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Screening and host suitability assessment of nematocidal plants for root-knot nematode control

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Summary – Root-knot nematodes (RKN), *Meloidogyne* species, are a top global threat associated with economic crop yield losses. They are difficult to detect and control, especially given the recent restrictions on environmentally harmful chemicals. There is a need for alternative solutions for sustainable RKN management, such as nematocidal plants (non-hosts or poor hosts). Despite extensive research, gaps remain in the understanding of nematocidal plant species and cultivars. Using our method, we evaluated the host suitability of 21 nematocidal plant candidates in climate chambers or glasshouses using a susceptible tomato control. Assessment was based on egg mass counts after one RKN cycle, as an indicator of reproduction. All the 21 candidates screened against *Meloidogyne incognita* were less infected than tomatoes, suggesting all the candidates are either non- or poor hosts. *Tagetes* species were evaluated against *M. incognita*, *M. arenaria* and *M. enterolobii*, with *T. patula* and *T. erecta* consistently non-hosts to the three RKN species. We also evaluated the number of galls as an indicator of the initiation of the RKN feeding sites and the plant's reaction. Only *Tagetes* spp. had no galls. *Tagetes* species *Foeniculum vulgare* and *Crotalaria juncea* were further assessed for *M. incognita* juvenile penetration and had significantly lower penetration than tomato, except for *C. juncea*. This suggests all *Tagetes* species and *F. vulgare* inhibit root penetration of most *M. incognita* juveniles at the rhizosphere level, while *C. juncea* attracts the nematodes and restricts reproduction. There is potential for most of the nematocidal plants to be used in cropping systems for sustainable integrated RKN management.

Keywords – biocontrol, egg mass, gall formation, host suitability, *Meloidogyne arenaria*, *Meloidogyne enterolobii*, *Meloidogyne incognita*, nematode penetration, non-host plant, poor host plant.

Root-knot nematodes (RKN), *Meloidogyne* species, rank among the most significant plant-parasitic nematodes globally in terms of scientific and economic impact (Jones *et al.*, 2013). Root-knot nematodes induce infection and ravage their host plant by feeding on the roots causing root galls, stunting, wilting, or chlorosis through limiting plant nutrient and water uptake, resulting in yield and quality loss (Wang, 2007; Djian-Caporalino, 2012). Several control techniques have been deployed to regulate RKN including the now-restricted chemical nematicides, soil solarisation, resistant crop cultivars, or biological control (Djian-Caporalino *et al.*, 2005; Wang, 2007; Moens *et al.*,

2009; Smith, 2015; Sorribas *et al.*, 2020). For instance, a few RKN-resistant genes have been identified (*e.g.*, *Mi-1* and *Me(s)* genes in tomato and pepper (Djian-Caporalino *et al.*, 2011; Regmi & Desaegeer, 2020) but they have limited durability, which is starting to be overcome, and ineffective when temperatures are over 30°C for *Mi-1*. Also, these genes seem highly specific and do not provide resistance against all *Meloidogyne* species (Brito *et al.*, 2007; Castagnone-Sereno, 2012). Root-knot nematodes are also exceedingly difficult to control because they are highly polyphagous and can remain hidden in the soil or plants.

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Agroecological alternatives to chemical nematicides are essential for integrated RKN management.

Nematicidal plants have proved effective in reducing plant-parasitic nematodes in vegetable production. They can be used in crop rotation, intercropping and cover cropping systems (Ploeg, 2002; Djian-Caporalino *et al.*, 2005). Particular attention could be paid to these plants for their traits related to RKN control. As their name suggests, these plants produce compounds that are toxic or repellent to nematodes or can trap them, making it impossible for them to complete their life cycle. Nematicidal compounds can be phytoanticipins (constitutive specialised metabolites), implying they exist regardless of whether pests or diseases are present, or phytoalexins (induced compounds), synthesised and accumulated *de novo* only upon detection of pests or diseases (VanEtten *et al.*, 1994; De Saint Germain & Kergunteuil, 2024). They could also be both phytoanticipins and phytoalexins as elucidated in the review on defence metabolites involved in plant-parasitic nematode control (Desmedt *et al.*, 2020). For example, marigolds, particularly *Tagetes patula*, *T. erecta* and *T. minuta*, are largely renowned for efficiently controlling a broad range of RKN species through mechanisms such as the presence of bioactive compounds like thiophenes and flavonoids, toxic compounds released from soil incorporated biomass, trapping, and fostering nematode-antagonistic flora and fauna. Sunn hemp, especially *Crotalaria juncea*, has also been studied for nematode management. It employs modes of action such as the production of allelochemicals such as monocrotaline, a pyrrolizidine alkaloid, trapping and promoting antagonistic flora and fauna (Wang *et al.*, 2002; Colegate *et al.*, 2012; Rech *et al.*, 2022). Additionally, toxic root exudates of *Sorghum* spp., including sorgoleone, may repel nematode juveniles (Czarnota *et al.*, 2003).

Based on these mechanisms of action, host suitability of plants to RKN can be categorised as good, poor or non-hosts, with nematicidal plants ideally falling within non- or poor hosts (Djian-Caporalino *et al.*, 2005). Susceptible hosts (good hosts) are attacked, permitting elevated accumulation and normal development of RKN. Poor host plants disrupt the prolific development and multiplication of RKN. Non-host plants are not attacked by RKN as they can inhibit hatching, root penetration, or subsequent RKN development and multiplication.

Several plants have been reported for their host suitability and potential use in nematode management. Although research on nematicidal plants has advanced, gaps remain regarding species coverage, consistency and performance

across cultivars. An example is a study of 18 plant species and cultivars, where three cultivars of *Crotalaria juncea*, three cultivars of *Sorghum bicolor* × *S. sudanense*, and *Avena strigosa* all interchangeably exhibited varied suitability for RKN, from non-host to poor host and susceptible to *M. incognita*, *M. arenaria* and *M. javanica* (Marquez *et al.*, 2022). Other studies highlight inconsistent responses of *C. juncea* to *Meloidogyne* spp. (McSorley, 1999; Bui & Desaegeer, 2021; Khanal & Harshman, 2022). Also, the host suitability of *Tagetes* spp. to RKN varies by plant species or variety and nematode species (Krueger *et al.*, 2007). Sorghum's response to *Meloidogyne* spp. has also been shown to vary from non-hosts, poor hosts to even good hosts (Djian-Caporalino *et al.*, 2019; Bui & Desaegeer, 2021; Khanal & Harshman, 2022). The differential resistance between sorghum genotypes is not due to dhurrin content as often thought, given that both low and high dhurrin cultivars showed similar poor host statuses (Djian-Caporalino *et al.*, 2019). Instead, inherited resistance factors in the sudangrass genome (Harris-Shultz *et al.*, 2015) and hypersensitive-like reactions, similar to those in *Mi-1.2* resistant tomatoes (Paulson & Webster, 1972), likely contribute to the lack of nematode reproduction. Brassicas like *Raphanus sativus* (radish) and *Diplotaxis tenuifolia* (perennial wall rocket) contain bioactive compounds such as glucosinolates (Bell & Wagstaff, 2014; Teklu *et al.*, 2014; Ngala *et al.*, 2015), but significant variability was observed among cultivars in their poor host status to different *Meloidogyne* spp. (Edwards & Ploeg, 2014; Daneel *et al.*, 2018; Waisen *et al.*, 2019).

The host suitability of several other plants to *Meloidogyne* species still needs to be explored. Millets (*Pennisetum glaucum*) are known to be susceptible to *M. ethiopica* (Lima *et al.*, 2009) yet non-hosts for *M. enterolobii* (Khanal & Harshman, 2022). *Avena strigosa* is a poor host for *M. ethiopica* (Lima *et al.*, 2009). According to a study by Carneiro & Carneiro (1982), *Phacelia tanacetifolia* (phacelia), which is well-known in insect pest management, suppresses the development of *M. incognita*. It is also difficult to find information on the nematode host status of *Valeriana locusta*, commonly known as corn salad, which is grown as a crop during winter in France and used by farmers as a poor host crop to manage RKN.

Characterising the host suitability of plants seems then crucial to identifying appropriate nematicidal plant species or cultivars. This study aims to provide a framework for testing plants for RKN host suitability and to determine their potential as nematicidal plants. By choos-

ing to screen various plant species and some cultivars from the same species, we also shed more light on some of the inconsistencies of the reports on the host suitability of nematicidal plants and their varietal effects on RKN exposure. This will aid in identifying nematicidal plants that pose a low risk of exacerbating nematode populations when grown.

To contribute to this, we propose a methodology to screen 21 nematicidal plant candidates to assess their host suitability to *M. incognita*, which is regarded as the most damaging crop pathogen worldwide (Sasser, 1977; Trudgill & Blok, 2001). Plant-nematode interactions start in the soil, the root interface and then inside the roots; thus, the RKN life cycle consists of the exophyte and endophyte phases (Ibrahim *et al.*, 2019), usually lasting 6 weeks depending on the host, temperature, moisture and soil type. The exophyte begins from the egg, from which the second-stage juveniles (J2) hatch, and the endophytic stage where the development of the feeding site at the central cylinder of the root occurs (often evidenced by gall formation), allowing the establishment, development and reproduction of the nematode, which would result in egg masses (EM) (Abad *et al.*, 2009).

Susceptible plants are expected to have several galls and EM. Poor hosts are expected to have galls and a few EM. Non-hosts are expected to have no EM and usually no galls too. Therefore, our set-up consists of counting galls and EM to prove the ability of nematodes to penetrate and reproduce inside the plant roots.

To go further, we set up a bioassay to evaluate root penetration of *M. incognita* on selected nematicidal plant species to determine the role that root penetration plays in the mechanism and host suitability of these plants. Desmedt *et al.* (2020) explained the importance of penetration tests that can reveal key information about the stage when plant resistance to nematodes occurs, ultimately influencing the choice and how to use a nematicidal plant.

We also applied our methodology to other *Meloidogyne* species in order to confirm the effectiveness of such screening on other RKN species and to compare the host suitability of some selected plants for the three different RKN species. We chose to work on *M. arenaria* as a previous survey reported that *M. incognita* often appears in a mix with *M. arenaria* in the farmers' fields in France (Djian-Caporalino, 2012). On the other hand, *M. enterolobii* is a recently emerging pathogen in worldwide vegetable systems (Philbrick *et al.*, 2020).

Materials and methods

PLANT SPECIES

We selected 21 plant cultivars, belonging to 12 species and seven plant families, which, according to the literature, are considered as non- or poor hosts, or have a controversial or unknown status (Table 1). Among them, we selected both summer and winter plants. Having a range of summer and winter nematicidal plants is crucial for RKN management, as the winter nematicidal plants or crops can be grown in rotation with summer crops. Some of these plants are already being used by farmers in the South of France as confirmed by a consultation with different stakeholders in France. Tomato 'Saint Pierre', usually susceptible to RKN, was used as control. Plants were grown from seeds provided by various seed companies depending on availability.

ROOT-KNOT NEMATODE SPECIES

Meloidogyne incognita Morelos populations are routinely reared and multiplied on susceptible tomato cultivar 'St Pierre' at the INRAE Sophia Antipolis experimental unit in France. After two propagation cycles (4 months after inoculating 2-month-old plants), cleaned roots with galls and EM were blended in chlorine solution at 0.5% to release the eggs from the surrounding mucilaginous mass and let them pass through a series of sieves to remove root debris and the chlorine solution. Lastly, the eggs were suspended in fresh water and counted under a microscope.

Meloidogyne arenaria Marmande and *M. enterolobii* Jan Mayric populations were extracted from the collection and multiplied as previously described to obtain sufficient nematodes for testing on a set of selected plants. *Meloidogyne enterolobii* is a recently emerging pest being detected in Europe in vegetable systems. Due to its quarantine status, its multiplication was carried out in a special authorised glasshouse compartment.

HOST SUITABILITY EXPERIMENTS

Two independent experiments were designed in 2020-2023 and randomly arranged in a complete block design, with 6-12 biological replicates ($n = 6-12$ plants), and with tomato as control. All plant species were grown in $7 \times 7 \times 7$ cm pots filled with sandy-loam autoclaved soil.

In the first experiment, the host suitability of 15 plant cultivars was tested on *M. incognita*. Summer plant species were grown at 24°C, 12 h light and relative

Table 1. List of the 12 summer and 9 winter nematocidal plant cultivars or accessions screened against *Meloidogyne incognita* with susceptible tomato as control.

Botanical name	Type	English/French common names	Cultivars or accessions	Family	Providers
<i>Solanum lycopersicum</i> L. *	S	Tomato/Tomate	'St Pierre'	Solanaceae	Syngenta
<i>Avena strigosa</i> Schreb.	W	Oats/Avoine rude	'Max'	Poaceae	Agrosems
<i>Crotalaria juncea</i> L.	S	Sunn hemp/Crotalaire	'Crescent Sunn', unknown	Fabaceae	unknown/ Lidea
<i>Diploaxis tenuifolia</i> (L.) de Candolle	W	Perennial wall rocket/Roquette	'Tiara', 'Sorta'	Brassicaceae	Semences de France /Gautier
<i>Foeniculum vulgare</i> Mill.	W	Fennel/Fenouil	'Rondo', 'Solaris'	Apiaceae	Bejo
<i>Pennisetum glaucum</i> (L.) Morrone	S	Millet/Millet perlé	'ADR 300'	Poaceae	Lidea/ Grab
<i>Phacelia tanacetifolia</i> Benth.	W	Lacy Phacelia/Phacelie	unknown	Boraginaceae	Grab
<i>Raphanus sativus</i> L. var. <i>oleiformis</i> Pers.	W	Radish/Radis	'Doublet'	Brassicaceae	Semences de France
<i>Sorghum bicolor</i> (L.) Moench× <i>S. sudanense</i>	S	Sorghum/Sorgho	'Jumbo Star', 'Piper', 'Sudal'	Poaceae	Lidea
<i>Tagetes erecta</i> L.	S	African marigold/Rose d'Inde	'CrackerJack'	Asteraceae	Lidea
<i>Tagetes patula</i> L.	S	French marigold /Fillet d'Inde	'Nana', 'Princess of Orange', 'Proud Mary', unknown	Asteraceae	Girard et fils/Lammers Seed Options BV/Lidea
<i>Tagetes minuta</i> L.	S	Mexican marigold/ <i>Tagetes</i> des decombres	unknown	Asteraceae	Germinance
<i>Valerianella locusta</i> (L.) Betcke	W	Corn salad/Mâche	'Gala', 'Trophy'	Caprifoliaceae	Clause

Names of cultivars are provided when known. S = summer plants; W = winter plants.

* Control.

humidity (RH) of 60-70%. Winter plant species were grown in a different climate chamber at 16°C, 11 h light and RH 60-70% throughout the experiment. There was an exception for radishes and oats that were kept together with the summer plants because they germinated and grew well at 24°C. After 1 month, plants were inoculated with 2000 eggs of *M. incognita*. The experiment was terminated 6 weeks after inoculation for plants at 24°C and 10 weeks for plants at 16°C as they needed more time to complete their nematode cycle. Plant roots were cleaned and stored in a freezer until counting for EM on the eosin B 0.045%-stained roots and for the galls a root gall index (GI) on a scale of 0 to 3 was used (0 = no galls, 1 = fewer than 20 galls, 2 = between 20 and 50 galls, and 3 = more than 50 galls).

In the second experiment, the first experiment was repeated on *M. incognita* with an improvement to the previous protocol: the winter plant species were only kept at 16°C until RKN inoculations, then transferred to the other plant species at 24°C to homogenise the environmental conditions for the RKN cycle and terminate the cycle at the same date, 6 weeks after inoculation. We also added three species of *Tagetes* (*T. erecta* 'CrackerJack', *T. patula* 'Nana' and an unknown accession) to verify the data in the literature. The number of EM and the number of galls were recorded.

In all experiments, non-host plants were categorised based solely on the total absence of EM regardless of the presence of galls. Plants with more than ten EM were considered susceptible (good hosts) as in Fazari *et al.* (2005). Galls simply indicate that the juveniles have reached the vascular cylinder and attempted to initiate some giant cells for their feeding site, resulting in a plant reaction. Some plants can show galls but cannot multiply RKN (no EM). Conversely, some plants may develop a few EM without noticeable galls (Djian-Caporalino *et al.*, 2019).

HOST SUITABILITY: VARIABILITY BETWEEN PLANT SPECIES/CULTIVARS AND RKN SPECIES

To check if the host suitability is species-specific or more generalist, we focused on those *Tagetes* species that had shown to be non-hosts to *M. incognita* in the second experiment and extended their screening to *M. arenaria* and *M. enterolobii*. We tested the two previously tested *Tagetes* species and added another species (*T. minuta*, unknown accession) to study the species effect, and other *T. patula* cultivars ('Princess of Orange' and 'Proud Mary') to study a potential varietal effect.

Plants for the *M. enterolobii* screening were maintained in a special glasshouse compartment because of the quarantine status of *M. enterolobii*, while *M. incognita* and *M. arenaria* tests were conducted in climate-controlled rooms. Six weeks post-inoculation (one nematode cycle), the number of EM and galls were counted. Host suitability was categorised as detailed in the previous experiments. As some plant species could not be included or repeated in both trials for *M. arenaria* due to mortality from unrelated factors, the corresponding data are provided in the Supplementary Material (Figs S1, S2).

MELOIDOGYNE INCOGNITA PENETRATION ASSAYS

According to their host suitability status, a selected number of nematocidal plants: *T. erecta*, *T. patula* (three accessions: 'Princess of Orange', 'Proud Mary', and an unknown accession) and *T. minuta*, and one *C. juncea*, or *F. vulgare* cultivar, were further tested for the penetration of *M. incognita* J2. *Tagetes* species were selected because of their non-host status, while *C. juncea* and *F. vulgare* (as representatives of the poor hosts) were included to compare with the non-hosts and the control tomato.

Plants were cultivated in 7 × 7 × 7 cm pots containing autoclaved sandy-loam soil at 24°C, with ten replicates per treatment (n = 10). At 1 month, 600-2000 *M. incognita* J2 were inoculated per plant. Eight days later, the plant roots were cleaned and stained with acid fuchsin (Byrd *et al.*, 1983) to count under a microscope the J2 that penetrated the roots, and compare the percentages of J2 penetration (compared to the initial number inoculated) with the tomato susceptible control.

DATA ANALYSIS

To categorise the plant host suitability to *M. incognita*, we compared the number of EM and galls across the various plant cultivars. Egg mass counts and gall counts/indices had a heavy presence of zeros, requiring a model that considered that. To analyse the gall index (ordinal outcomes), an ordered logistic regression was used using the 'polr' function in the 'MASS' package. This model accounts for the ordered nature of the gall index, while assuming proportional odds across the categories, thus preserving the rank structure of the data. A generalised linear model with a Poisson distribution (BRGLM) was then fitted to the number of galls or EM for all the data from all the experiments, using bias-reduction procedures implemented in the 'brglm2' R package. The 'brglmFit' a fitting method for GLM using bias reduc-

tion methods to the maximum likelihood estimates was applied.

Because of the quarantine situation for *M. enterolobii* and the different conditions for experiments, data between nematode species was not compared; thus, comparisons were done on the host suitability of *Tagetes* species and cultivars for each nematode species using similar models as previously mentioned.

The penetration of *M. incognita* J2 across different plant species was analysed using a GLM with a binomial family and logit link. The model was constructed to assess the impact of various treatments on the success of nematode penetration. The response variable was represented as the count of successful penetrations and failures, allowing for a robust evaluation of the data.

For all the statistical analyses we used 'emmeans' for *post-hoc* comparisons of estimated coefficients, adjusted using Tukey's HSD (honestly significance difference test) and the R software (version 4.4.1).

Results

PLANT HOST SUITABILITY TO *M. INCOGNITA*

In both experiments on *M. incognita* (Figs 1, 2), tomato plants were confirmed as good hosts, whilst all the nematicidal plants were significantly less infected with the RKN than tomato (EM: $\chi^2 = 569.84$, df = 15, $P < 0.001$; gall index: all z-values $> |2.3|$, $P < 0.001$).

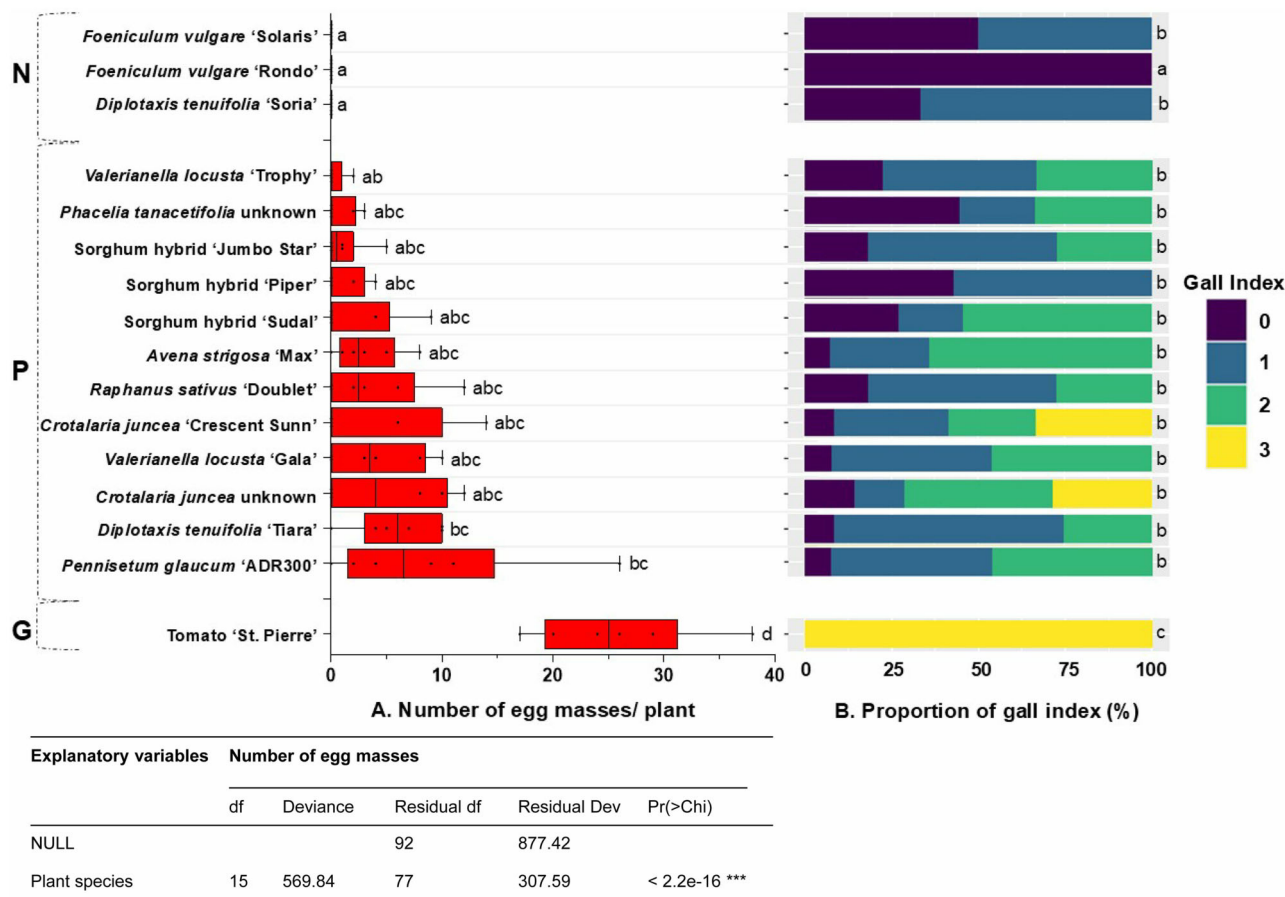
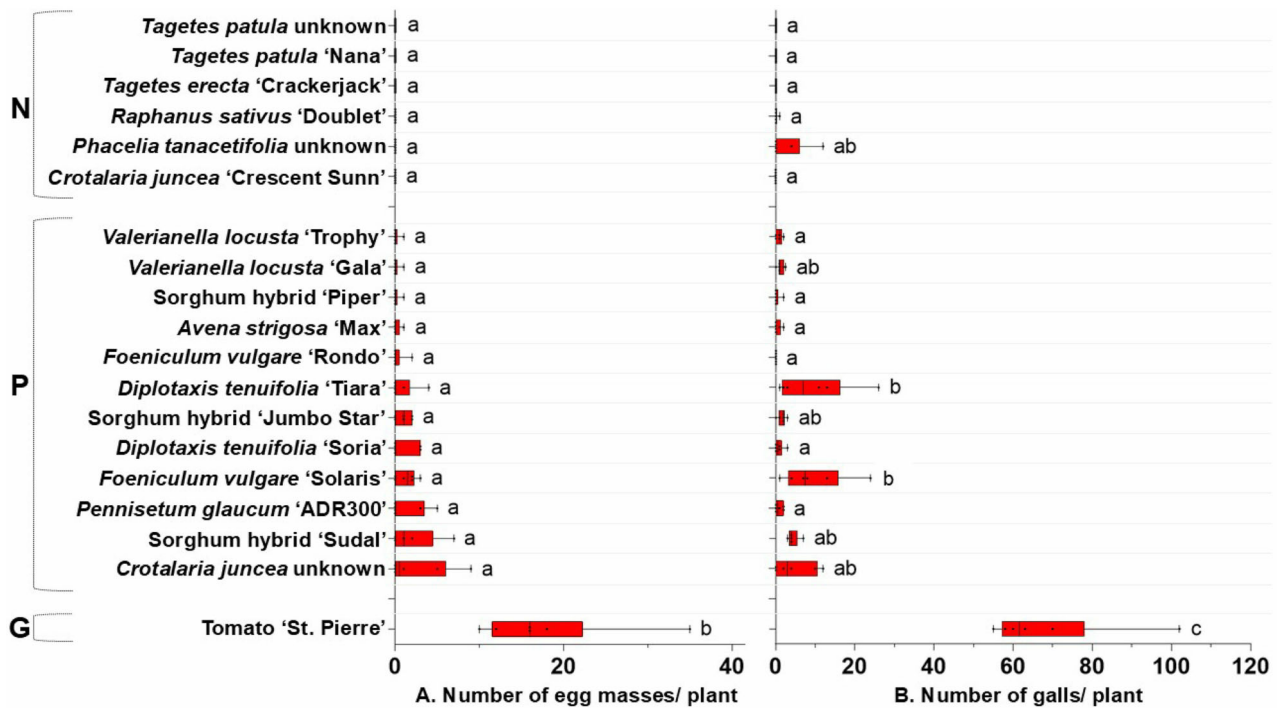


Fig. 1. Mean number of egg masses (A) and gall index on a scale from 0 to 3 (B) per plant species after inoculation with 2000 eggs of *Meloidogyne incognita* (first trial): means (n = 6) ± standard error. N = non-host; P = poor host; G = good host/ susceptible. Different letters indicating significant differences were computed for egg masses by the Bias Reduction GLM followed by Tukey's HSD *post hoc* test; $P < 0.05$ and Proportion-based gall index with ordered logistic regression and Tukey's HSD *post hoc* test. The results of the statistical tests are given in the table below the figures.



Explanatory variables	Number of egg masses					Number of galls				
	df	Deviance	Residual df	Residual Dev	Pr(>Chi)	df	Deviance	Residual df	Residual Dev	Pr(>Chi)
NULL			129	695.39				129	2400.31	
Plant species	18	546.08	111	149.31	< 2.2e-16 ***	18	2156.6	111	243.71	< 2.2e-16 ***

Fig. 2. Mean number of egg masses (A) and galls (B) per plant species after inoculation with 2000 eggs of *Meloidogyne incognita*: means (n = 6 and 12 for *Tagetes* spp.) $\pm$ standard error. Different letters indicating significant differences were computed by the Bias Reduction GLM followed by Tukey's HSD *post hoc* test; $P < 0.05$. N = non-host; P = poor host; G = good host/susceptible.

0.001; EM: $\chi^2 = 546.08$, df = 18, $P < 0.001$; galls: $\chi^2 = 2156.6$, df = 18, $P < 0.001$, respectively). Overall, all the nematocidal plant candidates were either non-hosts (no EM) or poor hosts (very few EM) of *M. incognita*, confirmed in both experiments. *Crotalaria juncea* 'Crescent Sunn', *Diplotaxis tenuifolia* 'Soria', *Foeniculum vulgare* ('Rondo' and 'Solaris'), *Phacelia tanacetifolia* and *Raphanus sativus* 'Doublet' had no EM in one experiment and only 2-10 EM in the other. Only *Tagetes* spp. were non-hosts (no EM) of *M. incognita* in both experiments (Figs 2, 3A). Considering the reaction of the plants (gall index or number of galls), *F. vulgare* 'Rondo' with zero gall index was significantly different from all the other plants, $P < 0.001$ (Fig. 1B), while *F. vulgare* 'Solaris' and *D. tenuifolia* 'Tiara' gall counts were significantly different from most of the plants ($P <$

0.001; Fig. 2). However, all of them had significantly fewer galls than the tomato in both experiments ($P < 0.001$). No galls were observed for *Tagetes* spp. in both experiments (Figs 2, 3A; Suppl. Figs S1, S2; Suppl. Table S1).

TAGETES HOST SUITABILITY TO THREE RKN SPECIES

Tomato was significantly infected with *M. incognita*, *M. enterolobii* and *M. arenaria* unlike all the *Tagetes* (EM and galls: $\chi^2 = 4497.7$ and 4063.8, df = 3, $P < 0.001$, Fig. 3A; $\chi^2 = 589.86$ and 715.29, df = 5, $P < 0.001$, Fig. 3B; $\chi^2 = 3758.9$ and 3323.2, df = 5, $P < 0.001$, Fig. 3C, respectively). *Tagetes patula* 'Nana' and cv. unknown, and *T. erecta* 'CrackerJack' were already tested in our previous experiment and found to be non-hosts for *M. incognita* (Fig. 2). We confirm in this experiment that all

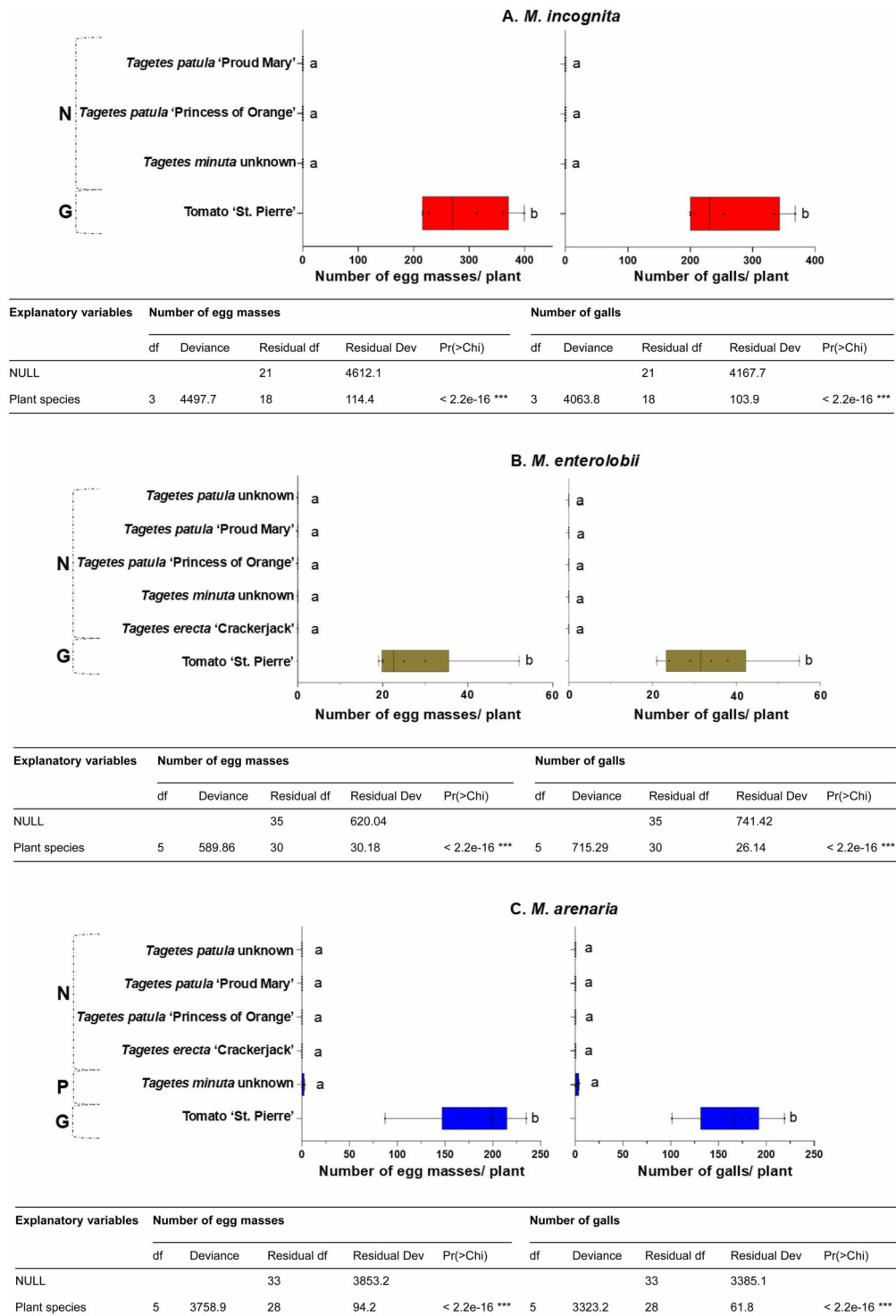


Fig. 3. Mean number of egg masses and galls for A: *Meloidogyne incognita*; B: *M. enterolobii*; C: *M. arenaria* per plant species after inoculation with 2000 eggs (third experiment): means ($n = 6$) $\pm$ standard error. Different letters indicate significant differences computed by Bias Reduction GLM followed by Tukey's HSD *post hoc* test; $P < 0.05$. N = non-host; P = poor host; G = good host/ susceptible.

the tested *Tagetes* species are non-hosts for *M. incognita* (no EM and no galls) (Fig. 3A). It is also the case for *M. enterolobii* (Fig. 3B) and *M. arenaria* (Fig. 3C), except for *T. minuta*, which was a non-host for *M. incognita* and *M. enterolobii*, whilst a poor host to *M. arenaria* with a few occasional EM and galls. Regardless, there was no statistical difference among all the non-host and poor host nematocidal plants ($P > 0.05$).

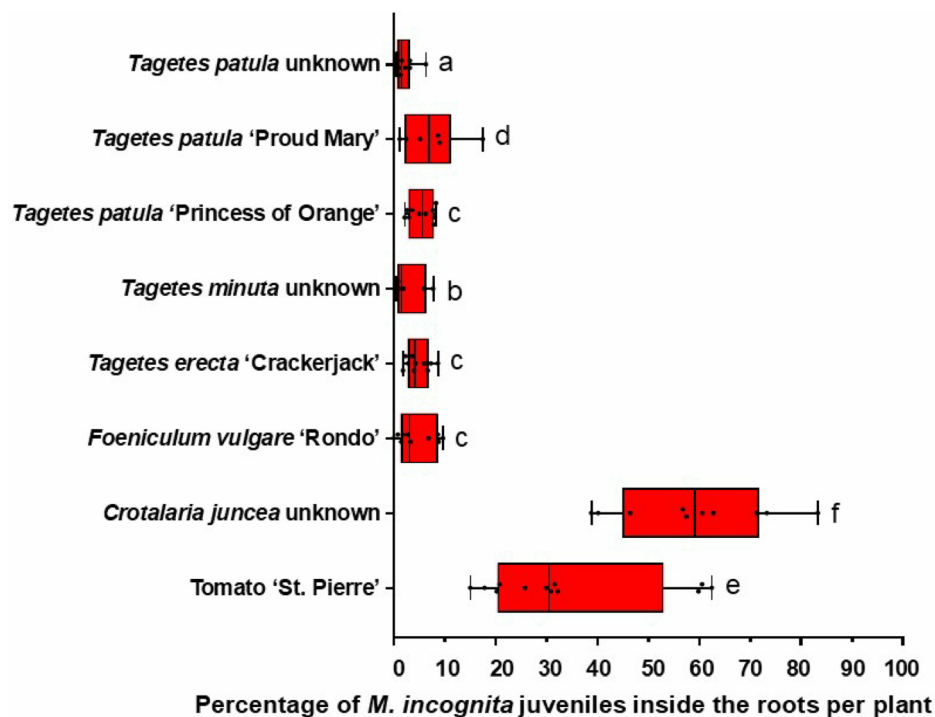
PENETRATION ASSESSMENT OF *M. INCOGNITA* JUVENILES IN ROOTS

A significantly lower number of *M. incognita* J2 were found to invade the roots of each *Tagetes* species compared to tomato ($F_{7,76} = 9.08$, $P < 0.001$; Fig. 4). Fewer

J2 penetrated also into the roots of the poor host *F. vulgare* (not significantly different from *T. erecta* and *T. patula* 'Princess of Orange'). By contrast, *Crotalaria juncea* had the most J2 counts inside its roots compared to all the plant species, including the tomato control.

Discussion

Our findings indicate that all tested nematocidal plants function as either non-hosts or poor hosts to *M. incognita*. Nematocidal plants were shown to be less infected with RKN than tomato showing potential for RKN suppression. Non-host status in this study was based on the absence of EM, regardless of the galls, which are not reli-



Explanatory variables	<i>M. incognita</i> J2 penetration/ 600-2000 J2 inoculation				
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Plant species	7	2685347	383621	9.08	4.23e-08 ***
Residuals	76	3211070	42251		

Fig. 4. Penetration (%) of *Meloidogyne incognita* second-stage juveniles (J2) inside the roots of the different plant species tested 8 days after nematode inoculation ($n = 6-12 \pm$ standard error). Different letters indicate significant differences at $P < 0.05$ (GLM binomial followed by Tukey's HSD *post hoc* test).

able indicators of the plant's susceptibility. Egg masses are the most important indicator of the host status of plants because they reflect the number of nematodes that make it to reproductive maturity. This was also noted by Hajihassani *et al.* (2020) and Marquez *et al.* (2022). Although we observed some inconsistencies, there were barely any significant differences between non-hosts and poor hosts, with a few exceptions. To further determine which plants react before, during or after penetration – and which could act as dead-end trap plants – selected nematicidal plants were assessed for the penetration of *M. incognita* J2. Root penetration tests provide knowledge of whether the plants impede nematode penetration, which brings more information to the host suitability categorisation.

So, when the objective was to distinguish between good hosts and poor/non-hosts, our methodology was good, and the EM are clearly a suitable assessment for making this classification. However, a plant may develop galls, indicating that nematodes have reached the vascular cylinder and initiated feeding, yet show no EM after one RKN cycle. But EM may appear in subsequent cycles. Hence, to distinguish further between poor and non-host, our methodology was also suitable with both EM and galls. Additionally, to check whether plants react before, during and after penetration, and to determine which are dead-end trap plants, our methodology was also helpful given the penetration rates. Finally, based on the three criteria (EM, galls and penetration rates), we were able to classify and gain more insights into the nematicidal plants tested.

GENERIC NON-HOST PLANTS

We consider as generic non-host plants all plant species/cultivars for which nematodes are almost unable to penetrate (low penetration rate), usually unable to produce galls and, most importantly, unable to reproduce (no EM). *Tagetes* species were the only ones following such criteria.

Tagetes erecta and all the *T. patula* cultivars in our study were consistently non-hosts to *M. incognita*, *M. arenaria* and *M. enterolobii* with no EM or galls and substantially low penetration by nematodes. Similarly, previous works have reported *T. erecta* and *T. patula* as non-hosts to *M. incognita*, *M. arenaria* and *M. javanica* (Buena *et al.*, 2008; Marquez *et al.*, 2022). Our study further fills the gap in the existing literature by demonstrating that both *T. erecta* and *T. patula* are non-hosts for the recently emerging vegetable pathogen, *M. enterolobii*. Furthermore, the non-host status appears to be consistent across different varieties: indeed, all three *T. patula* cultivars ('Princess

of Orange', 'Proud Mary', and the unknown) were non-hosts to the three *Meloidogyne* species. *Tagetes minuta* was also a non-host with no EM or galls for *M. incognita* and *M. enterolobii*, and could follow the same mode of action pathways of *T. erecta* and *T. patula*. However, we observed occasional egg masses of *M. arenaria* on *T. minuta*, which were inconsistent with observations from the other *Meloidogyne* species.

The nematicidal effects of *Tagetes* species could primarily be attributed to thiophene compounds, particularly α -terthienyl (Tang *et al.*, 1987; Arroo *et al.*, 1997; Szarka *et al.*, 2006; Marotti *et al.*, 2010) that can also be found in the rhizosphere and to a lesser extent other compounds like flavonoids. Alpha-terthienyl is an allelochemical that induces oxidative stress, infiltrating the nematode hypodermis and inducing its nematicidal effects (Hamaguchi *et al.*, 2019). Hence, the non-host and low nematode penetration we observed in the *Tagetes* species could be due to defence by thiophenes as constitutive phytoanticipins (Kagan, 1991; Hamaguchi *et al.*, 2019) in the rhizosphere by inhibiting hatching and repelling or killing the J2 in the soil before root penetration. Additionally, upon their attempt to penetrate roots, J2 could be killed by both phytoanticipins and induced phytoalexins. It is plausible that the nematicidal compounds in *Tagetes* could be both constitutive and induced, but the degree to which certain assumed typical thiophene components of *Tagetes* might be outcomes of phytoalexins remains uncertain. However, a nematicidal compound can be both a phytoanticipin and phytoalexin as explained by Desmedt *et al.* (2020). Whether the roots of *Tagetes* have a physical barrier effect to inhibit nematode penetration remains unclear. Those nematodes that manage to penetrate could be killed inside the roots by toxic compounds or starved, leading to a failure in the establishment of feeding sites, given that we observed no galls or any other morphological changes on the roots of our *Tagetes*. Nevertheless, some previous studies have also reported that *Tagetes* species/cultivars vary in metabolite composition, quality and quantity, and nematode species response (Krueger *et al.*, 2007; Marotti *et al.*, 2010; Karakas & Bolukbasi, 2019). This could explain the slight difference we observed for *T. minuta* to *M. arenaria* and the RKN penetration rate of *T. patula* 'Proud Mary'.

Fennel 'Rondo' also shows itself a poor host, with nearly non-host status. Similar to *Tagetes*, the mechanism of action of *F. vulgare* may occur primarily at the rhizosphere level, acting as a hatching inhibitor, repellent or toxin to J2. It may also kill J2 upon their attempt to

penetrate the root and further inhibit the establishment of those that successfully penetrate. Five terpene compounds – D-limonene, estragole, anethole, gamma-terpenes and beta-myrcene – were identified in fennel rhizosphere soil and root exudates (Yang *et al.*, 2022). These compounds were found to inhibit *Phytophthora capsica* infection. D-limonene, in particular, attracted zoospores through positive chemotaxis. Yang *et al.* (2022) showed that the combined effect of all five terpenes had a strong synergistic action, significantly disrupting the infection process through zoospore rupture. These compounds may also act against nematodes, and it would be interesting to test them against *Meloidogyne* in future experiments.

THE SPECIFIC PATTERN OF A TRAP PLANT

All plant species/cultivars that were invaded by *Meloidogyne* J2 but prevented or greatly restricted EM can be considered dead-end. It is important to note that some plants can serve solely as trap plants as they are susceptible to RKN. These plants must be destroyed and incorporated into the soil before nematode reproduction occurs. However, dead-end plants are different in the sense that they attract, trap and kill the RKN inside the roots, barely allowing any reproduction. One *Crotalaria juncea* cultivar followed such criteria. *Crotalaria juncea* cv. unknown was a poor host for *M. incognita*, yet it exhibited significantly higher *M. incognita* penetration, surpassing even tomato, which aligns with previous findings (Marla *et al.*, 2008; Curto *et al.*, 2015). Marla *et al.* (2008) observed all developmental stages of *M. incognita* within the roots of *C. juncea*. Additionally, a few mature females produced EM, but the J2 did not hatch from eggs after a week of incubation. Our study suggests that *C. juncea* cv. unknown could serve as a good dead-end trap plant, as it exhibited significant penetration but low nematode reproduction.

However, the other *C. juncea* ‘Crescent Sunn’ was in between a non-host and a poor host for *M. incognita*. Some *Crotalaria* spp. have different responses to RKN, with some non-hosts or poor hosts (trap plants) to certain nematode species. For example, *C. juncea* ‘P1207657’ and *C. juncea* ‘Tropic Sun’ were resistant to penetration by *M. javanica*, unlike a susceptible tomato (Araya & Caswell-Chen, 1994). Also, *C. juncea* root exudates had nematicidal effects on *M. incognita* (Danahap & Wonang, 2016). *Crotalaria* species have pyrrolizidine alkaloids like monocrotaline that are antagonistic to the RKN (Moens *et al.*, 2009; Colegate *et al.*, 2012; Rech *et al.*, 2022). Moreover, most of the research has focused on the use

of the *Crotalaria* genus as a biofumigant green manure to benefit the most from its aerial parts. This indicates varied modes of actions and varietal effects for the *Crotalaria* genus that have to be described more precisely.

POOR HOST PLANTS

For all the other plant species/cultivars, nematodes were more or less able to reproduce (few EM) and produce galls too (few galls). Because of the presence of these EM and galls, nematodes are clearly capable of penetrating the roots.

Our experiments showed sorghums to be poor hosts to *M. incognita*, as has been demonstrated in previous studies (Djian-Caporalino *et al.*, 2019). Other previous results have reported sorghums as either non-host or poor hosts to *M. ethiopicae*, *M. incognita*, *M. arenaria*, *M. javanica* and *M. enterolobii* and that their mode of action to control RKN may depend on their genotypes (Lima *et al.*, 2009; Curto *et al.*, 2012; Djian-Caporalino *et al.*, 2019; Bui & Desaegeer, 2021; Khanal & Harshman, 2022). The epidermal cells of sorghum, sudangrass and their hybrids contain dhurrin, a cyanogenic glucoside (De Nicola *et al.*, 2011). When root tissues are damaged, dhurrin is hydrolysed by dhurrinase in mesophyll cells, producing hydrogen cyanide (toxic to nematodes), p-hydroxybenzaldehyde and glucose. Nevertheless, the varying levels of resistance between genotypes could not be solely attributed to dhurrin content, as both low- and high-dhurrin cultivars were poor hosts, showing no significant differences in EM numbers on their roots (Djian-Caporalino *et al.*, 2019). The authors hypothesised inherited resistance factors that may be present in the sudangrass genome as already mapped (Harris-Shultz *et al.*, 2015), accounting for the lack of RKN reproduction on ‘Piper’. Several hypersensitive-like reaction (HR) sites also indicate a response to infection similar to that in *Mi-1.2* resistant tomato plants (Paulson & Webster, 1972). Their roots may also repel J2, due to the toxic root exudates, as reported for the hybrid *Sorghum bicolor* × *S. sudanense* ‘SX-15’ and ‘SX-17’ (Czarnota *et al.*, 2003). Sorgoleone, the phenolic compound identified as a predominant constituent in exudates, could be potentially responsible for this suppressive effect.

The other nematicidal plant candidates had varied responses across the two experiments: acting as non-hosts in one experiment and robust poor hosts in another, even when statistically similar. For example, *Phacelia tanacetifolia* was a non-host to *M. incognita* in the second experiment but a poor host in the first experiment. The

mechanisms and compounds involved in the nematocidal effects of *P. tanacetifolia* on RKN are less known, if not documented, and need to be studied.

Such inconsistencies were also observed for the Brassicaceous species tested, *Diplotaxis tenuifolia* ‘Soria’, and *Raphanus sativus* ‘Doublet’. This was previously reported for *R. sativus*: four cultivars had varied host statuses ranging from susceptible to poor host for *Pratylenchus penetrans*, a migratory semi-endoparasitic nematode (Neupane & Yan, 2023), whilst *R. sativus* was a poor host to *M. incognita*, *M. ethiopica* and *M. javanica* (Lima et al., 2009; Daneel et al., 2018; Waisen et al., 2019). Although *R. sativus* was a poor host of *M. incognita*, *M. hapla* and *M. javanica*, significant differences were still observed (Edwards & Ploeg, 2014). It follows that the application of *R. sativus* to plant-parasitic nematodes in the field is mired with mixed results, sometimes working, sometimes not (Ngala et al., 2015; Daneel et al., 2018; Waisen et al., 2019). However, there is a consensus that *R. sativus*, being used as a cover crop for nematode control, is capable of producing glucosinolates, which are precursors to isothiocyanates that are toxic to nematodes (Ngala et al., 2015; Waisen et al., 2019). Perhaps the inconsistencies that we observed in our study could be due to other factors that influence the production of these bio-toxic compounds, which are known to be actively produced through the plant growth phase. Regarding *D. tenuifolia*, there is a lack of information available on its host suitability, which we have shown to be a poor host to *M. incognita*. Like most Brassicaceae, our results could be attributed to glucosinolates, identified in *D. tenuifolia* (Bennett et al., 2007; Ntalli & Caboni, 2012; Bell & Wagstaff, 2014). Interestingly, we identified a varietal effect for *D. tenuifolia* (‘Soria’ and ‘Tiara’), which might be linked to differences in the quality/quantity of glucosinolates, highlighting the importance of testing several varieties and analysing their glucosinolate content.

These observations highlight the importance of understanding the cultivars to use in the field before advising the use of a given nematocidal plant. In some instances, there are no differences between varieties, such as that observed for *Valerianella locusta* (‘Gala’ and ‘Trophy’), which were strong poor hosts for *M. incognita* in the first and second experiments.

Conclusion and perspectives

With this work, we propose a screening method to help categorise the host suitability of nematocidal plant

species. Non-host plants like *Tagetes* can be used against at least the three tested *Meloidogyne* species, and the implementation strategy has been demonstrated to be key in some studies. Intercropping *Tagetes* species or growing them before the crop has been shown to suppress nematodes in tomato, cucumber and pepper (Ploeg, 1999, 2002; Tesleem et al., 2014; Taha, 2020). Poor host plants can also be used the same way as non-host plants: sorghum, for instance, could be effectively used as a rotation crop or green manure where their biomass is incorporated into the soil as has been successfully shown in the South of France where sorghum is the most widely used green manure in vegetable production (Djian-Caporalino et al., 2019, 2024). When they have an effective dead-end trapping effect, like *C. juncea*, nematocidal plants could be used as companion plants to attract nematodes away from the crop. The possibility of incorporating nematocidal plants also grown as crops, such as fennel, corn salads, radish and rockets into our crop rotation sequence to suppress RKN adds economic value from their yield.

Pending field validation, our results support the use of nematocidal plants in vegetable cropping systems year-round. For Cucurbitaceae crops, hybrid sorghums, *Crotalaria* and *Tagetes* can be used as summer intercrops to control nematodes. In Solanaceae systems, winter intercropping with plants like corn salad, rocket, phacelia or fennel can be effective. The duration of nematocidal plants’ action when used in co-culture, their planting density and distance from the associated culture are currently being studied (project ANR-20-PCPA-0003 “Cap Zero Phyto”).

The effectiveness of these nematocidal plants also depends on appropriate selection. Hence, the use of the nematocidal plants for RKN management would depend on their host suitability, their mode of action, agronomical considerations, the strategy to implement, the crop to protect and the species of RKN identified in the soil. Information on the varietal effect is crucial, as our results have shown that for some plant species, one variety may be more effective in controlling nematode species. Moreover, implementing these plants in the field requires considering several limiting factors, such as planting time, biofumigation timing, soil microbiota and soil type. Sorghum, for instance, is effective against root-knot nematodes but its success depends on these variables (Djian-Caporalino et al., 2019). Additionally, their significant root development and mycorrhizotrophic

nature, just like *Tagetes*, enhance their pest management capabilities (Rodriguez-Heredia *et al.*, 2020).

Further research should be conducted to fill the remaining gaps on nematicidal plants and fully understand their mechanisms of action. Comprehensive host suitability studies can aid breeders and growers in selecting effective nematicidal plants. A large pool of nematicidal plants is valuable to breeders as a confirmed source of resistance and to farmers as a diverse portfolio, offering options that suit their agronomic preferences. These preferences include the ease of cultivation, resource availability, labour requirements, production season and local climate.

Supplementary materials

Data is available on <https://doi.org/10.1163/15685411-bja10406> under Supplementary Materials.

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