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Chemical Ecology of Plant–Nematode Interactions : Mechanisms and Implications for Sustainable Crop Management

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ABSTRACT

Chemical ecology offers a powerful framework for understanding how root-knot nematodes (RKN) locate, invade and exploit plant hosts. These obligate parasites rely entirely on chemical signals to navigate soil environments, respond to plant root exudates and establish feeding sites. Differences in exudate chemistry among cultivars strongly influence nematode attraction, helping explain patterns of susceptibility and resistance observed in the field. Recent metabolomics studies in rice and tomato have highlighted the importance of specific soluble and volatile compounds in guiding host preference. Soil microbes add further complexity by masking attractant cues, producing deterrent metabolites and activating plant defence pathways. Beneficial endophytes such as *Aspergillus niger* F4 operate through dual mechanisms, direct nematicidal activity and priming of host defences, reducing nematode penetration and reproduction. By integrating insights from nematode behaviour, plant biochemistry and rhizosphere microbiology, chemical ecology provides new opportunities for developing sustainable management strategies. This article synthesises these mechanisms and highlights their relevance for designing cultivar-based, microbial-based and ecologically informed approaches for sustainable management of root knot nematodes.

Keywords : Chemical ecology, Nematode Chemotaxis, Host plant resistance, *Meloidogyne* spp., Rhizosphere microbiome, Biological control.

Introduction

Sustainable agriculture is the backbone of global food production to ensure steady supply of food for the growing population while preserving environmental balance. However apart from the commonly known abiotic stresses, various biotic stresses pose significant threat to sustainable crop productivity. Plant-parasitic nematodes are among the most serious yet often under-recognised threat to agricultural productivity worldwide. Despite their microscopic size, these obligate parasites cause extensive root damage that reduces water and nutrient uptake. Globally, nematodes cause annual yield losses exceeding USD 150 billion (Nicol *et al.,* 2011), affecting cereals, vegetables, pulses, fruit crops,

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ornamentals and plantation crops. In India, where smallholder agriculture dominates, losses of 15–40% have been reported in several crops, including rice and vegetables (Sasser and Freckman, 1987).

Table 1. Major plant-parasitic nematodes of India and their principal host plants

Nematode Species	Common Name	Key Host Crops in India	Notes on Economic Importance
Meloidogyne incognita	Root-knot nematode	Tomato, brinjal, okra, cucurbits,chilli, cotton, groundnut, tobacco	Most widespread RKN in India; causes severe losses in vegetable and cash crops
M. javanica	Root-knot nematode	Pulses, vegetables, groundnut, banana, sunflower	Highly polyphagous; major nematode in semi-arid regions
M. graminicola	Rice root-knot nematode	Rice (especially upland and DSR), some grasses	Major constraint in eastern and NE India; thrives under aerobic rice cultivation
M. arenaria	Peanut root-knot nematode	Groundnut, vegetables, tobacco	Important in peninsular India; damaging in groundnut-based systems
M. enterolobii	Guava root-knot nematode / Aggressive RKN	Guava, tomato, brinjal, okra, chilli, cotton	Highly aggressive; breaks many resistance genes; emerging threat in fruit orchards and vegetable systems
Heterodera avenae	Cereal cyst nematode	Wheat, barley, oats	Significant yield losses in the north-western plains
H. cajani	Pigeonpea cyst nematode	Pigeonpea, related legumes	Important in central and southern India; reduces vigour and nodule formation
H. zeae	Maize cyst nematode	Maize	Localised but increasing in north-western India
Radopholus similis	Burrowing nematode	Banana, black pepper, citrus, arecanut	Major factor in banana toppling disease; severe root destruction
Pratylenchus coffeae	Lesion nematode	Coffee, banana, turmeric, ginger, citrus	Migratory endoparasite; often interacts with fungal pathogens
P. zeae	Lesion nematode	Maize, sugarcane, rice, groundnut	Widespread in light-textured soils
Rotylenchulus reniformis	Reniform nematode	Cotton, okra, tomato, castor, pulses	Major nematode in rainfed cotton belts

Tylenchorhynchus spp.	Stunt nematodes	Cereals, fodder grasses, pulses	Common across soils; chronic yield suppression
Helicotylenchus spp.	Spiral nematodes	Vegetables, fruit crops, ornamentals	Moderate damage; problematic in high densities
Aphelenchoides besseyi	White-tip nematode	Rice	Seed-borne pathogen; causes white-tip disease
Ditylenchus dipsaci	Stem and bulb nematode	Onion, garlic, alfalfa, ornamentals	Survives desiccation; major pest of bulb crops

Among all plant-parasitic nematodes, root-knot nematodes (*Meloidogyne* spp.) are the most economically important. They parasitise more than 3000 plant species, including key food, fibre, and horticultural crops (Jones *et al.*, 2013). *Meloidogyne incognita*, *M. javanica* and *M. graminicola* are particularly widespread across Indian agroecosystems (Karssen *et al.*, 2013). Recently, *M. arenaria* and *M. enterolobii* have gained importance, with *M. enterolobii* recognised as a highly aggressive species capable of infecting a wide range of horticultural crops and breaking resistance in several hosts (Elling, 2013). These nematodes induce specialised multinucleate feeding cells, known as giant cells, inside the root, which subsequently develop into visible galls. By redirecting nutrients and altering vascular flow, they disrupt normal root physiology and weaken plant growth. In vegetable crops, particularly tomato, brinjal, cucurbits and solanaceous crops, *M. incognita* can cause up to 50% yield loss in heavily infested fields (Sikora and Fernandez, 2005). The symptoms, stunting, yellowing, nutrient deficiencies, wilting under mild moisture stress, and characteristic gall formation, are often confused with soil fertility problems, delaying diagnosis and allowing nematode populations to build up silently over seasons.

Management of root-knot nematodes remains a major challenge in India, particularly for resource-poor farmers. Historically, nematicides such as carbofuran and aldicarb provided effective control, but these compounds have been phased out due to toxicity and environmental risks (Chen *et al.*, 2020). Newer molecules, although safer, are expensive, often unavailable in rural markets, and lack label recommendations for smallholder-grown vegetable crops (Chen *et al.*, 2020). Additionally, nematodes reside inside roots, making them less accessible to contact nematicides. Cultural practices, crop rotation, soil solarisation, flooding, and organic amendments can manage nematode population but control success varies across regions, soil types,

Chemical ecology studies how plants, nematodes and microbes communicate using chemical signals.
These interactions shape host location, invasion and plant defence.

and climatic conditions (Stirling, 1988). Biological control using fungi and bacteria is promising but requires rigorous field validation to ensure consistent performance across diverse Indian agro-ecologies (Tian *et al.*, 2007). As a result, nematodes continue to persist as a chronic problem, especially in intensively cultivated vegetable systems.

This persistent challenge highlights the need for a deeper understanding of what drives nematode behaviour: how they locate host roots, choose susceptible varieties, avoid resistant cultivars, and manipulate plant cells to establish feeding sites. These behaviours are governed primarily by chemical signals exchanged between nematodes, plant roots, and associated soil microbes. This field of study, known as *chemical ecology*, examines how organisms use chemical cues for communication, survival, and interaction with their environment. For plant parasitic nematodes, chemical ecology provides a mechanistic understanding for several field observations: why nematodes thrive in some soils but not others, why certain crop varieties are consistently more susceptible, why some intercrops or organic amendments suppress nematode populations, and how microbial communities can alter nematode activity (Rasmann *et al.*, 2012).

Understanding these interactions is no longer merely academic. For agricultural practitioners, chemical ecology offers a scientific basis for devising practical, low-cost, and sustainable nematode management strategies. It provides a framework for explaining differences in susceptibility across crops and the influence of soil biological activity on nematode population. As knowledge in this field grows, it provides new opportunities for developing sustainable and scientifically grounded approaches to nematode management. As chemical ecology continues to uncover the molecular dialogue between plants, nematodes, and microbes, it provides new opportunities to integrate these insights into field-level decision-making (Dutta *et al.*, 2025; Dutta *et al.*, 2023; Dutta *et al.*, 2025).

This article synthesises current scientific knowledge on the chemical ecology of plant–nematode interactions with a focus on mechanisms relevant to field management. By linking root exudate chemistry to nematode chemotaxis, plant defence pathways, and soil microbial interactions, we aim to provide a mechanistic yet applied understanding that can support sustainable crop protection across India's diverse agroecosystems.

Biology of Root-Knot Nematodes and the Chemical Basis of Their Behaviour

Root-knot nematodes (*Meloidogyne* spp.) are microscopic, worm-like animals belonging to the kingdom *Animalia*. Most root-knot nematodes share a similar life cycle consisting of the egg, four juvenile stages (J1–J4), and the adult male or female (Jones *et al.*, 2013). The first moult occurs inside the egg, and the juvenile that emerges is the second-stage juvenile (J2). This J2 stage is the only infective stage capable of locating and penetrating a host root. Once inside the root, the nematode induces the formation of specialised multinucleated feeding cells and continues to grow. Females become swollen and sedentary, producing eggs either through mating or, commonly, parthenogenesis

(Jones *et al.*, 2013). Under optimal warm conditions, the complete egg-to-egg cycle may take only 2–4 weeks, allowing rapid population build-up in cropping systems (Jones *et al.*, 2013).

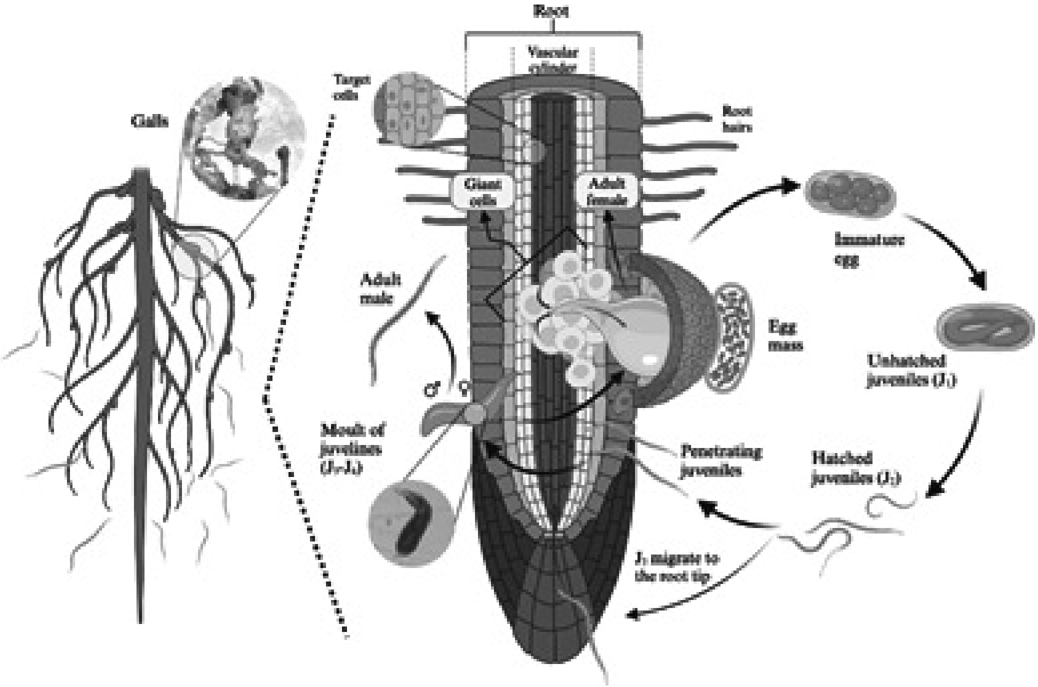

Figure 1. Life cycle of *Meloidogyne incognita* (Image courtesy: bioRender.com)

Chemical Ecology of Host Location

Host Location as a Chemically Guided Process

The infective second-stage juvenile (J2) of root-knot nematodes depends entirely on chemical signals in the soil to locate a suitable host. Unlike insects, nematodes do not use any visual cue and have very limited mechanosensory abilities; their survival relies on detecting and interpreting chemical gradients produced by plant roots and the surrounding microbiota (Rasmann *et al.*, 2012). Because J2s cannot feed until they enter the root, efficient host location is essential, and failure to find a host within a short period leads to starvation.

Host location therefore represents a critical ecological stage and is shaped by a wide array of chemical cues that diffuse through soil water films. These cues vary across plant species, cultivars, developmental stages and soil environments, creating a chemically heterogeneous landscape that nematodes must navigate. Understanding this chemically guided behaviour forms the basis for interpreting why nematode infestations differ across fields, why some varieties are consistently more susceptible and how soil biological activity affects nematode success (Rasmann *et al.*, 2012).

Nematode Chemosensory Structures : Amphids and Phasmids

Successful host location by root-knot nematodes relies on specialised chemosensory organs that detect and interpret chemical gradients in the soil. The two principal structures involved in this process are the amphids and phasmids, which together enable the infective juvenile (J2) to sense soluble compounds, volatiles and other chemical cues released from plant roots and soil microbes (Rasmann *et al.*, 2012).

A) Amphids : These are paired sensory organs located on the anterior end of the nematode. Each amphid contains multiple chemosensory neurons that open to the external environment through small pores near the lips. These are the primary structures responsible for :

- detecting root-derived soluble attractants such as amino acids, sugars and organic acids,
- sensing volatile organic compounds at low concentrations,
- interpreting directional chemical gradients by comparing changes in concentration as the nematode moves.

The amphids allow the J2 to orient towards zones of increasing attractant concentration, a behaviour known as chemo-orientation. This provides the nematode with the ability to locate host roots even in complex, heterogeneous soil environments.

B) Phasmids : These are posterior sensory organs located near the tail region. Although structurally simpler than amphids, they contribute to :

- confirming the direction of chemical gradients during movement,
- fine-scale navigation when the nematode is close to the root,
- responding to local cues that help identify suitable invasion sites.

Phasmids also play a role in assessing the immediate microenvironment and may help the juvenile evaluate whether the chemical conditions are favourable for initiating penetration.

Integration of Sensory Inputs

Together, amphids and phasmids provide a coordinated sensory system that allows nematodes to navigate towards host plants with high precision. By comparing chemical intensities along their body axis and adjusting movement patterns accordingly, J2 juveniles can efficiently locate the root tip or other preferred entry zones. This highly refined chemosensory ability underpins the ecological success of root-knot nematodes and explains their capacity to infect a wide range of crops under diverse soil conditions.

Types of Chemical Gradients: Long-Distance, Short-Distance and Local Attractants

Root-knot nematodes navigate through a chemically complex soil environment, where host plants release a wide range of soluble and volatile compounds. These substances create spatial gradients that vary in concentration with distance from the root surface. Based on behavioural studies and chemosensory assays, these gradients can be grouped into long-distance, short-distance and local attractants, each influencing a different stage of host location.

Long-Distance Attractants : Long-distance attractants operate several millimetres to centimetres away from the root and help orient J2 juveniles towards the general vicinity of the host plant (Rasmann *et al.*, 2012). These cues include :

- changes in pH and ionic composition around actively growing roots,
- CO_2 released during root respiration,
- low concentrations of soluble metabolites diffusing into the surrounding soil.

Such attractants provide broad directional information rather than precise guidance, allowing nematodes to move from bulk soil into the rhizosphere.

Short-Distance Attractants : As J2s approach the root surface, they encounter higher concentrations of more specific compounds (Rasmann *et al.*, 2012). Short-distance attractants guide the nematode towards the root body and include :

- amino acids, organic acids and simple sugars released from root exudates,
- certain volatiles associated with root metabolism,
- gradients associated with zones of active root growth.

These cues narrow the nematode's search to particular root regions and increase the likelihood of encountering suitable entry sites.

Local Attractants : Local attractants operate at very close range, usually within the immediate vicinity of the epidermis, and direct J2s to preferred penetration zones (Rasmann *et al.*, 2012). These cues often originate from:

- the elongation zone just behind the root tip,
- cells undergoing active division and expansion,
- surface features or micro-gradients produced by exudation from root hairs.

Local cues are essential for determining the exact site of infection. Behavioural studies show that J2 juveniles consistently orient towards the root tip or adjacent elongation zones, reflecting the influence of these highly localised signals.

Root Exudates and Volatile Signals That Attract J2s

Root exudates are central to the chemical ecology of host location by root-knot nematodes. They consist of a diverse mixture of soluble compounds and volatile organic molecules released from growing root tissues. As these substances diffuse into the surrounding soil, they create spatial gradients that nematodes use to orient themselves towards suitable hosts. The chemical composition of root exudates varies across plant species, cultivars and developmental stages, which in turn shapes the behavioural response of nematode juveniles (Rasmann *et al.*, 2012).

Soluble Exudates and Short-Distance Guidance : A range of soluble compounds, including amino acids, organic acids, sugars and ions, act as short-distance attractants. These substances accumulate around the rhizoplane and root elongation zone, where active growth produces characteristic chemical profiles. Behavioural studies show that J2 juveniles readily respond to gradients of these solutes, adjusting their movement to remain within increasing concentrations. This fine-scale orientation helps the nematode locate the epidermis and the preferred regions for penetration.

Volatile Organic Compounds (VOCs): Volatile compounds play a key role in guiding J2 juveniles through the immediate soil environment. Several VOCs have been identified from susceptible cultivars and shown to stimulate J2 chemotaxis. These include :

- á-pinene,
- limonene,
- 2-methoxy-3-(1-methylpropyl)-pyrazine,
- methyl salicylate,
- tridecane, and
- 4,5-diepi-aristolochene.

These volatiles act individually and in combination. In laboratory assays, a synthetic blend comprising five of these compounds produced significantly higher attraction compared to controls, suggesting that nematodes respond to the overall chemical profile rather than single components. This combinatorial response mirrors natural conditions, where roots release complex mixtures rather than isolated compounds.

Cultivar-Specific Chemical Signatures

Root exudate profiles differ substantially between susceptible and resistant cultivars. Susceptible varieties tend to release chemical mixtures that stimulate J2 movement and enhance orientation towards the root surface. In contrast, resistant lines may produce lower levels of attractant volatiles or show higher concentrations of deterrent compounds. These cultivar-specific signatures help explain why nematodes consistently prefer certain varieties even under identical environmental conditions (Dutta *et al.*, 2025).

Findings from recent metabolomic and volatile analysis also indicate that resistant cultivars accumulate defence-associated metabolites that reduce attraction or impair nematode behaviour. These observations support a chemical basis for host preference and contribute to the broader ecological understanding of nematode–plant interactions.

Integration of Soluble and Volatile Cues

Host location is not governed by a single class of chemicals but by a coordinated sequence of signals. Volatiles and coarse gradients bring nematodes into the rhizosphere, while soluble exudates near the root surface provide precise directional cues for locating entry points. This chemical signalling cascade enables J2s to navigate effectively through soil and precise location of suitable hosts.

Table 2. Chemical Attractants of Root-Knot Nematodes (*Meloidogyne* spp.)

Chemical / Group	**Distance Class**	**Source**	**Notes on Activity**
CO,	Long-distance	Root respiration	Guides J2s from bulk soil toward rhizosphere.
pH and ion gradients	Long-distance	Root physiological activity	Provide broad directional cues.
Amino acids	Short-distance	Root exudates	Stimulate movement toward root surface; indicate metabolically active zones.
Sugars (e.g., glucose, fructose)	Short-distance	Root exudates	Associated with root growth; enhance orientation.
Organic acids (general)	Short-distance	Root exudates	Influence fine-scale movement toward elongation zone.
α-Pinene	Short-distance (volatile)	Root volatiles of susceptible cultivars	Part of volatile blend attracting J2s.
Limonene	Short-distance (volatile)	Root volatiles	Behaviourally active in chemotaxis assays.
2-Methoxy-3-(1-methylpropyl)-pyrazine	Short-distance (volatile)	Root volatiles	Enhances J2 chemotaxis; identified in susceptible lines.
Methyl salicylate	Short-distance / signalling volatile	Plant volatile	Acts as an attractant in in vitro assays.
Tridecane	Short-distance (volatile)	Root volatile	Component of a validated attractant blend.
4,5-Diepi-aristolochene	Short-distance (volatile)	Root volatile	Attracts J2 in behavioural assays.
Synthetic 5-component blend	Short-distance (volatile mixture)	Laboratory-constructed blend	Demonstrated strong attraction to J2 juveniles.

Table 3. Chemical Repellents, Deterrents and Nematicidal Compounds Affecting Root-Knot Nematodes

Chemical / Group	Distance Class	Source	Notes on Activity
Myristic acid	Short-distance cucumber metabolomics study	Resistant varieties;	Suppresses egg hatching and reduces infectivity.
Palmitic acid	Short-distance	Resistant or *Tagetes* spp.	Shows inhibitory and repellent effects.
Stearic acid	Short-distance	Resistant or *Tagetes* spp.	Associated with nematicidal properties.
Dodecanoic acid	Short-distance	*Tagetes* spp.	Strong nematicidal effect on J2s.
Sesquiphellandrene (α- and â- forms)	Short-distance (volatile)	*Tagetes* spp.	Known for nematode deterrence.
Other long-chain alkanes (octaeicosane-8-one, triacontane-1-ol, trieicosane)	Short-distance	*Tagetes* spp.	Reported to reduce J2 survival and orientation.
Phenolic acids	Local / short-distance	Resistant cultivars; defence activation	Accumulate during plant defence; reduce nematode success.
Flavonoids	Local	Endophyte-induced or resistance-associated	Inhibit nematode migration and feeding-site establishment.
Stress-related enzymes (catalase, PPO, â-1,3-glucanase)	Indirect, local	Endophyte-treated roots	Modify chemical micro-environment; reduce attraction and penetration.

Host Specificity in Attraction: Chemical Basis for Susceptible versus Resistant Varieties

Root-knot nematodes do not respond uniformly to all host plants. Instead, juveniles show clear preferences that reflect differences in the chemical composition of root exudates. These cultivar-dependent signatures strongly influence the likelihood of host encounter, early recognition and successful penetration. In susceptible crop varieties, root exudates often contain higher concentrations of attractant volatiles and soluble compounds, whereas resistant varieties tend to release lower amounts of attractants or produce deterrent or defence-associated metabolites (Rasmann *et al.*, 2012).

General Patterns of Chemical Variation : Studies across several crops, including rice, tomato, cucumber and various horticultural species, show that susceptible cultivars typically create stronger chemical gradients around their roots. These gradients are enriched in amino acids, organic acids, terpenoids and simple sugars that facilitate short-distance orientation and attract infective juveniles towards the rhizoplane. Resistant cultivars, on the other hand, often accumulate metabolites associated with defence, such as phenolics, flavonoids and certain fatty acids, which may reduce nematode movement, impair recognition or interfere with feeding-site formation. These differences in root chemistry form a major component of host resistance or susceptibility.

Behavioural Evidence from Olfactometer Assays : Behavioural assays using multi-arm or dual-choice olfactometers support the idea that nematodes discriminate among cultivars based on their chemical cues. Infective J2s consistently migrate towards exudates from susceptible varieties, while showing weaker or no attraction to those from resistant ones. Such directed movement confirms that nematodes rely on chemical signals to assess host suitability before attempting root penetration.

Example – Cultivar-Specific Exudate Chemistry in Rice : In a recent study, root exudates from the nematode-resistant rice cultivar Kalo Bhutia-213 (KB 213) and the nematode-susceptible cultivar Pusa Basmati 1121 (PB 1121) were compared using GC–MS-based metabolite profiling and olfactometer assays. Juveniles displayed a marked preference for PB 1121, supporting the broader pattern that susceptible cultivars produce stronger attractant cues.

Chemical analysis revealed clear differences in exudate composition between the two cultivars. PB 1121 released higher levels of several volatile and semi-volatile compounds associated with nematode attraction, including terpenoid and hydrocarbon derivatives. In contrast, KB 213 produced greater amounts of defence-associated metabolites such as phenolics and specific fatty acids, which are known to reduce nematode activity or interfere with early infection processes. Multivariate analyses (PCA and PLS-DA) showed distinct separation between KB 213 and PB 1121, further emphasising that the two cultivars generate chemically different rhizosphere environments (Dutta *et al.*, 2025).

Implications – These findings illustrate how cultivar-specific chemical signatures shape nematode attraction and contribute to differences in field susceptibility. The example of KB 213 and PB 1121 demonstrates how resistant cultivars may create a chemically less favourable environment for nematode orientation, while susceptible cultivars may inadvertently produce attractant-rich exudates. Such chemical contrasts highlight the importance of considering root chemistry in breeding and selection of resistant varieties, and in designing integrated nematode management strategies.

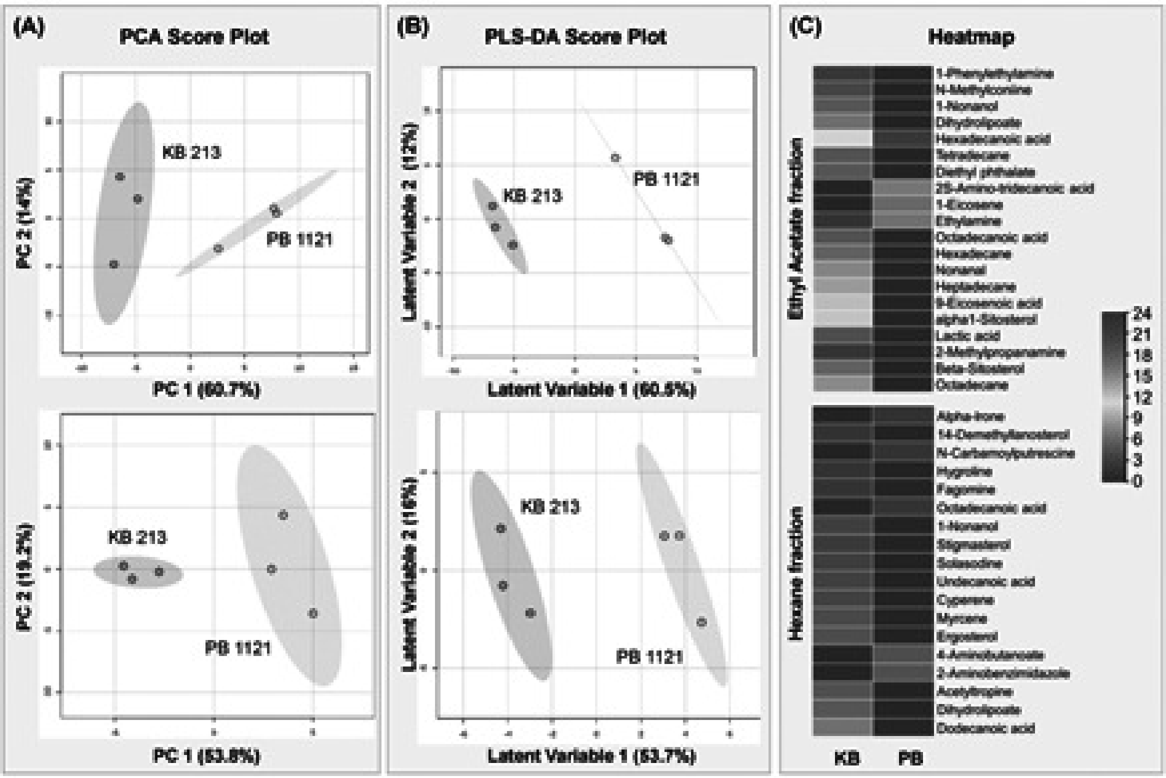

Figure 2. GC–MS-based comparison of root exudate constituents from the nematode-resistant rice cultivar Kalo Bhutia-213 (KB 213) and the nematode-susceptible rice cultivar Pusa Basmati 1121 (PB 1121). (A) PCA analysis of metabolites found in the Ethyl Acetate fraction (EA, above) and hexane fraction (HE, below) of PB 1121 and KB 213 rice cultivars. (B) PLS-DA analysis of metabolites found in the EA (above) and HE (below) fractions of the two rice cultivars. (C) Heat map of the top 20 compounds presents in PB 1121 and KB 213 in the EA fraction (above) and HE fraction (below). Together, these panels illustrate the cultivar-specific chemical signatures of KB and PB 1121, providing a mechanistic basis for the contrasting nematode attraction patterns observed in behavioural assays. (Figure adapted from Dutta *et al.*, 2025)

Microbial Mediation of Nematode Behaviour and Host Defence Responses

Soil and root-associated microorganisms strongly influence the chemical ecology of plant–nematode interactions. Many microbes produce secondary metabolites that directly affect nematodes, while others modulate plant physiology by priming defence pathways. Together, these processes can alter nematode attraction, penetration, development, and reproduction. A growing body of work now shows that fungi and bacteria associated with roots, rhizosphere soil, and even nematode-induced galls can interfere with host location cues, suppress nematode activity, and enhance the plant's innate resistance.

Microbial effects on nematodes broadly fall under **two complementary mechanisms** :

1. **Direct Effects on Nematodes**
   - nematicidal metabolites causing mortality, paralysis, or reduced egg hatching
   - altered amphid or phasmid-based chemotaxis, reducing host attraction
   - developmental disruption during juvenile moulting or feeding-site establishment
2. **Indirect Effects via Host-mediated Defence Activation**
   - induction of jasmonic acid, ethylene, or salicylic acid defence pathways
   - enhanced activity of oxidative enzymes and structural fortification of root tissues
   - increased accumulation of phenolics and flavonoids that suppress nematode development

Microbial Interference with Nematode Chemotaxis and Host Location Microbial communities associated with plant roots can substantially alter the chemical environment that nematodes perceive. Several soil and root-associated microbes release volatile or soluble compounds that modify chemical gradients around the root surface, leading to reduced nematode migration towards preferred hosts. Studies in vegetable and cereal systems consistently show lower juvenile attraction when roots are colonised by beneficial endophytes or treated with their culture filtrates. Microbial metabolites may mask attractive cues such as amino acids, organic acids and simple sugars, or introduce deterrent compounds into the rhizosphere, thereby disrupting the chemical signals that guide nematodes during host location.

Endophytes isolated from nematode galls provide useful examples of this process. Many of these fungi produce bioactive molecules that directly impair J2 mobility or interfere with chemosensory perception. In some cases, metabolites induce rapid cellular damage in nematodes, including the formation of large vacuoles and other stress-associated structures that lead to death. These effects highlight the potential of microbial metabolites to disrupt the early stages of nematode host finding and invasion.

Beyond direct toxicity, microbes can also influence nematode behaviour and infection success by modulating plant defence pathways. A well-studied example is *Aspergillus niger* F4, a gall associated endophyte shown to act through both direct and indirect mechanisms. In in-vitro assays, metabolites from F4 caused high J2 mortality and demonstrated cellular damage. At the same time, F4-treated plants exhibited increased activity of defence-related enzymes and greater accumulation of phenolics, flavonoids and other compounds associated with enhanced resistance. These biochemical changes were accompanied by reduced nematode attraction, fewer galls and lower reproductive success across different host–nematode systems, including rice–*Meloidogyne graminicola* (Dutta *et al.*, 2023) and tomato–*M. incognita* (Dutta *et al.*, 2025).

Together, these findings illustrate how a single microbial endophyte can reshape the chemical landscape of the rhizosphere, interfere with nematode chemotaxis and reinforce plant defences. Microbial modulation therefore represents an important dimension of nematode chemical ecology and offers promising opportunities for sustainable nematode management.

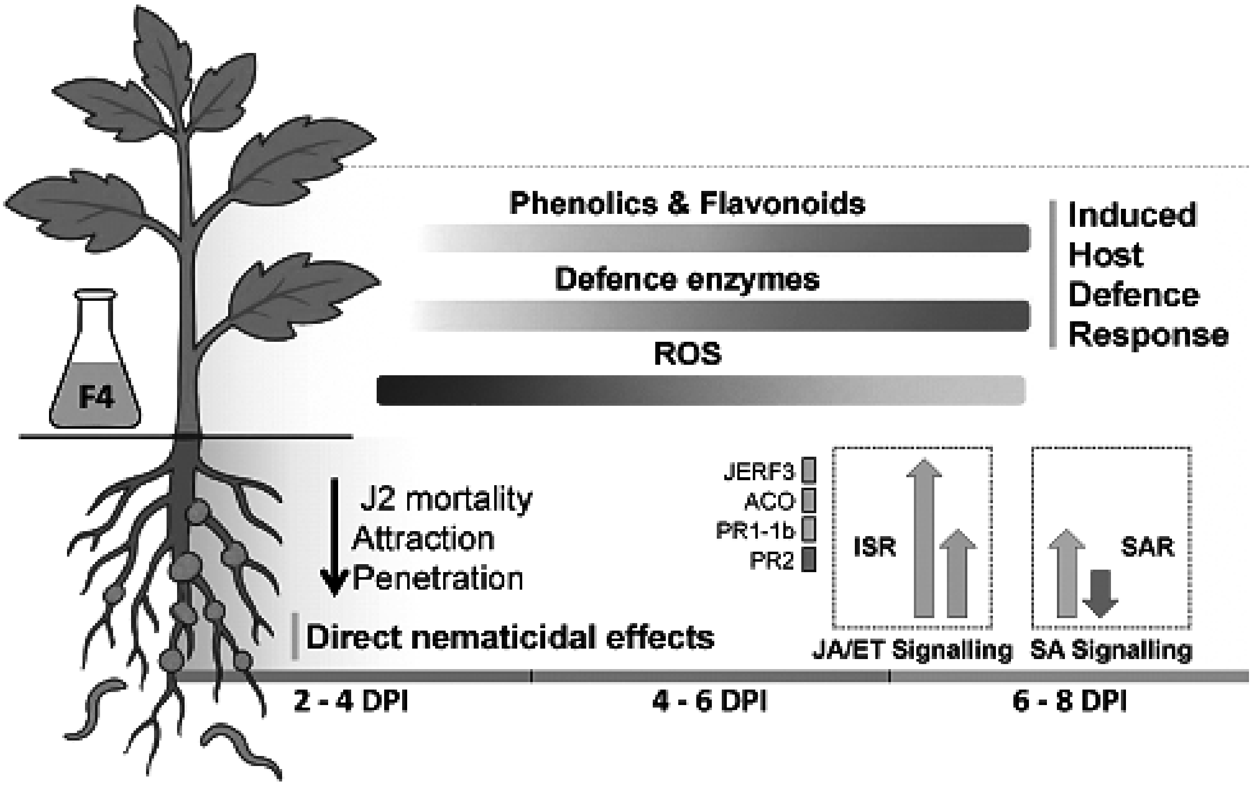

Figure 3. Schematic diagram illustrating the dual mode of action of *Aspergillus niger* F4 culture filtrate in tomato roots infected with *Meloidogyne incognita*. It summarises the timeline of direct nematicidal effects and activation of host defence responses. Enzyme activity (POD, APX, PAL, etc.) and ROS levels are shown to vary across time, contributing to early induced systemic resistance (ISR), followed by partial activation of systemic acquired resistance (SAR). Darker colour intensity in enzyme blocks indicates higher activity, while arrow height and direction represent gene expression intensity and direction, respectively. Together, these panels demonstrate that *A. niger* F4 protects tomato against *M. incognita* through a dual mechanism: (1) direct toxicity to juveniles and suppression of early infection steps, and (2) strong activation of plant defence pathways that reduce nematode establishment and reproduction. (Figure adapted from Dutta *et al.*, 2025).

Implications for Nematode Management

Understanding the chemical ecology of plant–nematode interactions provides a mechanistic foundation for interpreting why nematode problems vary across fields, seasons and cultivars. Chemical signals produced by plants, nematodes and associated microbes shape every stage of the infection process from host location to feeding-site establishment and therefore have direct relevance for sustainable crop management.

Differences in root exudate chemistry among cultivars help explain why some varieties remain consistently more susceptible, even under similar environmental conditions. Susceptible cultivars release stronger attractant cues, whereas resistant cultivars often produce deterrent metabolites or rapidly accumulate defence-related compounds. Recognising these chemical differences supports informed selection of cultivars and assists in breeding programmes aiming to enhance nematode resistance using traits linked to root chemistry.

The influence of soil microbes adds an additional layer of complexity. Microbial communities can modify chemical gradients around roots, mask attractant signals or introduce deterrent compounds into the rhizosphere. Beneficial endophytes and rhizosphere fungi may also prime host defences, leading to reduced attraction, penetration and nematode reproduction. Such microbe-mediated effects complement host genetic resistance and suggest opportunities for developing biological inputs that operate through predictable chemical mechanisms.

These insights collectively underscore the importance of viewing nematode management not only through agronomic practices but also through the chemical environment surrounding roots. Approaches that integrate resistant cultivars, beneficial microbes and practices that maintain a diverse and active soil biological community are more likely to succeed than strategies that target nematodes in isolation. As research continues to identify key attractants, repellents and microbially derived metabolites, there is increasing potential to design management tools that directly manipulate nematode behaviour, disrupt host location or strengthen plant defences in a targeted and environmentally sound manner.

Conclusion

Chemical ecology provides a unifying framework for understanding how root-knot nematodes locate their hosts, initiate infection and overcome plant defences. Host location is guided by coordinated chemical cues in soil, including volatiles and soluble compounds released from roots, as well as metabolites produced by nematodes and associated microbes. Differences in these cues across cultivars explain variability in susceptibility and highlight the crucial role of root exudate chemistry in shaping nematode behaviour.

Key Takeaways

- Nematodes depend on chemical cues to locate and infect host plants.
- Root exudate chemistry differs across cultivars and strongly influences nematode attraction.
- Resistant cultivars often produce deterrent or defence-related metabolites.
- Beneficial microbes can disrupt nematode chemotaxis and activate plant defences.
- Chemical ecology offers eco-friendly avenues for breeding, biocontrol and sustainable nematode

Microbial communities add further complexity by altering chemical gradients, masking attractants or introducing deterrents. Beneficial endophytes and rhizosphere fungi can strengthen plant defences and reduce nematode success through both direct and indirect mechanisms. These interactions demonstrate that nematode management is influenced not only by nematode biology but also by the broader chemical environment created by plants and microbes.

Future research should focus on identifying the specific metabolites that strongly influence nematode orientation and assessing how these compounds vary across cultivars, soils and management practices. Advances in metabolomics, imaging and behavioural assays offer opportunities to map the chemical landscape around roots with increasing precision. Such knowledge can guide the development of resistant varieties, microbe-based interventions and strategies that deliberately manipulate chemical cues to reduce nematode infestation.

As understanding grows, chemical ecology has the potential to become a practical foundation for sustainable nematode management. Integrating resistant cultivars, beneficial microbes and practices that support soil biological activity can help reduce reliance on chemical nematicides while improving crop resilience. These insights highlight a promising path forward, where manipulation of chemical signals in the rhizosphere can be used to manage nematodes in a targeted, effective and environmentally sound manner.

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