crops (El-Haddad et al. 2003; El-Hamawi et al. 2004; Verma 2006; Kamunya et al. 2008; Tringovska et al. 2015; Xie et al. 2016). In this work, intercropping marigold (*T. patula*) with lettuce reduced the total number of *M. javanica* eggs per pot. As far as we know, there are no previous studies investigating the cultivation of Madagascar periwinkle or yarrow intercropped with other crops to assist in the management of RKN in tomato or lettuce. By intercropping garlic along with tomato or lettuce, there was a reduction in the population of *M. javanica*. Garlic and other species of the genus *Allium* were able to reduce *Meloidogyne* spp. population and promote plant growth when used in different intercropping systems (Abdel-Baset and Allah 2020; Seman et al. 2020; Nie et al. 2021; Detrey et al. 2022).

The cultivation of non-host plants to manage RKN can provide other benefits such as improving plant growth and increasing the yield (Tringovska et al. 2015). Garlic, Madagascar periwinkle and yarrow not only reduced the RKN population but also improved tomato and lettuce growth, which may have occurred due to different plant-plant, plant-soil, and plant-microbial interactions (da Silva et al. 2018; Brosset and Blande 2022; Das et al. 2022). In this work, it was demonstrated that before performing field tests of non-hosts, the attraction of roots and their exudates, the verification of J2 development inside the roots, as well as pot intercropping studies would provide more insights into the potential effects of intercropping plants to control RKN populations and promote host plant growth.

Conclusion

The attractiveness of *M. javanica* J2 to yarrow and garlic roots was lower than the other evaluated non-hosts. However, marigold and Madagascar periwinkle attracted the J2s to their roots, but they did not successfully complete their cycle inside the roots. Consequently, all the plants intercropped with RKN hosts significantly reduced the egg formation of the nematode. Additionally, the non-hosts Madagascar periwinkle, yarrow and garlic improved tomato and lettuce shoot growth. The estimation of root attraction, exudates chemotaxis, J2 penetration and development, along with the growth promotion of tomato and lettuce supported the potential use of the evaluated non-host plants in the RKN management.

Acknowledgements This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001. The authors thank the CAPES, FAPEMIG and CNPq institutions for granting scholarships and for supporting research in our institution. They also thank the Laboratory of Nematology of the Plant Pathology Department (DFP) and the Plant Tissue Culture Laboratory of the Department of Agriculture (DAG) of the Federal University of Lavras (Universidade Federal de Lavras - UFLA) for the structure provided for the experiments and for the support of the technicians and teachers. The authors thank the Clerio Rodrigues Ribeiro, Sansão Augusto Germano, Regiane Alves Belizario and Maria Luiza Paiva de Oliveira for assisting in the laboratory activities.

Author contributions V.P.C.: investigation, formal analysis, visualization, writing – original draft. W.C.T.: formal analysis, visualization, writing – original draft, writing – review & editing. J.C.P.S.: conceptualization, visualization, writing – review & editing. A.J.M.O.: formal analysis, visualization, writing – original draft. K.M.F.F.: investigation, writing – original draft. B.M.S.: investigation, writing – original draft. V.P.C.: resources, writing – review & editing. F.A.R.: visualization, writing – review & editing, supervision. F.H.V.M.: conceptualization, writing – review & editing, supervision. J.D.: conceptualization, writing – review & editing, supervision.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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