Chemotaxis in Root-Knot Nematodes

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Abstract

For a long time, chemotaxis in root-knot nematodes has received scant attention. In recent years, however, this topic has captured the attention of several researchers worldwide. Chemotaxis refers to the movement of living organisms towards or away from a chemical gradient. Second-stage juveniles (J2s) hatching from eggs are the only infective stage of *Meloidogyne* spp., and they locate their host through chemotaxis by sensing host-secreted chemoattractants. Despite its importance in the host location process, the structures and properties of compounds that are attractive to *Meloidogyne* spp. J2s are not well understood. This chapter will present a compilation of information on the attractiveness of volatile and non-volatile compounds identified in emissions from plant roots and microorganisms. The obstacles in chemotaxis studies, which include the characterization of compounds that attract or repel, the limitations of in vitro methodologies, such as Petri dishes filled with agar and the challenges of studies using soil, will be presented. On the other hand, the advances achieved in the recent years and how chemotaxis can be manipulated to manage these important soil-borne pathogens will also be discussed.

Keywords

Attraction · Chemical gradients · *Meloidogyne* spp. · Repellence

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F. Ahmad, G. Nombela (eds.), *Root-Galling Disease of Vegetable Plants*,
https://doi.org/10.1007/978-981-99-3892-6_3

3.1 Introduction

Root-knot nematodes (*Meloidogyne* spp.) are the most widespread and damaging among the plant-parasitic nematodes. These pathogens cause losses in agriculture that are estimated to be around US$157 billion per year (Coyne et al. 2018). These nematodes are obligate biotrophic parasites that penetrate into the roots of host plants to obtain food. They molt once inside the eggs, and the second-stage juveniles (J2s) hatch and move through the soil to find suitable hosts before their energy reserves are depleted. They enter just behind the root tips and establish the feeding site at the vascular tissue, known as giant cells and the external symptom as gall or root-knot. The nematode feeds and molts three more times before it reaches maturity when females lay eggs in a gelatinous matrix. The eggs hatch, and J2s, the only infective stage, will spread in the soil again, searching for new penetration sites in the same host or new hosts.

Molecules produced by one organism with the property of influencing the behaviour of other organisms are called semiochemicals or signaling molecules (Robinson and Perry 2006). When these interactions involve members of different species, they are named allelochemicals (Perry 1996). Semiochemicals influence all relationships among living organisms in nature. The process by which *Meloidogyne* spp. J2s follow chemical gradients to find a suitable host plant is known as chemotaxis. Nematodes use chemotaxis to locate food, for mating, to avoid predators and many other behavioural responses (Zuckerman and Jansson 1984). The most important semiochemicals that attract or repel *Meloidogyne* spp. are the ones produced by plants (Kihika et al. 2017; Murungi et al. 2018; Sikder and Vestergård 2020). Factors such as the presence of microorganisms, root zone and age, soil composition and texture heavily influence the attractiveness to *Meloidogyne* spp. J2s (Perry 1996; Rocha et al. 2016). Water-soluble compounds are used for short distance, whereas volatile organic compounds (VOCs) are used in long range chemotaxis (Čepulytė et al. 2018; Wang et al. 2019; Sikder and Vestergård 2020). Chemotaxis in *Meloidogyne* spp. has been extensively studied since its first demonstration (Lindford 1939), but only recently, due to the use of modern techniques, the compounds that exert chemotaxis are being revealed (Van Dam and Bouwmeester 2016).

Our objective in this chapter is to review the information on chemotaxis in *Meloidogyne* spp. J2s towards or away from the emitting source, with emphasis on chemicals produced by plants and microorganisms. The possible applications of chemotaxis in managing these pathogens are also discussed.

3.2 Perception of Environmental Stimuli by *Meloidogyne* spp.

In order to find suitable hosts, nematodes need to assimilate information from their external environment via sensing organs or sensilla (Perry 1996), most of which are located in the anterior end of the nematode body. Of all the nematode sensilla, the amphids are considered to be the primary chemosensilla. These organs are situated

on either side of the nematode mouth, open to the exterior via a prominent pore (Bargmann 2006). Each amphid contains sensory cilia, dendrites of chemosensory neurons, that are exposed to the environment via a pore in the cuticle (Siddique et al. 2022). Axonal processes from these neurons project into the circumpharyngeal nerve ring, the main mass of the nematode central nervous system, where much of the sensory integration takes place. Sensory organs in the tail region are known as phasmids, and they are similar in general structure to the amphids, each consisting of an external pore. Anatomy and chemosensation in functional studies implicate amphid and phasmid neurons in chemosensation (Robinson and Perry 2006).

Migration of the nematode is enabled by separate innervation of dorsal and ventral muscle trunks by their respective nerve chords along most of the body length. Innervation is achieved via somatic muscle arms that extend to and synapse only with their respective dorsal or ventral nerve chords (Robinson and Perry 2006).

3.3 Rhizosphere Gradients

Meloidogyne species chemotaxis can be defined as the migration oriented with respect to a chemical stimulus gradient. The soil volume affected by roots—the rhizosphere—establishes several chemical gradients that affect the *Meloidogyne* spp. J2 movement (Fig. 3.1). It is certain that some of these gradients constitute cues that allow the migration of nematodes towards the root region.

Several authors have shown that most gradients in the rhizosphere extent for 0.5–4 mm, but gases may exceed this limit (Kuzyakov and Razavi 2019). The following are some of the gradients formed in the rhizosphere that are thought to help J2s find roots and establish a feeding site before their energy reserves are completely depleted (Rocha et al. 2010).

3.3.1 Carbon dioxide (CO_2)

The most frequently suggested attractant for plant-parasitic nematodes has been CO_2 (Klingler 1965; Pline and Dusenbery 1987). Carbon dioxide was long regarded as the most common and potent nematode attractant in nature (Robinson and Perry 2006).

By using planar optodes, a non-destructive visualization technique, gradients of CO_2 were clearly visible around root tips but less pronounced around mature root parts, probably due to high root respiration and microbial activity around the tips (Holz et al. 2020). The mean CO_2 concentration at the root center of young roots was 0.26 μmol L^{-1}, which was higher than in bulk soil. This CO_2-sensitive sensor revealed a CO_2 rhizosphere range of 1.5–3 mm (Holz et al. 2020). This seems to be a relatively short distance considering the gaseous nature of carbon dioxide. It is important to note that *Meloidogyne* spp. J2s only penetrate at a region just after the root tip.

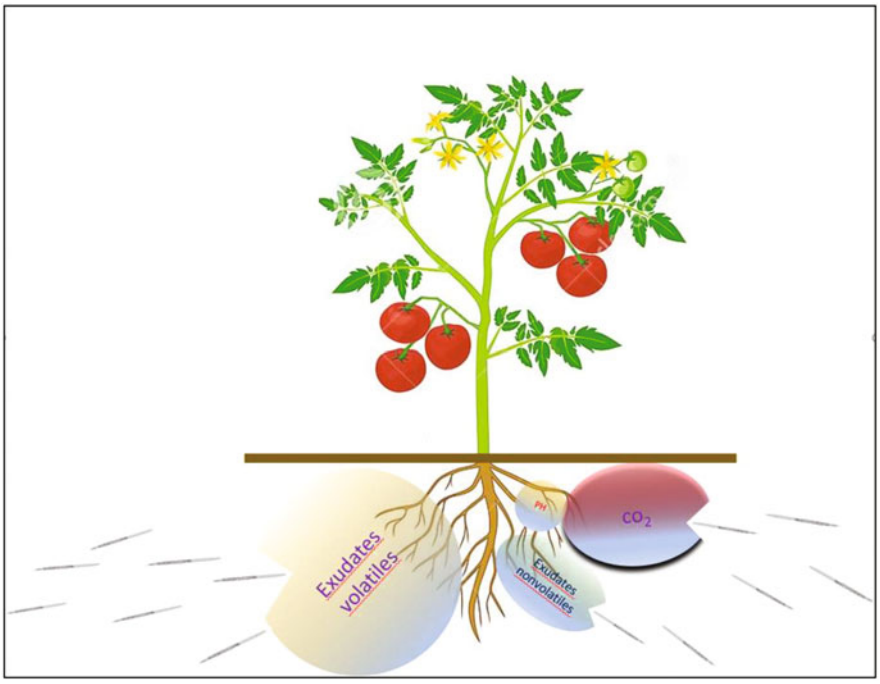

Fig. 3.1 Gradients in the rhizosphere that affect the chemotaxis of second-stage juvenile (J2s) of *Meloidogyne* spp. towards the root system. These gradients include root exudates, volatile organic compounds (VOCs), organic compounds, CO_2 and pH, all of them under the influence of the microbes inhabiting the rhizosphere

3.3.2 pH

The release of H^+ by roots into slightly acidic, neutral and alkaline soils (without N fertilization) is one of the dominant mechanisms of plants to mobilize nutrients and maintain the electrochemical potential on the root surface (Kuzyakov and Razavi 2019). The common distance of root-induced pH changes is about 2–3 mm (Blossfeld et al. 2010).

Meloidogyne hapla was shown to be attracted to pH gradients between 4.5 and 5.4 formed by acetic acid and several other Brønsted acids (Wang et al. 2009). This observation is consistent with the idea that low pH is an attractant for nematodes. As mentioned above, root-knot nematodes have been reported to be attracted to CO_2; however, the study suggested that this attraction may be due to CO_2-acidified solutions rather than to CO_2 itself.

3.3.3 Organic Compounds

The organic compounds released by living roots into the soil are collectively referred to as rhizodeposits. It is estimated that approximately 3% of the assimilated C is released by plants as rhizodeposits, including the continuously and passively released exudates and the dynamically and actively released mucilage, secretions and enzymes from various root zones (Pausch and Kuzyakov 2018). Most root exudation takes place at the root tips, and two main mechanisms decrease the concentration of organic compounds in soil solution: (1) microbial uptake and utilization/modification and (2) sorption on surfaces of minerals or organic matter (Kuzyakov and Razavi 2019). The rhizosphere extent measured by ^{14}C imaging of exudates is usually only 2–3 mm (Holz et al. 2018).

In recent years, a variety of volatile and non-volatile organic compounds released by roots of host plants have been identified as attractants or repellents to *Meloidogyne* spp. J2s (Kirwa et al. 2018; Tsai et al. 2021). Oota et al. (2019), using cryo time-of-flight secondary ion mass spectrometry/scanning electron microscopy (cryo-TOF-SIMS/SEM) analyzes, techniques used to visualize the distribution of water-soluble compounds in freeze-fixed samples at microscopic resolution level, demonstrated that propane-1,3-diamine, putrescine and especially cadaverine (Fig. 3.2), are potent attractants to J2s of *M. incognita*. These compounds are produced and released by soybean root tips and form a gradient up to 250 μm from the root surface.

The evaluation of rhizosphere extent and shape are more complicated for signalling compounds like secondary metabolites and other chemoattractants because most of them are volatile and are not strongly absorbed by soil minerals. Consequently,

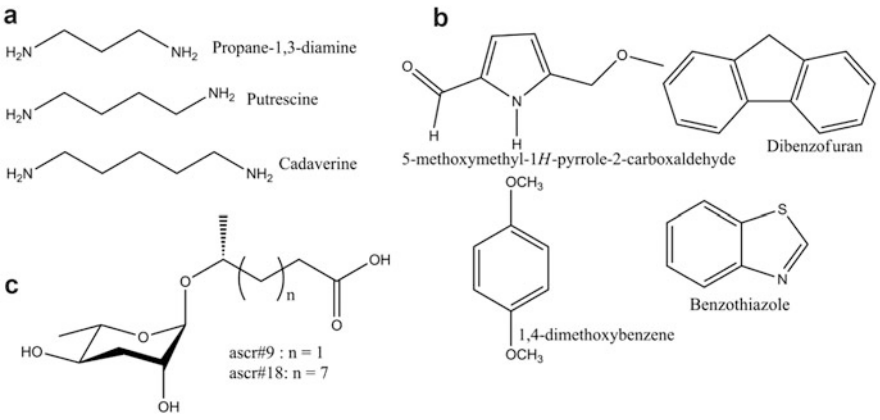

Fig. 3.2 Chemical structures of semiochemicals shown to influence *Meloidogyne* spp. chemotaxis. (**a**) Diamines produced by soybean roots that attract J2s of *M. incognita*. (**b**) Chemical structures of heterocyclic organic compounds produced by microorganisms. (**c**) Ascarosides produced by *Meloidogyne* spp. affect chemotaxis towards plant roots and nematode-trapping fungi

the travel distances and concentration gradients of some signalling compounds are very dynamic and dependent on soil properties (Kuzyakov and Razavi 2019).

3.4 Distances Root-Knot Nematodes Move

After hatching from the egg, *Meloidogyne* spp. J2s have to find a suitable host plant root to penetrate, otherwise, they will starve to death in approximately 7 days (Rocha et al. 2010; Campos et al. 2011). After the perception of chemical signals through the sensory organs, J2s start moving towards attractive gradients or in the opposite direction of repellent gradients. An issue still not well understood is the distance that J2s can migrate before losing their infective capacity.

Studies on the distances *Meloidogyne* spp. J2s move have generated a wide range of results. While some studies indicated that *Meloidogyne* spp. J2s were able to migrate more than 50 cm and infect the host plant; other studies showed a drastic reduction in migration and infectivity when J2s were placed 5 cm away from the host (Prot 1976; Rocha et al. 2016).

Nematode migration depends on the relation between pore size and J2 body diameter and the thickness of water films adhered to soil particles (Wallace 1968), among many other factors. Soil moisture has been kept close to ideal for the nematode movement in migration studies. On the other hand, soil texture and the three-dimensional environment in which J2s are inserted have varied. Vertical and horizontal migration of *Meloidogyne* spp. J2s have been studied mainly in three-dimensional systems using columns filled with sand (Prot 1976; Prot and van Gundy 1981; Pinkerton et al. 1987; Oliveira et al. 2020; Leitão et al. 2021a, b). In these apparatuses, the test nematode is placed at one end of the column and a bait plant at the opposite end, where J2s can migrate over different distances and periods of time (Leitão et al. 2021a).

Using columns with a diameter of 1.2 cm, Prot (1976) observed that J2s of *M. javanica* placed 75 cm vertically and 50 cm horizontally from tomato plants were capable of penetrating the roots in large numbers. Using the same apparatus, Prot and Van Gundy (1981) reported that up to 34% of *M. incognita* J2s were able to penetrate tomato roots after migrating 20 cm from the infestation point. Probably the small diameter used in these studies restricted nematode horizontal dispersal and imposed a vertical migration. In vertical columns with 4 cm of diameter assembled with metal or PVC rings, approximately 40% of *M. enterolobii* (Oliveira et al. 2020), 5% of the *M. floridensis* (Leitão et al. 2021b) and 1.6% of *M. incognita* (Leitão et al. 2021a) J2s were able to migrate 13 cm upwards after 9 days of infestation. By using a similar apparatus, Eo et al. (2007) reported that less than 10% of the *M. incognita* J2s migrated more than 7.5 cm 10 days after soil infestation. On the other hand, Pinkerton et al. (1987), using columns with a larger diameter (8.25 cm), filled with soil containing 16% clay plus silt, observed that less than 0.1% of the J2s of *M. chitwoodii* were able to migrate 45 cm and penetrate tomato roots.

After reaching the roots, only a small percentage will effectively penetrate and this percentage is highly dependent on the energy reserves. For example, when J2s of

M. javanica were placed 7.5 cm away from soybean roots in plastic pots, only 0.2% of them were able to penetrate the roots in a period of 5 days (L. Andrade-Souza, unpublished data).

These studies were performed with different set-ups, nematode species and soil characteristics and therefore are difficult to compare. Species such as *M. marylandi* and *M. javanica* are more motile than *M. incognita* (Oka 2020; Leitão et al. 2021b) and are expected to move longer distances. Nematodes appear to move longer distances in clayey than in sandy soils (Rocha et al. 2016). In addition to the *Meloidogyne* species and soil textures, migration distances are also influenced by the presence of bait plants, soil humidity, nutrients and salts, microorganisms and the amount of lipid reserves in the J2 body (Rocha et al. 2010, 2016). Probably, although there is no information on this topic, the amounts of reserves influence the capacity of these J2s to perceive and respond to chemical cues.

3.5 Compounds that Influence *Meloidogyne* Chemotaxis

The search for attractants and repellents to phytonematodes has been an ongoing endeavour. The chemical composition and identity of the plant-derived compounds that elicit nematode responses are mostly unknown. However, the precise and high-throughput detection and identification of semiochemicals from soils and rhizospheres have improved in recent times due to the development and higher sensitivity of scientific instrumentation (Torto et al. 2018). Interest in such molecules has increased with the need for new technologies to control nematodes (Oka 2021).

3.5.1 Plant Exudates

The main source of chemoattractants are exudates released by plants and metabolites secreted by microorganisms. Exudates are composed of high-molecular-weight polysaccharides and lower-molecular-weight organic compounds such as sugars, amino acids, flavonoids, tannins and other phenolic compounds, enzymes, fatty acids, growth regulators, nucleotides, carbohydrates, steroids, terpenes, alkaloids, polyacetylenes and vitamins (Bertin et al. 2003). They are released as a product of the interaction of the plant or microorganism with the environment that surrounds them (Kihika et al. 2017; Oota et al. 2019). The molecules perceived by nematodes include carbohydrates, amino acids, flavonoids, thiazoles, benzoxazinoids, terpenoids, alkaloids and many others (Sikder and Vestergård 2020; Sikder et al. 2021; Tsai et al. 2021).

Studies on the attractiveness and repellence of chemical compounds require specific tools. In vitro studies are carried out in Petri plates (Fig. 3.3), using water agar, agarose or pluronic F-127 gel (Williamson et al. 2009; Shivakumara et al. 2018; Liu et al. 2019; Oota et al. 2019; Oka 2020) or in adapted olfactometers filled with sand (Reynolds et al. 2011; Kihika et al. 2017; Murungi et al. 2018; Kirwa et al.

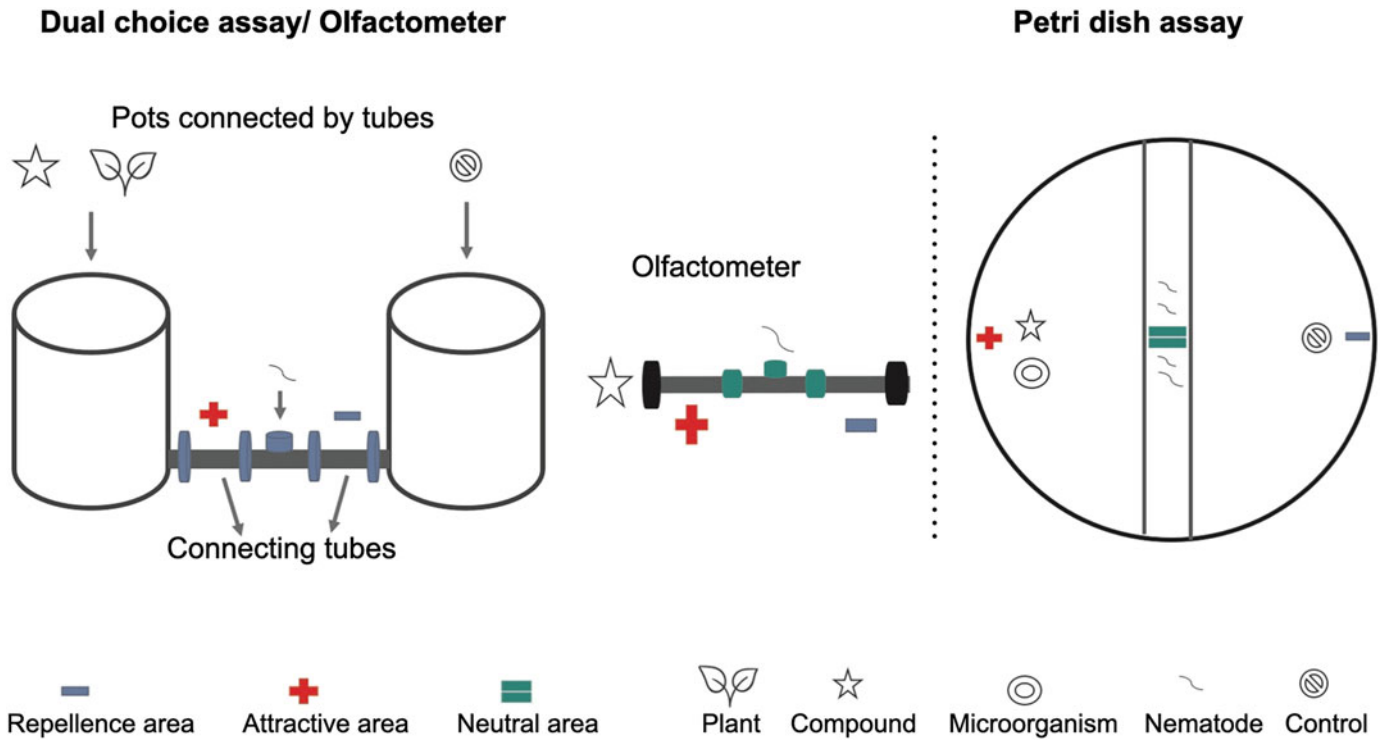

Fig. 3.3 Main techniques used to study the attraction and repellency of phytonematodes to chemical compounds or microorganisms

2018; Torto et al. 2018). Evaluations include most commonly counting the number of J2s that migrate to determined zones in the plates or olfactometers (Pacheco et al. 2021), number of stylet thrusts in selected specimens (Dutta et al. 2012; Kirwa et al. 2018) and time-lapse photographic evaluations of nematode tracks (Wuyts et al. 2006). Experiments with plants are generally carried out using pots connected by tubes (Kihika et al. 2017; Wang et al. 2019; Pacheco et al. 2021; Fig. 3.3), where recovery of nematodes from soil or sand may be challenging due to the low efficacy of the extraction methods.

VOCs are among the metabolites that compose exudates and are currently one of the most explored. They have up to 20 carbon atoms in their chemical structures and tend to present high vapour pressure, being easily released and dispersed in the environment (Dudareva et al. 2006). Several VOCs from different chemical groups had their toxicity to nematodes verified, and recently their attractiveness and repellence potential have been studied (Murungi et al. 2018; Oka 2021; Pacheco et al. 2021).

Nematode responses to plants are complex, and to illustrate this point, Wang et al. (2018a) measured the attractiveness of root tips, root exudates and extracts of marigold, a known trap plant and of soybean and pepper. They found that the root tips of all three species attracted *M. incognita* J2s, but only soybean root tips attracted *Heterodera glycines*. On the other hand, these three species' root exudates and root extracts attracted *H. glycines*, but repelled *M. incognita*. Although the chemoattractants were fractionated and found to be polar in their chemical nature, they were not identified. Similar species-dependent responses were also found for root border cells of different plant species to *M. incognita* (Zhao et al. 2000).

Susceptible and resistant cultivars of *Capsicum annum* and tomato showed that root exudates and VOCs emitted by susceptible plants are more attractive to *M. incognita* J2s than those emitted by resistant cultivars (Yang et al. 2016; Kihika et al. 2017). In addition to VOCs, some carbohydrates and proteins were related to the attractiveness of root-knot nematodes. *Arabidopsis* seeds attract *M. incognita* J2s, but it was dependent on the composition and presence of the seed-coat mucilage. Mutants that did not produce mucilage did not attract. Mucilage itself was not able to attract J2s, other components, such as carbohydrates and proteins, were determinant (Tsai et al. 2019).

3.5.2 Pure Chemical Compounds

Root-knot nematode species are among the most used in chemotaxis studies, especially *M. incognita*. A common approach adopted by many authors is the detection and identification of plant-derived chemicals by different techniques, such as gas chromatography (GC) coupled with mass spectrometry (MS) for volatiles and high-performance liquid chromatography (HPLC) coupled with MS for non-volatiles, followed by testing the pure chemicals in chemotaxis bioassays. Many compounds derived from plants were tested in their pure form, and their effects on chemotaxis have been confirmed (Table 3.1). These studies are difficult to compare because they

Table 3.1 Pure synthetic compounds or chemicals derived from plants and their activity on the chemotaxis of root-knot nematodes

Compound	Source	*Meloidogyne* species	Chemotaxis				
			Evaluation[a]	Assays[b]	Attractant +[c]	Repellent −[c]	References
p-Coumaric acid	Pure compounds from the Phenylpropanoid pathway	*M. incognita*	Chemotaxis factor (Cf) done in plates with water agar and time-lapse photographs of nematode tracks			Repellent	Wuyts et al. (2006)
Caffeic acid						Repellent	
Ferulic acid						Repellent	
Kaempferol						Repellent	
Quercetin						Repellent	
Myricetin						Repellent	
Salicylic acid					Attractant		
Lauric acid – 0.5–2 mM	Crown daisy exudates	*M. incognita*	Chemotaxis index (CI) in agar plates	3	0.17–0.22		Dong et al. (2014)
Lauric acid – 4 mM				1		0.08	
Dibutyl phthalate	Tomato root exudates	*M. incognita*	CI in Petri plates with agar water	3		0.3–0.49	Yang et al. (2016)
Methyl salicylate	*Capsicum annum* root volatiles	*M. incognita*	CI determined in dual choice olfactometer filled with sand	3	0.4–0.62		Kihika et al. (2017)
α-Pinene				3	0.1–0.24		
(+)-Limonene				3	0.22–0.28		
Tridecane				3	0.12–0.2		
2-Methoxy-3-(1-methylpropyl)-pyrazine				2	0.05–0.1		
Thymol				3		0.2–0.64	
Ethephon[d]	Synthetic plant phytochemicals	*M. incognita*	CI in agar plates		0.6		Fleming et al. (2017)
Salicylic acid					0.42		
Mannitol					0.31		
Indole-3-acetic acid					0.26		
Gibberellic acid					0.47		

6-Dimethylallylamino purine					0.46		
Vanillic acid					0.45		
Coumaric acid						0.63	
trans-Cinnamic acid						0.31	
Palmitic acid	Castor bean exudates	*M. incognita*	CI in water agar			0.08–0.18	Dong et al. (2018)
Linoleic acid						0.02–0.12	
Methyl salicylate	Tomato root exudates	*M. incognita*	CI in sand	3	0.16–0.52		Kirwa et al. (2018)
Zeatin				5	0.14–0.44		
Luteolin				4		0.1–0.36	
Quercetin – low conc.[e]				3	0.08–0.38		
Quercetin – high conc.[e]				2		0.04–0.24	
Solasodine				4		0.06–0.16	
Tomatidine				3		0.12–0.2	
3-Methylbutan-1-ol	Pure compounds	*M. incognita*	CI in pluronic gel	6	0.4–0.9		Shivakumara et al. (2018)
Butan-1-ol				6	0.23–0.83		
Benzaldehyde – high conc.				6		0.44 (1)[f]	
Benzaldehyde – low conc.				6	0.1–0.64 (5)[f]		
Butan-2-one				6	0.25–0.8		
Octan-1-ol				6		0.1–0.42	
Methyl salicylate	Exudates from tomato and spinach	*M. incognita*	CI in olfactometer with sand		0.2–0.48		Murungi et al. (2018)
Tridecane					0.02–0.28		
Sabinene					0.04–0.2		
2-Isopropyl-3-methoxypyrazine					0.04–0.2		
Cadaverine		*M. incognita*	CI with pluronic gel		0.81		

(continued)

Table 3.1 (continued)

Compound	Source	*Meloidogyne* species	Chemotaxis				References
			Evaluation[a]	Assays[b]	Attractant +[c]	Repellent −[c]	
Putrescine	Soybean and tomato root exudates				0.71		Oota et al. (2020)
Propane-1,3-diamine					0.58		
Ethylenediamine					0.22		
Propylamine					0.07		
Spermidine					0.3		
Spermine					0.27		
Octane-1,8-diamine					0.11		
Heptane-1,7-diamine					0.07		
Hexane-1,6-diamine					0.06		
Nonane-1,9-diamine						0.02	
trans-Cinnamic acid	Pure compounds	*M. javanica/M. marylandi/M. hapla*	Relative density (RD) of J2 in pre-defined zones in agar plates. RD > 2.0 was defined as attractant		8.3/7.0/ 3.7[f]		Oka (2020)
Salicylic acid					6.0/13.4/ 2.3		
4′-Hydroxy-3′-methoxyacetophenone					3.0/4.1/ 5.2		
O-vanillin					5.1/11.6/ 5.0		
Carvacrol					9.6/11.3/ 4.2		
2-Methoxybenzaldehyde					6.1/8.3/ 6.6		
3-Methoxybenzoic acid					7.4/10.3/ 4.9		

3-Methoxybenzyl alcohol					3.0/6.8/5.3		
2-Methoxycinnamaldehyde					10.6/8.8/5.2		
trans-p-methoxycinnamaldehyde					2.8/10.9/2.5		
4-Methoxy-3-methylbenzaldehyde					11.0/7.4/5.6		
2-Methoxy-4-propenylphenol					7.3/5.0/4.9		
Thymol					3.2/10.0/2.5		
Salicylic acid	Pure compounds	*M. javanica*, *M. Marylandi*, *M. hapla*, *M. incognita*	CI calculated with the number of J2s trapped in tubes placed in sterile sand dune		0.96/0.95/0.083/0.09[g]		Oka (2021)
Carvacrol					0.31/0.88/0.78/0.74		
O-vanillin					–/0.90/0.64/–		
trans-Cinnamic acid					0.66/–/–/–/0.91		
2-Methoxycinnamaldehyde					0.85/0.95/0.65/0.65		
3-Methoxybenzoic acid					0.89/0.73/0.81/0.76		
4-Methoxybenzoic acid					0.96/0.85/0.63/0.83		
2-Methoxybenzaldehyde					0.90/0.94/0.85/0.80		

(continued)

Table 3.1 (continued)

Compound	Source	*Meloidogyne* species	Chemotaxis				References
			Evaluation[a]	Assays[b]	Attractant +[c]	Repellent −[c]	
Tridecane	Root exudates of tomato, radish, cucumber, alfalfa, lettuce and pepper	*M. incognita*	CI in pluronic gel	9	0.03–0.22 (5)	0.02–0.25 (4)	Wang et al. (2021)
Octadec-1-ene				9	0.04–0.22 (9)		
2-Hexyldecan-1-ol				9	0.04–0.26 (7)*	0.03–0.20 (2)	
Docos-1-ene				9	0.23 (1)	0.04–0.24 (8)*	
Malic acid				5	0.01–0.23 (4)*	0.03 (1)	
Tartaric acid				5	0.05–0.15 (4)*	0.07 (1)	
Maleic acid				5	0.07–0.10 (4)*	0.05) (1)	
Oxalic acid				5	0.23 (1)	0.07–0.43 (4)*	
Lactic acid				5	0.04–0.20 (4)*	0.02 (1)	
Glycolic acid				5	0.06–0.16 (4)*	0.05 (1)	
4-aminobenzoic acid				5	0.03–0.22 (4)*	0.16 (1)	
Ferulic acid				5	0.02–0.08 (4)*	0.03 (1)	
Amygdalic acid				5	0.10 (1)	0.01–0.19 (4)*	

Rhamnogalacturonan-I (RG-I)	From flaxseed mucilage	*M. incognita*	CI in Petri plates with pluronic gel		0.47		Tsai et al. (2021)
L-Gal(α1–3)-L-Rha(1) – RG-I side chain					0.35		

[a]The chemotaxis index (CI) is calculated with the formula: (Number of J2s in the test area – number of J2s in the control area)/number of J2s in both test and control areas. When the CI was not given by the authors, the numbers in the figures were extracted with the program WebPlotDigitizer (https://automeris.io/WebPlotDigitizer) and the CI index calculated to facilitate comparisons
[b]Number of assays with different concentrations done in the study
[c]Classification of the compounds as attractant when the CI is shown in this column or repellent when the CI is presented in the column. A dash between two numbers indicates a range of values
[d]Ethephon is a synthetic product used as growth regulator, therefore cannot be considered a plant-derived hormone
[e]High and low concentrations of the compound
[f]The numbers between parenthesis indicate the number of assays in which the response is either attractant or repellent to J2s
[g]The numbers separated by slashes refer to the respective *Meloidogyne* species. A dash just before a slash indicates that the species was not tested for this compound
*Asterisks indicate the predominant activity of the compound on the basis of the number of assays with different concentrations performed in the study

were done with different methods, nematode species and populations and chemicals, without any standardized controls across studies. In this chapter, we made an effort to compile the studies with purified chemicals tested in chemotaxis of *Meloidogyne* species in a quantitative way, whenever possible (Table 3.1). The determination of a chemotaxis index (CI) is the most common way of presenting the data. This is a convenient way to make comparisons, especially when the methods are the same, but one should always keep the differences in mind. For example, salicylic acid was used in four different studies and in only one of them, it did not attract *M. incognita*, although it did not repel (Table 3.1). In these four studies, the chemotaxis index varied from 0.09 to 0.42 and four different methods were used to determine CI (Table 3.1), illustrating the difficulties of comparing these data. Nevertheless, when the methods are the same, there is value in comparing the CIs obtained in different studies. As an example, the CI of methyl salicylate (MeSA) in sand varied from 0.16 to 0.52 in one study and from 0.2 to 0.48 in another, both in the same range (Table 3.1).

Although studies on chemotaxis are done with pure compounds, semiochemicals are not expected to exert their activities isolated, but in complex mixtures. In some studies, this aspect was taken into consideration. For example, MeSA was detected in tomato roots and shown to contribute to the attractiveness of tomato to *M. incognita*, whereas 2-isopropyl-3-methoxypyrazine and tridecane contributed to the attractiveness of spinach. MeSA exerted a stronger attraction even when mixed with other compounds and was responsible for the preference of tomato over spinach by *M. incognita* (Murungi et al. 2018). The blend composed of α-pinene + limonene +2-methoxy-3-(1-methylpropyl)-pyrazine + tridecane + MeSA was highly attractive to J2s of *M. incognita*. However, when MeSA was removed from the blend, the attractiveness was drastically reduced. Similarly, thymol induced negative chemotaxis (repellence) when it was added in any blend (Kihika et al. 2017).

There is an effect of the concentration for many of these chemical compounds, where lower concentrations attract nematodes and higher concentrations repel them and vice versa (Li et al. 2019; Tables 3.1 and 3.2). This is another factor that makes comparisons across studies difficult because there is no standardization among studies. Additionally, some compounds detected in root exudates might be contaminants from soil, microorganisms or the extraction process. One possible example is dibutyl phthalate, a common plasticizing agent, that was detected in tomato root exudates (Yang et al. 2016). Although its origin is unknown, it has been reported to be produced by filamentous fungi in nature (Tian et al. 2016).

It appears that there is no universal chemical that will function in the same way for all *Meloidogyne* spp. However, some chemical characteristics gave some hints in determined systems. For example, Oota et al. (2019) found that only diamines with a backbone containing three to five carbons, including cadaverine, putrescine and propane-1,3-diamine attracted J2s of *M. incognita* among the 376 compounds tested. Cadaverine was the most attractive compound to J2s of *M. incognita*, but it had no effect on *M. arenaria* and *M. enterolobii*, showing that this specificity may determine the host range of different *Meloidogyne* spp. (Oota et al. 2019). According to the authors, cadaverine is released by stressed plants, leading nematodes to potential

Table 3.2 Pure compounds from microorganisms with activity on *Meloidogyne* chemotaxis

				Chemotaxis			
Compound	Source	*Meloidogyne* species	Evaluation[a]	assays[b]	Attractant +[c]	Repellent -[c]	References
Acetone	VOCs from *Paenibacillus polymixa* KM2501–1	*M. incognita*	CI in agar plates	5	0.10–0.27		Cheng et al. (2017)
Decan-2-ol				5	0.06–0.17		
Furfural acetone				5	0.29–0.47		
Undecan-2-one				5		0.09–0.44	
4-Acetylbenzoic acid				5	0.09–0.24 (2)[d]	0.06–0.23 (3)[d]	
(*Z*)-Hexen-1-ol acetate	VOCs from *Pseudomonas putida* 1A00316	*M. incognita*	CI in 2% agar plates	5		0.42–0.58	Zhai et al. (2018)
Octan-2-one				5		0.41–056	
Undec-1-ene				5		0.33–0.56	
1-(Ethenyloxy)octadecane				5		0.23–0.49	
Dimethyl-disulfide				5		0.45–054	
Undecan-2-one				5		0.49–0.73	
Nonan-2-one				5		0.42–0.48	
3,3-Dimethyloctane	Tomato exudates with *Bacillus cereus* BCM2	*M. incognita*	CI in agar plates	3	0.46 (1)	0.18 (1)	Li et al. (2019)
Tridecane				3	0.08 (1)	0.06–0.08 (2)	
2,4-Di-tert-butylphenol				3	0.2–0.26		
Benzothiazole	VOCs from *Streptomyces plicatus* G	*M. incognit*a	CI in plates with 1% agarose	3		0.04–0.4	Wang et al. (2019)
Dibenzofuran				3	0.22–0.46		
Benzothiazole + dibenzofuran				3	0.06–0.38		
1,4-Dimethoxybenzene	VOC from *Purpureocillium chlamydosporia* Pc-10	*M. incognita*	CI in agar plates	5	0.29–0.8		Pacheco et al. (2021)
5-Methoxymethyl-1*H*-pyrrole-2-carboxaldehyde—high conc.[e]	From *Purpureocillium lavendulum* YMF1.00683	*M. incognita*	CI in plates with agarose	3		0.07–0.38	Bao et al. (2022)

(continued)

Table 3.2 (continued)

				Chemotaxis			
Compound	Source	*Meloidogyne* species	Evaluation[a]	assays[b]	Attractant +[c]	Repellent -[c]	References
5-Methoxymethyl-1*H*-pyrrole-2-carboxaldehyde—low conc.[e]				3	0.02–0.13		

[a]The chemotaxis index (CI) is calculated with the formula: (Number of J2s in the test area – number of J2s in the control area)/number of J2s in both test and control areas. When the CI was not given by the authors, the numbers in the figures were extracted with the program WebPlotDigitizer (https://automeris.io/WebPlotDigitizer) and the CI index calculated to facilitate comparisons
[b]Number of assays with different concentrations done in the study
[c]Classification of the compounds as attractant when the CI appears in this column or repellent when the CI is presented in the column
[d]The numbers between parenthesis indicate the number of assays in which the response is either attractant or repellent to J2s
[e]High and low concentrations of the compound

hosts with a compromised immunity. In another study, Oka (2020) found that the most attractive chemicals to three different *Meloidogyne* spp. in a screening of 60 pure compounds contained a methoxy group (OCH_3) and postulated that its presence may play a role in attraction. Although the methoxy group was present in the attractants reported by Oka (2020), it is absent from widely known list of semiochemicals such as salicylic acid and carvacrol (attractants) and thymol and *trans*-cinnamic acid (repellents).

Non-volatile compounds from tomato root exudates were fractionated and the phytohormone zeatin (cytokinin) was shown to be attractive to the *M. incognita* J2s, whereas the flavonoid quercetin elicited concentration-dependent responses, being attractive at low concentrations and repellent at high concentrations (Kirwa et al. 2018). These results indicate that the concentration of certain chemicals and the ratio among compounds in mixtures determine the complex responses of *Meloidogyne* spp. (Kirwa et al. 2018). Furthermore, zeatin was shown to be secreted by *M. incognita* and is probably used in the manipulation of plant hormone balance in the initial stages of invasion for the establishment of feeding sites (Dowd et al. 2017; Kirwa et al. 2018). It appears that most phytohormones are somehow involved in the attractiveness of *Meloidogyne* to plants, including indolacetic acid (IAA), salicylic acid, jasmonic acid and ethylene (Wuyts et al. 2006; Bhattarai et al. 2008; Curtis 2008; Fudali et al. 2013; Fleming et al. 2017; Zinovieva et al. 2021). Salicylic acid was shown to be an attractant of *M. incognita* J2s, but it also inhibited egg hatching and had nematicidal effects (Wuyts et al. 2006). Foliar or drench applications of salicylic acid suppressed *M. incognita* (Maheshwari and Anwar 1990; Nandi et al. 2003), probably by increasing the level of plant resistance. However, exogenous application of IAA decreased the resistance of plants to *M. incognita* (Curtis 2008). Mutants deficient in the accumulation of salicylic acid and ethylene attracted more J2s than the wild type (Fudali et al. 2013; Čepulyté et al. 2018), whereas the role of jasmonic acid in chemotaxis is less understood (Bhattarai et al. 2008). In addition to VOCs and phytohormones, *Meloidogyne* spp. also responds to fatty acids, such as lauric acid that was found in exudates of crown daisy (Dong et al. 2014) and palmitic and linoleic acid from roots of castor bean (Dong et al. 2018).

In a relatively large-scale screening, Oka (2020) tested 60 pure aromatic compounds against *M. incognita*, *M. javanica*, *M. marylandi* and *M. hapla* and found that none of the compounds was repellent, even the ones with nematicidal activity, such as carvacrol. *Meloidogyne incognita* did not respond to any of the compounds and 35 of them attracted at least one of the three other species, and 13 were considered highly attractive (Table 3.1). Although *M. javanica* and *M. hapla* are considered species with a broad host range, the specialist *M. marylandi* was attracted to more chemicals. In this study, thymol and salicylic acid, previously found to be repellent and attractant, respectively, by other authors (Fleming et al. 2017; Kihika et al. 2017; Wuyts et al. 2006), did not elicit any response from *M. incognita*. These results raise awareness to the fact that either the methodology used by Oka (2020) needs to be further evaluated or populations of *M. incognita* are responding differently to the same chemicals as implied by Wang

et al. (2009). In a follow-up study, Oka (2021) used a bioassay with trap tubes filled with sand. In contrast with the other study (Oka 2020), the author was able to show attraction of *M. incognita* J2s to salicylic acid and less attractiveness of all species of *Meloidogyne* to carvacrol (Table 3.1). Differential responses are known to occur among *Meloidogyne* species and their nature is still unknown. More investigations in this area will uncover if there is any link between chemotaxis and host range. Additionally, the concentrations used in laboratory assays are not always realistic in the field.

3.5.3 Nematode-Derived Compounds

The semiochemical compounds described up to now are produced either by plants or by microorganisms in soil or in the rhizosphere. However, there is a large class of glycosidic hormones called ascarosides, universally conserved among nematodes that function in mate location, aggregation and regulation of development (Choe et al. 2012; Schroeder 2015). Ascarosides seem to be devoid of antimicrobial activity and sometimes may act against parasitic nematodes as they are also perceived by other microorganisms such as nematophagous fungi, that are induced to produce trapping structures to capture nematodes moving in soil (Hsueh et al. 2013). These molecules are also perceived by plant roots at pico to nano molar concentrations and elicit systemic resistance to nematodes and other pathogens, in plants as diverse as tomato, *Arabidopsis* and barley (Manosalva et al. 2015).

Ascaroside ascr#18 (Fig. 3.2), the most common in *Meloidogyne* spp. and other nematodes, is a weak attractant to nemadodes (Hamada et al. 2020). This compound was shown to be metabolized by plants and transformed into ascr#9 (Fig. 3.2), which in mixtures with asc#18 repelled J2s of *M. incognita* (Manohar et al. 2020). It has also been shown that repellence, rather than systemic resistance, was mainly responsible for the reduced infection by *M. incognita* (Manohar et al. 2020). Therefore, these mixtures of ascarosides seem to interfere with the plant-nematode interaction by reducing the level of infection.

3.5.4 Inorganic Compounds

Inorganic salts and ions were investigated for their effect on the chemotaxis of *M. incognita* J2s and most of them were found to be repellent. No salt was found to be a consistent attractant to the J2s of this species. In some cases, higher concentrations resulted in stronger repellence (Qi et al. 2015). Salts of nitrate (NO_3^-), ammonium (NH_4^+), thiocyanate (SCN^-), cesium (Cs^+), potassium (K^+) and sodium (Na^+) were among the most repellent (Castro et al. 1990; Le Saux and Quénehervé 2002; Qi et al. 2015). Salts of chloride (Cl^-), sulfate (SO_4^{2-}), hidrogenphosphate (HPO_4^-), carbonate (CO_3^{2-}) and hydroxide (OH^-) repelled at

a lower extent, whereas salts of calcium (Ca^{2+}) had no effect (Castro et al. 1990; Le Saux and Quénéhervé 2002; Qi et al. 2015).

Many of these salts are used as fertilizers and may have a disruptive effect on nematode orientation in soil (Qi et al. 2015). Besides repelling nematodes, some salts, such as the ones containing ammonium have a nematicidal activity (Oka and Pivonia 2002). It would be interesting to determine if these salts can increase the efficacy of chemical nematicides when they are combined in joint field applications.

3.6 Microorganisms Affecting *Meloidogyne* Chemotaxis

Plant roots are metabolically active organs that produce exudates and when these compounds are released, they attract microorganisms of different trophic levels, including saprophytes, symbionts and phytopathogens, such as plant-parasitic nematodes (Hol et al. 2013). The rhizosphere is one of the most complex ecosystems on earth, fostering millions of microbial cells that can affect the migration of nematodes (Korenblum et al. 2020). Surprisingly, despite the extensive number of reports demonstrating the influence of root exudates from host plants on the behaviour of plant-parasitic nematodes, there have been few studies on the behaviour of nematodes with respect to soil microorganisms. Several authors have demonstrated that bacteria, mainly in the genera *Bacillus* and *Pseudomonas*, are able to reduce *Meloidogyne* spp. penetration and reproduction (Leontopoulos et al. 2017; Cruz-Magalhães et al. 2021; Antil et al. 2022; Gowda et al. 2022). It is thought that microorganisms, in general, can alter the production of root exudates or modify their composition after secretion, thereby affecting nematode chemotaxis. One of the main effects of microorganisms is to decrease the attractiveness of the root exudates (Padgham and Sikora 2007; Hu et al. 2017; Zhao et al. 2022).

Bacteria such as *Pseudomonas oryzihabitans* were shown to inhibit the migration of *M. javanica* J2s by modifying the root exudates, making it less attractive to the nematode (Leontopoulos et al. 2017). The efficient colonization of roots by the biological control agent *Bacillus cereus* strain BCM2 was fundamental to repelling J2s of *M. incognita*, leading to 80% reduction in the number of galls (Hu et al. 2017). Based on these results, Li et al. (2019) studied the composition of root exudates released by tomato plants colonized by *B. cereus* BCM2 and showed that the bacterium changed the composition of the exudates, increasing the number of molecules produced, including 2,4-di-tert-butylphenol and 3,3-dimethiloctane, which reduced the number of galls and the number of nematodes in soil and plant tissue. The VOCs furfural acetone and decan-2-ol from the bacterium *Paenibacillus polymyxa* KM25021–1 attracted J2s of *M. incognita* in a strategy named "honey-trap" by the authors (Cheng et al. 2017). These J2s were subsequently killed either through fumigation or direct contact with the bacterium, which probably used the nematode as a food source.

In a screening of actinomycetes performed by Wang et al. (2019), 17% of the isolates attracted J2s of *M. incognita*, while 8% repelled them. The selected actinomycete *Streptomyces plicatus* strain G produced the VOC dibenzofuran (Fig. 3.2),

that was a potent attractant to J2s, whereas benzothiazole (Fig. 3.2) was a repellent. The attractive effect prevailed when the mixture of purified VOCs or cultures of the bacterium were applied to tomato roots. This bacterium may attract the nematodes to the roots to use them for their nutrition.

Fungi were also shown to affect the chemotaxis of *Meloidogyne* species J2s. Common endophytic fungi such as *Fusarium* spp. were shown to alter the composition of root exudates (Hallmann and Sikora 2011) and thereby affect chemotaxis. *Purpureocillium lavendulum* produced the compound 5-methoxymethyl-1*H*-pyrrole-2-carboxaldehyde (Fig. 3.2), which attracted J2s of *M. incognita* at low concentrations and was toxic at high concentrations, causing up to 98% mortality and inhibiting egg hatching by 81% (Bao et al. 2022). The fungal species *Pochonia clamydosporia* has been widely studied for its antagonistic interaction with plant-parasitic nematodes. This fungal species produced several VOCs and among them, 1,4-dimethoxybenzene (Fig. 3.2), which attracted J2s of *M. incognita,* causing 89% mortality and reduced hatching by 86% (Pacheco et al. 2021). The nematophagous fungus *Arthrobotrys oligospora* perceives the presence of nematodes by detecting their ascarosides (Hsueh et al. 2013) and is then able to attract these nematodes with volatile furanones and at the same time increase the number of traps to capture nematodes by signaling with pyrones (Wang et al. 2018b).

Some of these rhizosphere microorganisms are active ingredients of commercial products because they reduce the reproduction of *Meloidogyne* spp. on plants. However, the mode of action of some of them is still unknown, but part of them is expected to act by disrupting chemoreception in J2s.

3.7 Prospects and Potential Uses of Chemotaxis to Manage *Meloidogyne* Species

Plants and microorganisms rely on chemical communication networks to determine the outcome of their interactions (Van Dam and Bouwmeester 2016). The composition and concentration of semiochemicals impact plant development and health as plants evolved strategies to interact with beneficial microorganisms and protect themselves against pathogens, such as nematodes (Siddique et al. 2022).

Several techniques were employed to study chemotaxis in vivo and in vitro (Dusenbery 1980, 1983; Castro et al. 1988; Haseeb and Fried 1988; Perry 1996; Rocha et al. 2016; Wang et al. 2009; Oka 2020, 2021; Pacheco et al. 2021). These techniques have advantages and disadvantages, but none of them is superior. The most used in vitro approach is agar plates with demarcated zones to calculate the chemotaxis index (Cheng et al. 2017; Zhai et al. 2018) and in vivo/*in planta* assays are pots connected with tubes filled with soil or sand (Wang et al. 2019; Oliveira et al. 2020). The most challenging task is extracting the nematodes from the soil (Oka 2021). Although assays in sand or soil may best simulate the natural environment, nematodes cannot be seen in these opaque substrates, instead, they must be extracted to monitor migration (Siddique et al. 2022). Nematode extraction techniques recover only around 10% of the total number of nematodes placed in

soil (Oka 2020; Viglierchio and Schmitt 1983). Together these two factors may explain why most chemotaxis studies are conducted in vitro with Petri dishes. These in vitro assays are difficult to standardize because of the variation in set-ups. New apparatuses with microchannels filled with a gel appear to allow the quantitative and high-throughput efficient determination of chemotaxis in nematodes (Hida et al. 2015) or standardized chambers made by 3D printers could help standardize the chemotaxis tests (Laloum et al. 2020).

Many chemicals from plants and microorganisms that play a role in chemotaxis are being revealed. These chemicals may be used in nematode management in different ways, such as the development of synthetic nematicides by using them as lead structures. This may be necessary if the chemicals are not stable enough to be used in their natural form. Some chemicals such as carvacrol have dual effects as they attract and kill nematodes at the same time (Oka 2020) and can be used directly as a nematicide. Plants may not produce enough of these semiochemicals or may depend on specific conditions such as temperature and nutrition, and therefore the direct application of the purified product might be more efficient, especially when they can be produced at low costs. One of the difficulties with synthetic semiochemicals is that they appear to be highly specific. Finding compounds that would attract a broad range of parasitic nematodes seems to be impossible. Up to this moment, there is no universal attractant to all *Meloidogyne* species.

Interference with chemotaxis is one of the most promising management strategies for nematodes in general. Interference could be applied by using plants or/and microorganisms that produce or modify the semiochemicals in order to decrease or eliminate chemotaxis, produce repellents or increase the amount of attractive chemicals. The final outcome would be the impedance of host location by lack of attractants, presence of repellents and a confounding effect that would lead J2s overwhelmed and incapable of locating the host. Plants already naturally interfere with chemotaxis by perceiving nematode ascarosides, for example, and synthesizing chemicals that repel nematodes and induce systemic resistance (Manohar et al. 2020). Repellence may be selected in different plants, as shown for peppers, where resistant cultivars repelled *M. incognita* J2s whereas the susceptible ones attracted (Hu et al. 2017; Kihika et al. 2017). The selection of plants that host more microorganisms, such as bacteria and fungi that produce repellent semiochemicals, is a strategy that has not yet been exploited but holds promise. Another strategy of interest is the modification of plant root exudates by microorganisms. Exudates of lettuce are normally attractive to *M. incognita*, but the inoculation of roots with an isolate of *Bacillus subtilis* turned them repulsive to the nematode (VP Cavalcanti, unpublished data). Trap plants are regarded as attractive to *Meloidogyne* spp. and their use is considered effective, especially in small plots. For example, Dong et al. (2014) reported that five crown daisy plants can protect one tomato plant from *M. incognita*. Yet another way of interfering with chemotaxis is inserting a physical barrier between the nematode and plant roots, such as wrapping with banana tissue employed in Africa to control the potato cyst nematode (Ochola et al. 2022).

Transgenic plants, although not yet widely accepted, are interesting alternatives to manage nematodes through chemotaxis. Transgenic potato plants secreting peptides that interfere with chemoreception decreased *Globodera pallida* infection and development (Liu et al. 2005). This strategy, which aims to interfere with the invasion process rather than with the feeding process adopted in most transgenic plants (Atkinson et al. 2003), may be further explored to control *Meloidogyne* spp.

The number of studies with the olfactory genes in *Meloidogyne* spp. is still relatively small, but at least 14 genes were characterized in the genome of *M. incognita* (Dong et al. 2014; Shivakumara et al. 2019; Li et al. 2022). When these genes were interfered with iRNA by soaking, the J2s lost their attraction towards or repulsion away from different semiochemicals that were previously known to affect the chemotaxis of J2s of this species (Shivakumara et al. 2019; Li et al. 2022). These results indicate that these genes are targets for the development of new chemical nematicides that interfere with chemotaxis, new iRNA-based nematicides directed to these genes or the development of transgenic plants through host-induced gene silencing that would interfere with these genes and disrupt chemotaxis.

Nematode chemotaxis is tightly associated with microorganisms that colonize the rhizosphere and soil. Chemicals released by bacteria and fungi (Table 3.2) and other interactions that are not yet well understood influence chemotaxis. For example, most studies report that mycorrhized plants reduced the ability of nematodes to locate and penetrate plant roots by interfering with chemotaxis (Bacetty et al. 2009; Vos et al. 2012). Some studies show the contrary, increased infection in mycorrhized plants due to a decreased resistance induced by the symbiont (Borowicz 2001; Hol and Cook 2005; Frew et al. 2018). However, most studies showing increases in nematode populations were done with migratory nematodes, which appear to influence the outcome (Gough et al. 2020). Metataxonomic studies on the whole microbiome with NGS sequencing will shed more light on the complex interactions between nematodes and the other microorganisms with whom they share the infection court. In this context, the microbiome in nematode-suppressive soils may harbour the clues needed to build an unfavourable environment for these parasites (Topalovic et al. 2020). These types of studies showed changes in the bacterial and fungal communities (Wang et al. 2014; Toju and Tanaka 2019; Yergalieyev et al. 2020; Zhang et al. 2020; Liu et al. 2022) and nematode populations (Sikder et al. 2021) influenced by semiochemicals or by the presence of nematodes. However, in order to turn this knowledge into control measures, more field experiments with these anti-nematode microorganisms need to be pursued.

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