

MICROBIOME-DRIVEN PLANT DEFENCE AGAINST ROOT-KNOT NEMATODES: INTEGRATIVE MECHANISMS AND APPLICATIONS

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ABSTRACT:

Root knot nematodes (RKNs) (*Meloidogyne spp.*) are among the most destructive plant parasitic nematodes (PPNs), causing severe yield losses across global agriculture. They establish permanent feeding sites known as giant cells within the vascular tissues of host roots disrupting nutrient transport and predisposing plants to secondary infections. Conventional nematicides and cultural practices are increasingly limited by environmental concerns, regulatory restrictions, broad host ranges, and the emergence of highly virulent species such as *M. enterolobii*. The plant microbiome that comprising rhizosphere, rhizoplane, endophytic, and phyllosphere communities functions as an extended defence system that enhances plant resilience to nematode attack. Beneficial microorganisms including *Bacillus*, *Pseudomonas*, *Paenibacillus*, *Streptomyces*, *Trichoderma*, *Pochonia*, *Purpureocillium*, and arbuscular mycorrhizal fungi suppress RKNs through direct antagonism (nematicidal metabolites, hydrolytic enzymes, parasitism), modulation of root architecture and exudation, and activation of induced systemic resistance (ISR), systemic acquired resistance (SAR), and mycorrhiza induced resistance (MIR). Microbial metabolites such as lipopeptides, phenazines, peptaibols, VOCs (e.g., dimethyl disulfide, 1 octen 3 ol), and fatty acids (lauric, palmitic) alter nematode behaviour, inhibit egg hatching, and prime plant immune pathways involving JA, SA, ET, ROS signaling, and antioxidant enzymes. Advances in metagenomics, meta-transcriptomics, metabolomics, and effector biology have revealed the molecular basis of plant-microbe-nematode interactions and identified key microbial taxa associated with disease suppressive soils. Microbiome engineering, synthetic microbial communities (SynComs), host mediated microbiome selection, and soil health management offer promising avenues for sustainable nematode control. This review integrates ecological, physiological, and molecular insights into microbiome driven defence against RKNs, highlights key microbial players and their synergistic interactions, and outlines future directions for precision microbiome engineering, climate resilient biodefence, and field level translation. Harnessing microbiome enabled resilience provides a scalable, eco friendly alternative to chemical nematicides and represents a transformative strategy for sustainable nematode management in modern agriculture.

KEYWORDS: Root knot nematode, Microbiome, Induced Systemic Resistance, Systemic Acquired Resistance, Mycorrhiza-Induced Resistance, Hormonal Interaction.

Abbreviation	Full form
AMF	Arbuscular mycorrhizal fungi
AI	Artificial intelligence
ACO	1-Aminocyclopropane-1-carboxylate oxidase
DAPG	2,4-Diacetylphloroglucinol
DNA	Deoxyribonucleic acid
ET	Ethylene
EPNs	Entomopathogenic nematodes
GC-MS	Gas chromatography-mass spectrometry
GLR3.5	Glutamate receptor-like 3.5
HY5	ELONGATED HYPOCOTYL 5
ISR	Induced systemic resistance
ITS	Internal transcribed spacer
JA	Jasmonic acid
J2	Second-stage juvenile
J3	Third-stage juvenile
J4	Fourth-stage juvenile

JERF3	Jasmonate and ethylene responsive factor 3
LC ₅₀	Median lethal concentration
MAPK	Mitogen-activated protein kinase
MIR	Mycorrhiza-induced resistance
NVOCs	Non-volatile organic compounds
PGPB	Plant growth-promoting bacteria
PGPR	Plant growth-promoting rhizobacteria
PPNs	Plant-parasitic nematodes
PR	Pathogenesis-related
RKNs	Root-knot nematodes
RNA	Ribonucleic acid
ROS	Reactive oxygen species
SA	Salicylic acid
SAR	Systemic acquired resistance
SynComs	Synthetic microbial communities
VOCs	Volatile organic compounds
16S rRNA	16S ribosomal RNA
18S rRNA	18S ribosomal RNA

INTRODUCTION

Root knot nematodes (*Meloidogyne* spp.) are among the most destructive plant-parasitic nematodes, causing severe yield losses across agricultural and horticultural systems worldwide. These sedentary endoparasites establish permanent feeding sites known as giant cells within the vascular tissues of host roots, leading to characteristic gall formation that disrupts water and nutrient uptake, reduces plant vigour, and predisposes plants to secondary infections by pathogens. Major species such as *Meloidogyne incognita*, *M. javanica*, *M. arenaria*, and *M. hapla*, are responsible for significant economic losses in both tropical and temperate regions (Migunova & Sasanelli, 2021). Among them, *Meloidogyne enterolobii* (syn. *M. mayaguensis*) has emerged as one of the most virulent species because of its rapid reproduction, broad host range, and ability to overcome resistance genes, including the widely deployed Mi-1 gene in tomato. Consequently, *M. enterolobii* has become an important phytosanitary concern worldwide (Singh, 2020).

The plant microbiome comprises a diverse and complex community of microorganisms, including bacteria, fungi, archaea, and protists, that colonize plant tissues and associated rhizosphere soil environments. This dynamic microbial ecosystem exists in delicate equilibrium, where beneficial microbes (e.g., mycorrhizal fungi, plant-growth-promoting bacteria, and fungal biocontrol agents) coexist with plant pathogens, including parasitic nematodes and other harmful microorganisms. The rhizosphere microbiome is particularly rich in microbial diversity and represents a critical interface where plants and microbes engage in multifaceted interactions that profoundly influence plant health, productivity, and resistance to stress and pathogenic attack. The structure and function of plant-associated microbiota are shaped by plant genotype, soil physicochemical properties, agricultural management practices, and environmental conditions, collectively determining the balance between beneficial and pathogenic microorganisms (Trivedi et al., 2020; Chaparro et al., 2012).

The plant microbiome consists of both beneficial and detrimental members, whose interactions ultimately determine plant health. Beneficial microorganisms, including plant growth-promoting rhizobacteria (PGPR), arbuscular mycorrhizal fungi (AMF), endophytic bacteria and fungi, actinomycetes, and antagonistic fungi such as *Trichoderma*, *Purpureocillium*, and *Pochonia*, contribute to plant protection through nutrient mobilization, phytohormone production, niche competition, secretion of antimicrobial and nematocidal metabolites, and activation of induced systemic resistance (ISR), systemic acquired resistance (SAR), and mycorrhiza-induced resistance (MIR). In contrast, non-beneficial microorganisms and pests—including phytopathogenic fungi, bacteria, viruses, oomycetes, and plant-parasitic nematodes—exploit host resources, interfere with normal physiological processes, and suppress plant immunity, leading to disease development and significant crop losses. Among the detrimental members of the plant-associated microbiome, PPNs, particularly root-knot nematodes (*Meloidogyne* spp.), represent one of the most destructive components of the belowground biotic community (Compant et al., 2019; Vandenkoornhuyse et al., 2015).

In recent years, the concept of microbiome-enabled resilience has gained considerable attention as a sustainable strategy for managing plant diseases. Rather than functioning as isolated biocontrol agents, beneficial microorganisms form complex and dynamic communities that interact with plants and soil to enhance disease resistance and maintain ecosystem stability. The integrated view has been studied in crops such as rice and cucumber, as well as in broader rhizosphere systems, encompassing factors such as AMF colonization timing, dehydroascorbic acid (DHA)-triggered systemic resistance, and nematode-associated microbial interactions (Vos et al., 2012; Desmedt et al., 2022). These microbial consortia suppress plant pathogens through multiple mechanisms, including competition for nutrients and ecological niches, production of antimicrobial metabolites, induction of systemic resistance, modulation of root exudation, and improvement of soil health (Topalović et al., 2020; Vashisth et al., 2024). Advances in high-throughput sequencing, metagenomics, metatranscriptomics, metabolomics, and synthetic microbial community engineering have substantially improved our understanding

of these intricate plant-microbiome interactions, creating new opportunities for environmentally sustainable nematode management (Trivedi et al., 2020).

This review summarizes current knowledge on plant-microbiome interactions associated with *Meloidogyne* infestation. It discusses the ecological and molecular mechanisms through which beneficial microorganisms suppress nematode infection, activate host immune responses, and improved plant health. Furthermore, recent advances in microbiome engineering, induced systemic resistance (ISR), systemic acquired resistance (SAR), mycorrhiza-induced resistance (MIR), microbial metabolites and multi-omics technologies are highlighted to identify further research priorities for sustainable nematode management.

Limitations of conventional nematode management strategies

Traditional nematode management strategies including chemical nematicides, resistant cultivars, crop rotation, soil fumigation and cultural practices to suppress nematode populations. However, chemical nematicides pose risks of environmental toxicity, non-target effects and disruption of beneficial soil microbiota, regulatory restrictions and resistance development in nematode populations. Soil fumigants are costly and often incompatible with smallholder systems, while genetic resistance is frequently overcome by virulent pathotypes such as *M. enterolobii*. Modern fluorinated nematicides like fluazaindolizine, fluopyram, and fluensulfone demonstrate variable efficacy against *Meloidogyne* suggesting that reliance on single mode of action risks nematode adaptation (Grabau et al., 2024). Cultural practices such as crop rotation are frequently ineffective against root knot nematodes because of their broad host range, persistence in soil, and the occurrence of mixed nematode populations. These constraints have driven the search for ecologically sound, biologically based alternatives (Tian et al., 2025).

Emergence of micro-biome-based plant protection

Recent advances in plant-microbe interaction research underscore the pivotal role of the plant microbiome in conferring resilience against nematode infestation. Soils with low infestations of *M. incognita* contain more plant-beneficial microbes with nematocidal activities, such as *Bacillus amyloliquefaciens* W1, compared to heavily infested soils, suggesting that microbial community composition directly influences nematode suppression (Zhao et al., 2023). The plant microbiome, comprising rhizosphere, rhizoplane, endophytic, and phyllosphere microbial communities, functions as an extended plant defense system by influencing nutrient acquisition, plant growth, immune responses, and stress tolerance (Tian et al., 2025). Beneficial microorganisms including rhizobacteria, endophytes, fungi and arbuscular mycorrhizal fungi (AMF) suppress nematodes through multifaceted mechanisms such as production of nematocidal metabolites and volatile organic compounds (VOCs), modulation of root exudation, niche competition, direct parasitism and activation of host defense pathways. Rhizobacteria such as *Bacillus velezensis* produce volatile organic compounds (VOCs), including 3-methyl-1-butanol and 2-heptanone, that exhibit multiple modes of action against root-knot nematode juveniles, including direct-contact nematocidal activity, fumigant activity, and repellent activity, resulting in mortality rates exceeding 97% at 48 h. Similarly, endophytic fungi produce bioactive VOCs; for example, *Daldinia* cf. *concentrica* volatiles caused 67% reduction in *M. javanica* J2 viability, with synthetic volatile mixtures achieving 99% nematocidal efficacy. Nitrogen-fixing PGPB strains, including *Rhizobium*, *Mesorhizobium*, *Sinorhizobium*, *Bradyrhizobium* spp. and the nitrogen-fixing *Paenibacillus polymyxa*, promote plant growth by supplying nitrogen and increase plant resistance to root-knot nematodes (Aioub et al., 2022). The manuscript emphasizes that “beneficial microorganisms form complex and dynamic communities that interact with plants and soil [to] enhance disease resistance and maintain ecosystem stability.”

Scope and objectives of the review

This review synthesizes current knowledge on microbiome-mediated plant defense against RKNs, integrating ecological, physiological and molecular perspectives. Specifically, it aims to: i) Describe the biology and parasitism of *Meloidogyne* spp.; ii) Summarize the composition and functional diversity of plant-associated microbiomes.; iii) Elucidate microbiome-mediated defense mechanisms, including direct antagonism, induced systemic resistance (ISR), systemic acquired resistance (SAR), and modulation of root architecture and exudation.; iv) Highlight key microbial players and their synergistic interactions in RKN suppression.; v) Integrate omics-based insights into plant-microbe-nematode interactions.; vi) Discuss strategies for engineering and manipulating the plant micro-biome for sustainable nematode management.; vi) Identify challenges, limitations and future research directions for micro-biome-driven bio-defense in agriculture.

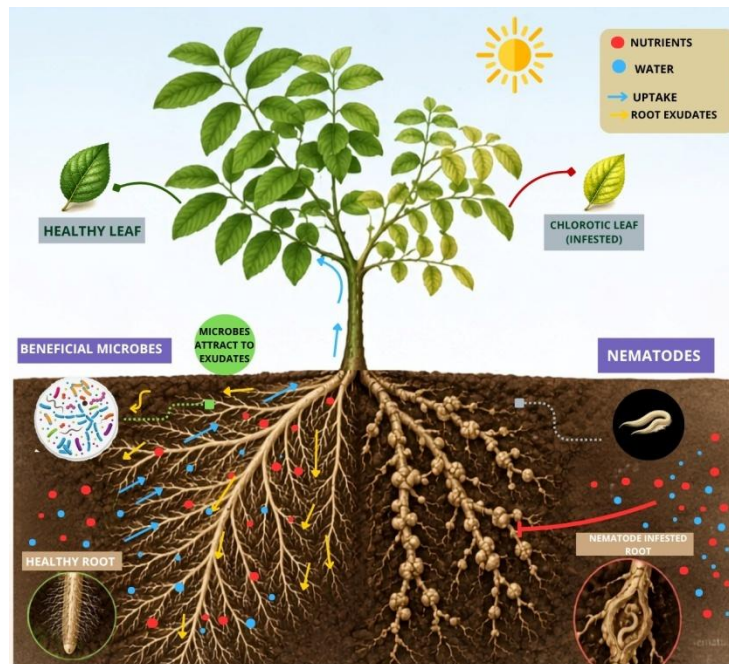


Fig I: Overview of plant–microbiome–root-knot nematode interactions in the rhizosphere.

Beneficial rhizosphere microorganisms are recruited by root exudates and enhance plant health by improving nutrient and water uptake, promoting root development, and suppressing root-knot nematodes (*Meloidogyne spp.*). In contrast, nematode infection induces root gall formation, disrupts root function, reduces nutrient and water acquisition, and leads to chlorosis and impaired plant growth.

2. Biology and Parasitism of Root-Knot Nematodes

2.1. Life cycle and infection process of *Meloidogyne* spp.

RKNs exhibit a relatively simple yet highly specialized life cycle. Eggs are deposited in gelatinous matrices on or within roots. Second-stage juveniles (J2s) hatch from eggs and migrate through soil, guided by root-derived chemical cues. Upon reaching the root surface, J2s penetrate near the elongation zone and migrate intercellularly towards the vascular cylinder. There, they induce the formation of giant cells—hypertrophied, multinucleate cells that serve as nutrient sinks. The nematodes then become sedentary, undergo successive molts to J3, J4 and adult stages, and females produce new egg masses, completing the cycle (Abad et al., 2008).

Root exudates from soybean, tomato, *Medicago*, and pea are known to attract RKN J2s, with specific chemical structures of polysaccharides in root mucilage, including 1-galactose side chains of rhamnogalacturonan-I, serving as potent chemo attractants. Recently, neuropeptides such as MjFLP-14-2 were identified as endogenous modulators of J2 chemotaxis towards tomato root tips, representing novel molecular targets for nematode behavioral disruption (Mo et al., 2024). Upon reaching the root surface, J2 penetrate root, and migrate intercellularly towards the apical meristematic region, then turn around and migrate back away from the root tip until they reach the differentiating vascular tissue where they induce feeding site formation (Bozbugaet al., 2018). The establishment of feeding sites involves penetration through the root epidermis at the zone of root elongation, moving beyond the casparian strip to the root tip, and then returning to the vascular cylinder of the roots in search of potential feeding sites. Effectors secreted by the esophageal glands through the RKN stylet play a crucial role in modulating the transcriptional programming of plant parenchymal cells, leading to the development of giant cells at the feeding site (Yadav et al., 2025)

2.2. Host–parasite interactions and feeding site establishment

Feeding site establishment is a defining feature of RKN parasitism. Nematode secretions reprogram host cell development, leading to giant cell formation and surrounding gall tissue. These changes disrupt normal root architecture, impair water and nutrient transport, and alter hormonal balance. Giant cells disrupt vascular function and nutrient transport, creating a metabolic sink that diverts resources from plant growth to nematode development and increases susceptibility to secondary infections, highlighting the broader impact of localized root damage (Yadav et al., 2025).

2.3. Molecular basis of nematode parasitism

At the molecular level, RKNs deploy a suite of effector proteins secreted from esophageal glands into host tissues (Mantelin et al., 2022; Habteweld et al., 2024). These effectors modulate cell cycle, cytoskeleton organization, chromatin remodeling, vesicle trafficking, cell wall modification, hormone signaling (auxin, cytokinin, ethylene), and defense pathways (SA, JA, ET), enabling successful invasion and feeding site maintenance. Some effectors suppress SA-dependent PR gene expression, while others interfere with JA signaling, thereby dampening basal immunity and facilitating chronic infection.

Virulent species such as *M. enterolobii* possess effector repertoires capable of overcoming major resistance genes, underscoring the evolutionary arms race between host and parasite (Domínguez-Figueroa et al., 2024).

For instant, in transcriptome analyses show that all salicylic acid (SA)- responsive genes tested (PR-1, PR-2, PR-4b, PR-5) are down-regulated in response to nematode infection, while jasmonic acid (JA) – responsive genes, including ACO and JERF3, remain largely unaffected. This selective suppression of the SA- dependent immune axis highlights the precision of RKN immune modulation (Molinari et al., 2024).

3. The Plant Microbiome: Composition and Functional Diversity

3.1. Rhizosphere, endosphere, and phyllosphere microbiomes

The plant micro-biome encompasses diverse microbial communities inhabiting the rhizosphere (soil closely associated with roots), endosphere (internal tissues) and phyllosphere (leaf and stem surfaces) collectively forming an interconnected network that profoundly influences plant health and pathogen resilience. (Santoyo, G. 2025). Rhizosphere microbiomes act as primarily defense against RKN interactions, as they mediate root colonization, nutrient cycling and antagonism against soil borne pathogens. The rhizosphere soil is a narrow zone most strongly influenced by plant roots, rich in nutrients and act as a hotspot for microbial interactions, harboring beneficial microorganisms, soil-borne pathogens and their competing communities, with soil microorganisms intimately involved in the decomposition of organic matter directly linked with plant growth and diseases spread (Lu et al., 2026). Endophytic bacteria and fungi colonize root cortical and vascular tissues, often exerting systemic effects on plant growth and defense. Phyllosphere communities, though less directly involved in root infection, can contribute to systemic signaling and ISR (Jung et al., 2024).

3.2. Core vs. transient microbial communities

Plant-associated microbiomes comprise core taxa that are consistently associated with a given host species or genotype, and transient taxa that fluctuate with environmental conditions, management practices and developmental stage. Diverse plant genotypes growing in similar habitats interact with a common set of microbial groups, through some core groups are species- or environment-specific (Durán et al., 2024). Core microbiota often include *Bacillus*, *Pseudomonas*, *Streptomyces*, *Trichoderma* and AMF, which are repeatedly implicated in disease suppressing capabilities and plant growth promoting. Transient members may provide context-dependent benefits or costs, and their recruitment is strongly influenced by root exudates and soil properties (Romão et al., 2025).

3.3. Factors shaping plant-associated micro-biomes

Four important factors shape micro-biome composition and functions are i) Host genotype and physiology - Root architecture, exudates profile and immune status influence microbial recruitment. Host genotype governs root exudation and developmental traits, which in turn orchestrate micro-biome assembly and plant-environment adaptation (Raza et al., 2023); ii) Soil type and management - Texture, pH, organic matter, fertilization and tillage alter microbial diversity and abundance.; iii) Cropping system - Intercropping, rotation and cover crops modulate rhizosphere communities and nematode pressure. Compared to monocultures, the complexity and robustness of soil networks comprising bacterial, fungal, and nematode communities increased in intercropped maize soils, but densities of plant parasitic nematodes and β - glucosidase activity were reduced (Li et al., 2021); iv) Environmental conditions - Temperature, moisture and light (e.g. red light in watermelon inducing systemic defense) affect both plant physiology and microbial activity. Advances in high-throughput DNA and RNA sequencing, , metagenomics, meta-transcriptomics and metabolomics have substantially improved our understanding of these intricate plant–micro-biome interactions, “creating new opportunities for environmentally sustainable nematode management” (Pinto et al., 2024).

4. Microbiome-Mediated Plant defence Mechanisms against RKNs

4.1 Direct antagonism of nematodes

4.1.1. Production of nematicidal metabolites (toxins, enzymes)

Rhizosphere microorganisms produce diverse soluble and volatile metabolites with nematicidal activity against *Meloidogyne* spp. These compounds inhibit egg hatching and cause J2 mortality that reduce root galling, and nematode reproduction (Adam et al., 2014; Migunova et al., 2021).

Bacterial metabolites: *Bacillus*, *Pseudomonas*, *Paenibacillus*, and *Streptomyces*, produce potent nematicidal metabolites such as surfactin, iturin, fengycin, phenazines, pyrrolnitrin, and 2,4-diacetylphloroglucinol (DAPG), which disrupt nematode cellular integrity, inhibit egg hatching, and reduce juvenile survival (Ayaz et al., 2024).

Fungal metabolites: *Purpureocillium lilacinum*, *Pochonia chlamydosporia*, and *Trichoderma* spp., secrete secondary metabolites such as leucinostatins, gliotoxin, harzianolide, and peptaibols, which interfere with nematode development and reproduction while simultaneously enhancing host defense responses (Parveen et al., 2025).

Extracellular enzymes: Chitinases, proteases, collagenases and lipases degrade nematode eggshells and cuticles, reducing hatching success and increasing susceptibility to microbial attack (Topalović et al., 2020).

Non-volatile organic compounds (NVOCs): Antibiotics, cyclic lipopeptides (surfactin, iturin, fengycin), phenazines, pyrrolnitrin, siderophores, phenolics, alkaloids, organic acids, phytohormones and hydrolytic enzymes. These metabolites are primarily synthesized by rhizobacteria, endophytes, actinomycetes, and fungi associated with root tissues (Yang et al., 2013). Many NVOCs also act as signaling molecules that stimulate ISR and SAR via SA, JA and ET pathways, thereby coupling direct toxicity with systemic defense (Yang et al., 2013; Liang et al., 2019).

NVOCs require direct contact or close proximity to exert their effects.

4.1.2. Parasitism and predation of nematodes

Certain fungi and bacteria act as true nematophagous organisms, parasitizing eggs, juveniles or adults. *Paecilomyces (Purpureocillium) lilacinus* and *Pochonia chlamydosporia* colonize egg masses, penetrate eggshells and consume developing embryos, achieving up to 95% egg parasitism in tomato–*M. incognita* systems (Giné et al., 2017). Nematode-trapping fungi (e.g. *Arthrobotrys*, *Duddingtonia*) form adhesive nets or constricting rings that capture J2s, followed by hyphal invasion and digestion (Youssar et al., 2019). These parasitic interactions reduce nematode population density and complement metabolite-mediated suppression (Liang et al., 2019).

4.2 Induced systemic resistance (ISR)

4.2.1. Role of jasmonic acid (JA), salicylic acid (SA), and ethylene pathways

ISR provides whole-plant protection against RKNs when locally triggered by beneficial microorganisms, chemical elicitors or environmental stimuli. Nahar et al. (2011) critically defined ISR for nematode control as “complex hormonal crosstalk, primarily mediated through jasmonic acid and ethylene signaling pathways, which regulate defense gene expression, strengthen cell walls, increase lignifications, and restrict nematode penetration”. Notably, ET- triggered systemic defense against RKN has been shown to depend on intact JA-responsive genes in roots even though JA signaling itself remains functional independent of ET. This JA/ET-dominant crosstalk in root tissue contrasts with the SA- centered signaling more typical of above-ground defense responses, indicating that RKN-targeted ISR relies on a distinct, root- specific hormonal circuit (Martinez-Medina et al., 2017).

Beneficial microbes such as *Bacillus*, *Pseudomonas*, *Trichoderma* and *Streptomyces* activate JA/ET-dependent induced systemic resistance (ISR), which frequently interacts with salicylic acid (SA)-mediated systemic acquired resistance (SAR) to enhance plant immunity against root-knot nematodes (Pieterse et al., 2021).

4.2.2. Priming of plant immune responses

ISR is characterized by priming where plants mount faster and stronger responses upon subsequent nematode challenge (Jung et al., 2024). Localized ROS bursts act as early defense signals, creating a hostile environment for nematodes while activating downstream defense genes. Concurrently, antioxidant enzymes such as superoxide dismutase, peroxidase and catalase are upregulated to balance ROS levels and maintain cellular integrity (De Kock et al., 2024). ISR also stimulates biosynthesis of secondary metabolites (phenolics, flavonoids, alkaloids and terpenoids) with antimicrobial and nematocidal effects. Root system remodeling (increased branching, root hair formation and improved nutrient uptake) strengthens plant vigour and reduces susceptibility to invasion. Systemic signal transmission ensures that defense signals generated at the site of elicitation are conveyed to distal tissues, equipping the entire plant with heightened resistance (Ismail et al., 2022; Faizi et al., 2011).

4.3 Modulation of root architecture and exudation

4.3.1. Changes in root morphology affecting nematode infection

Micro-biome-mediated changes in root architecture can alter nematode infection dynamics. Enhanced root branching, thicker cortical tissues, increased lignifications and modified root hair density may reduce suitable penetration sites or alter chemotactic gradients. AMF colonization, for example, can modify root system architecture and nutrient status, indirectly affecting nematode behavior and feeding site establishment (Veronico et al., 2018).

4.3.2. Micro-biome-driven alteration of root exudates

Root exudates represent a complex mixture of primary and secondary metabolites secreted into the rhizosphere, playing a pivotal role in nematode–plant interactions (Bais et al., 2006). These compounds act as chemical signals that influence nematode attraction, repellence, paralysis, inhibition of egg hatching, or juvenile mortality. Phenolic acids, flavonoids, alkaloids and terpenoids can repel nematodes or kill juveniles directly, while sugars and amino acids may attract them (Kirwa et al., 2018).

Microbiome-driven modulation of exudates can shift this balance. For example: a) Lauric acid in tomato-crown daisy intercropping attracts *M. incognita* at low concentrations but repels them at higher concentrations, illustrating concentration-dependent chemotaxis (Dong et al., 2014) b) Palmitic acid in pepper-cucumber rotation recruits *Pseudarthrobacter oxydans*, a nematocidal bacterium that degrades nematode-promoting compounds and induces ISR in cucumber (Tian et al., 2025); c) Caffeic acid, coumarin and SA in *M. incognita*-infested tomato enhance colonization by *Proteus vulgaris* BX-1, a nematocidal strain, demonstrating exudates-mediated recruitment of beneficial rhizobacteria (Yue et al., 2024). Thus, root exudates serve as a central interface linking plant physiology, nematode behavior and micro-biome assembly. The major root exudate compounds involved in nematode interaction are presented in Table 1.

Table1. Root exudates compounds and their roles in mediating Plant-Nematode and Microbial Interactions

Plant System	Species /	Key exudate compound	Observed effect on Nematodes	Associated Microbial Interaction / Mechanism	Reference
Tomato rootstock		Mixed root	suppressed	Alters nematode behavior	Yang et al.,

	exudates	M.incognita egg hatch and reduced J2 survival	and infection success	2016
Tomato intercropped with crown daisy (<i>Chrysanthemum coronarium</i> L.)	Lauric acid	Attracts M. incognita at 0.5-2 mM; repels them at ≥ 4 mM.	Concentration dependent signaling affecting nematode chemotaxis	Dong et al., 2013
Onion	4-hydroxy-benzenethanol (n-butanol extract)	Reduced egg hatchability to $<10\%$ And inhibited J2 viability	Direct nematicidal activity through toxic phenolic metabolites	Li et al., (2018)
Guava	Enriched root exudates with 1, 5-dinitrobiuret producing microbes	Altered root physiology and innate immunity and reduced susceptibility to M. enterolobii	Promotes microbial-mediated defense, stimulation of Induced Systemic Resistance	Souza et al., 2023
Marigold, Pepper, Soybean	Seedling root exudates	Attract Heterodera glycines (Cyst nematode) but repel Meloidogyne species, while root tips attract both species	Species specific chemical signalling regulating nematode host selection	Wang et al., 2018
Pepper-cucumber rotation	Palmitic acid	Recruits Pseudathrobacter oxydans; a nematicidal, degrades a nematode-promoting compound, and induce ISR in cucumber	Selective recruitment of beneficial microbes leading to induce systemic resistance and suppression of nematode infection	Tian et al., 2024
Tomato (<i>M.incognita</i> infested)	Caffeic acid, coumarin, salicylic acid	Enhances colonization of <i>Proteus vulgaris</i> BX-1 (nematicidal strain)	Root exudate-mediated recruitment of beneficial rhizobacteria microbe-assisted nematode suppression	Yue et al., 2024
<i>Arabidopsis</i>	Malic acid	Recruited <i>Bacillus subtilis</i> FB17, enhancing resistance to root pathogens and improving rhizosphere health	Chemotactic attraction of beneficial bacteria and activation of ISR	Rudrappa et al., 2008
Rice	Flavonoids and organic acids	Reduced invasion by <i>M.graminicola</i> through enhanced recruitment of beneficial rhizobacteria	Rhizosphere microbiome restricting and activation of plant defense pathways	Anil et al., 2024

5. Key Microbial Players in RKN Suppression

5.1. Plant growth-promoting rhizobacteria (PGPR)

PGPR such as *Bacillus*, *Pseudomonas*, *Paenibacillus* and *Streptomyces* spp. are repeatedly associated with RKN suppression. They produce lipopeptides (surfactin, iturin, fengycin), DAPG, phenazines, siderophores and VOCs that impair nematode mobility, inhibit egg hatching and prime ISR (Mata et al., 2025). *Pseudomonas fluorescens* strains reduce egg hatching and juvenile survival by 80–90%, while *Bacillus subtilis* can achieve 62% reduction in nematode infestation in tomato pot experiments (Choudhary et al., 2023; Araújo et al., 2009). *Pseudomonas fluorescens* F113 has strongly affected *Globodera rostochiensis* J2 stage nematode mobility and egg hatchability. Many PGPR also enhance nutrient acquisition and root growth, improving plant tolerance to residual nematode damage (Ye et al., 2022).

5.2. Fungal biocontrol agents (*Trichoderma*, *Pochonia*, *Purpureocillium*)

Fungal antagonists play multiple roles:

Trichoderma spp. produce peptaibols, cellulases and VOCs (e.g. 6-pentyl- α -pyrone, 1-octen-3-ol) that degrade eggshells, induce oxidative stress in nematodes and activate host defence responses, reducing gall formation and egg masses (Contreras-Cornejo et al., 2018).

Pochonia chlamydosporia parasitizes eggs and secretes chitinases and proteases, contributing to egg mortality and SAR/ISR activation (Escudero et al., 2016).

Purpureocillium lilacinum (formerly *Paecilomyces lilacinus*) achieves high egg parasitism and produces leucinostatins and hydrolytic enzymes, combining direct parasitism with metabolite toxicity (Xie et al., 2016).

These fungi also stimulate accumulation of flavonoids, phenolics, lignin and cell wall-related enzymes, reinforcing physical and chemical barriers against nematodes.

5.3. Endophytes and their multifunctional roles

Endophytic bacteria and fungi colonize internal root tissues and can exert systemic effects on plant defence (Gómez-Lama Cabanás et al., 2014). They may produce nematocidal metabolites in situ, modulate hormone signaling, and prime ISR/SAR (Shoresh et al., 2010; Hermosa et al., 2012). Some endophytes enhance tolerance to abiotic stress (drought, salinity), thereby indirectly improving resilience to nematode infection. Their intimate association with host tissues makes them promising candidates for durable, heritable resistance. Notably, *Trichoderma*-induced defense in tomato has been shown to persist across progeny, suggesting potential for transgenerational protection (de Medeiros et al., 2017).

5.4. Microbial consortia and synergistic interactions

Beneficial microorganisms rarely act in isolation; instead they form complex consortia that interact synergistically. Combinations of PGPR, fungi and AMF can provide additive or synergistic suppression of RKNs while enhancing growth and nutrient status (Ayaz et al., 2024). Microbial consortia can occupy multiple niches (rhizosphere, endosphere, phyllosphere), produce complementary metabolite profiles and reinforce multi-layered defense (direct antagonism, ISR, SAR, MIR). Harnessing such consortia is central to microbiome-enabled resilience.

PGPR strains that successfully colonize the rhizosphere can act as keystone species, anchoring the assembly of broader nematode-suppressive microbial communities and amplifying overall biocontrol activity beyond what any single introduced strain could achieve alone (Kumar et al., 2026). Such synergy is further reinforced when AMF, PGPR and *Trichoderma* spp. co-occur, since their combined activity initiates multiple defense pathways simultaneously, producing a stronger and more durable resistance response than any one partner acting in isolation (Ansabayeva et al., 2025). Harnessing such consortia is central to microbiome-enabled resilience.

6. Molecular and Omics Insights into Microbiome–Nematode Interactions

6.1. Metagenomics and microbiome profiling

Metagenomic sequencing and amplicon-based profiling (16S rRNA, ITS) have revealed shifts in rhizosphere and endosphere communities in response to nematode infestation and biocontrol treatments (Kudjordjie et al., 2024; Yao et al., 2025). For instance, amplicon sequencing of bacterial 16S rRNA, fungal ITS and eukaryotic 18S rRNA genes in tomato showed that *Meloidogyne incognita* parasitism produced distinct, time-dependent shifts in bacterial, fungal and eukaryotic community structure in both the rhizosphere and roots, together with stronger microbial network connectivity in infected compared with non-infected sample (Yao et al., 2025). Disease-suppressive soils often exhibit enrichment of specific taxa (e.g. *Bacillus*, *Pseudomonas*, *Streptomyces*, *Trichoderma*, nematophagous fungi) and higher functional gene diversity related to secondary metabolism and hydrolytic enzymes. Comparative metagenomics can identify keystone taxa and functional modules associated with RKN suppression (Topalović et al., 2020; Lu et al., 2026).

6.2. Transcriptomics of plant–microbe–nematode interactions

Transcriptomic analyses of plant roots and shoots under RKN attack, with or without beneficial microbes, reveal extensive reprogramming of defence, hormone and stress-related genes (Molinari et al., 2024). Biocontrol agents upregulate SA-dependent PR genes, JA/ET-responsive defence genes, ROS-scavenging enzymes and cell wall biosynthesis pathways, while nematodes attempt to suppress these responses via effectors early RKN infection, for instance, has been shown to specifically downregulate SA-responsive genes (*PR-1*, *PR-2*, *PR-4b*, *PR-5*) while leaving JA/ET-responsive genes largely unaffected, indicating a targeted, hormone-selective suppression strategy rather than blanket immune shutdown (Molinari et al., 2024). MAPK cascades, electrical signals and root–shoot feedback loops (e.g. JA accumulation in leaves following root infection) integrate local and systemic responses; recent work in tomato has shown that RKN attack triggers a phyB-dependent accumulation of the transcription factor HY5 in leaves, which activates JA biosynthesis genes, while GLR3.5-dependent electrical signals traveling from roots to shoots amplify this HY5–JA circuit to coordinate whole-plant defense (Sun et al., 2025).

6.3. Metabolomics and signaling molecules

Metabolomic profiling of root exudates, rhizosphere soil and plant tissues identifies key signaling molecules involved in microbiome–nematode interactions: phenolics, flavonoids, organic acids, fatty acids (lauric, palmitic), benzoxazinoids, saponins, phytoalexins and VOCs (Dong et al., 2024; Lu et al., 2020). Among these, lauric acid identified by GC-MS in crown daisy root exudate has been shown to directly regulate root-knot

nematode chemotaxis and infection by disrupting expression of the *Mi-18* neuropeptide gene, explaining the protective effect observed when crown daisy is intercropped with susceptible tomato (Dong et al., 2024). These metabolites mediate chemotaxis, microbial recruitment, ISR/SAR induction and direct nematicidal activity.

VOCs such as dimethyl disulfide, benzaldehyde, 1-octen-3-ol and 6-pentyl- α -pyrone exhibit LC50 values comparable to commercial nematicides and significantly reduce nematode infection (Pereira et al., 2026) (Table 2). VOCs are diverse metabolites with multifunctional roles in plant growth, defense, and rhizosphere ecology. They act directly on nematodes and pathogens and indirectly by priming plant immunity.

Table 2. VOCs and their effects in Nematode Suppression

Crop species	Major VOCs	Microbial Source	Mode of action	Effects on RKNs	Reference
Tomato	Dimethyl disulfide, Dimethyl trisulfide, volatile sulfur compounds	<i>Ochrobactrum pseudogrignone</i> , <i>Bacillus cereus</i> , <i>Bacillus tropica</i> , <i>Burkholderia ambifaria</i> , <i>Pseudomonas fluorescens</i> , <i>Pseudomonas chlororaphis</i> , <i>Serratia plymuthica</i>	Disruption of mitochondrial respiration, neurotoxicity, membrane damage, reduced infectivity	Strain NC1 produced potent nematicidal VOCs, causing high J2 mortality and 88-100% suppression of root knot formation	Yan et al., 2021
Tomato	Benzaldehyde	<i>Ochrobacterum pseudogrignone</i> , Several soil bacteria including <i>Bacillus</i> and <i>Pseudomonas</i> spp.	Interferes with embryonic development and juvenile movement	Exhibited nematicidal activity by inhibiting egg hatching and reducing J2 survival	Yan et al., 2021
Cucumber	1-Octen-3-ol, 3-Octanone, 3-Octanol	<i>Metarhizium anisopliae</i>	Membrane disruption, oxidative stress, chemorepellent activity	Caused approx. 50% J2 mortality, significantly inhibited egg hatching, and repelled infective J2s	Fang et al., 2023
Cucumber	1-Octen-3-ol, 3-Octanone	<i>Beauveria bassiana</i>	Disruption of membrane integrity and inhibition of nematode mobility	Induced high J2 mortality and significantly suppressed egg hatching through volatile mediated toxicity	Fang et al., 2023
Soil/Rhizosphere	1-octen-3-ol, 3-octanone, Benzaldehyde	Nematophagous fungi (<i>Arthrobotrys</i> , <i>Monacrosporium</i> , <i>Duddingtonia</i> , and <i>Pochonia</i> spp.)	Neurotoxicity, repellence, inhibition of feeding and reproduction	VOCs exhibited LC50 values comparable to commercial nematicides and significantly reduced nematode in plant	Pereira et al., 2026
Rice	Dimethyl disulfide, and other volatile sulfur compounds	<i>Bacillus cereus</i> , <i>Pseudomonas aeruginosa</i>	Sulfur VOCs impair respiration and reduce root penetration	Suppression of nematode population by 78% and decreased root galling by 55- 70% under soil microcosm conditions.	Hang et al., 2012
Eggplant	1-Octen-3-ol, 3-octanol, volatile esters	<i>Beauveria bassiana</i>	Volatile-induced paralysis and inhibition of egg development	Caused 55-70% J2 mortality, reduced root galling by 50-68% and suppressed nematode reproduction by 45-	Fang et al., 2023

				60%.	
Watermelon	Dimethyl disulfide, volatile sulfur compounds, volatile esters	<i>Bacillus cereus</i> , <i>Serratia plymuthica</i>	Sulfur VOCs inhibit host location and invasion	Suppressed root galling by 55-70%; reduced J2 penetration into roots by 65-78% and decreased nematode establishment under sand culture.	Yang et al., 2022
Tomato	Dimethyl disulfide, acetoin, 2,3-butanediol	<i>Bacillus velezensis</i>	Respiratory inhibition and oxidative damage	Volatile sulfur compounds disrupt respiration and neuromuscular function while priming host immunity.	Gao et al., 2016
Laboratory bioassays	Isobutyric acid, alcohols, esters, sesquiterpenes	<i>Muscodoralbusi</i>	Volatile organic compounds (VOCs) act as biofumigants, disrupting nematode physiology and causing paralysis and mortality through synergistic action of multiple VOCs	Nearly 100% mortality after fumigation	Strobel et al., 2006
Tomato	6-Pentyl- α -pyrone, 1-Octen-3-ol	<i>Trichoderma harzianum</i>	VOC-mediated toxicity and activation of host defense responses	Reduced gall formation and egg masses	Yan et al., 2021

6.4. Role of effector molecules and microbiome-derived compounds

On the nematode side, effector molecules manipulate host immunity and development (Niu et al., 2016). On the microbiome side, effector-like compounds (lipopeptides, peptaibols, terpenes, lactones, macrocyclic lactones) target nematode neuromuscular systems, membranes and signaling pathways. Macrocyclic lactones such as abamectin and emamectin bind glutamate-gated chloride channels, causing hyperpolarization, flaccid paralysis and death of nematodes. Although originally developed as chemical nematicides, similar modes of action may be exploited by microbial metabolites or engineered strains (Wolstenholme et al., 2005).

Macrocyclic lactones are non-volatile compounds that include abamectin, emamectin, avermectin B2 and mibemectin. These molecules exhibit potent nematicidal activity and are particularly effective against root-knot nematodes (*Meloidogyne* spp.), where they particularly suppress egg hatching, immobilize or kill second stage juveniles (J2), and reduce root invasion and reproduction (Talavera-Rubia et al., 2020; Radwan et al., 2019). In tomato, abamectin and emamectin significantly reduced egg hatching, increased J2 mortality, lowered gall formation and over performed the spinosyns, with the greatest gall reductions observed for emamectin and abamectin (Radwan et al., 2019).

The primary mechanism of action of macrocyclic lactones involves high affinity binding to glutamate-gated chloride channels, leading to hyperpolarization, flaccid paralysis and eventual death of nematodes (Lifschitz et al., 2024; Lamassiaude et al., 2021). In PPNs, chloride-channel involvement is indirectly inhibition of *M. incognita* motility, although the exact receptor subtype in *Meloidogyne* remains unresolved (Smus et al., 2017). Important nematicidal VOCs and their role in nematode suppression are presented in table 3.

Table3. Nematicidal Volatile Organic Compounds (NVOCs) and their role in Nematode suppression

Microbial Source	Target Stage Impacted	Maximum Efficacy Achieved	Key Bioactive Compounds (NVOCs)	Mechanism of action	Host crop and Experimental system	Reference
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<i>Ochrobactrum spp.</i>	Eggs and J2 juveniles	100% inhibition of hatching; complete J2 mortality	3-Epimacronine, Heraclenin, secondary metabolites	Alkaloid like compounds inducing rapid paralysis of J2 juveniles and inhibit embryonic development; metabolite mediated toxicity to developing stages	Guava - M. enterolobii (in vitro)	Krithika et al., 2024
<i>Bionectria ochroleuca</i>	Eggs and J2 juveniles	Egg hatching reduced to 5.64% and 95.4% J2 mortality	Secondary metabolites	Inhibits egg hatching and causes irreversible damage to infective juveniles	Guava - M. enterolobii (in vitro)	Shravani, 2024
<i>Trichoderma citrinoviride</i>	Eggs, egg masses and galls	~90% egg hatching inhibition	Peptaibols, Cellulases, secondary metabolites	Degrades eggshells enzymatically and induces oxidative stress in nematodes; cellulase-mediated	Laboratory assays	Fan et al., 2020
<i>Bacillus subtilis</i>	Egg masses and J2 juveniles	62% reduction in nematode infestation	Surfactin, iturin, fengycin	Lipopeptide disrupt nematode cuticle and activate ISR priming via cell wall components and enhanced plant defenses in host plants	Tomato (pot experiments)	Adam et al., 2014
<i>Streptomyces laurentii</i> and other <i>Streptomyces spp.</i>	Egg and J2 juveniles	33% reduction in disease suppression in JA deficient plants	Secondary metabolites	Dual mechanism: Secreted metabolites immobilize J2s and death; Activating JA mediated plant immunity, counteracting RKN-induced JA suppression; JA-dependent confirmed via lox8 mutant experiments	Maize-Meloidogyne spp.	Zheng et al., 2024
<i>Pseudomonas fluorescens</i>	Eggs and J2 juveniles	70-90% reduction in egg hatching and juvenile survival	2,4-diacetylphloroglucinol (DAPG), pyoluteorin, VOCs	Produces antimicrobial metabolites and VOCs that impair nematode mobility, inhibit egg hatching, and induce systemic resistance.	Tomato-M. incognita	Siddique and Shaukat 2003
<i>Paecilomyces lilacinus</i>	Egg and females	Upto 95% egg parasitism	Leucinostatins, chitinases, proteases	Parasitizes eggs and degrades eggshells through hydrolytic enzymes and toxic	Tomato-M. incognita	Kiewnick & Sikora 2006

				metabolites.		
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Beneficial microorganisms activate jasmonic acid (JA)- and salicylic acid (SA)-mediated signaling pathways, triggering systemic resistance in plants. These signaling networks induce pathogenesis-related (PR) proteins, antioxidant enzymes, and the deposition of callose and lignin, thereby strengthening plant defense and limiting root-knot nematode infection and gall development

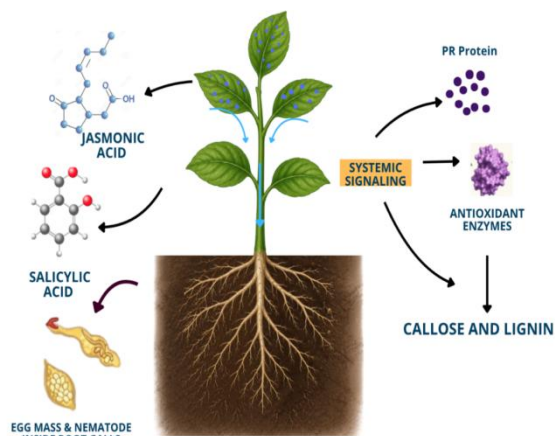


Fig II Microbiome-induced systemic defense responses against root-knot nematodes

7. Engineering and Manipulating the Plant Microbiome

7.1. Microbiome engineering and synthetic communities (SynComs)

Microbiome engineering involves designing and deploying synthetic microbial communities (SynComs) with defined composition and function (Martins et al., 2023). SynComs can be assembled from well-characterized PGPR, fungi and AMF that collectively provide robust RKN suppression and growth promotion, with AMF increasingly recognized as a keystone functional group that stabilizes community assembly and extends the ecological fitness of otherwise transient bacterial consortia (Zeng et al., 2025). By controlling community structure, researchers can dissect interaction networks, optimize metabolite production and minimize negative interactions compared with single-strain inoculants, defined SynComs exhibit greater resilience, more stable colonization, and broader beneficial metabolite profiles under controlled, reproducible conditions (Yu et al., 2025). SynComs can be delivered as seed coatings, root dips or soil inoculants (Martins et al., 2023).

7.2. Host-mediated microbiome selection

Plants can be bred or engineered to preferentially recruit beneficial microbiota via root exudate profiles and immune traits (Zhang et al., 2023). Host-mediated microbiome selection leverages natural variation in exudate composition (e.g. flavonoids, organic acids, fatty acids) and receptor repertoires to favour disease-suppressive communities. For example, malic acid secretion in *Arabidopsis* recruits *Bacillus subtilis* FB17, enhancing resistance to root pathogens and improving rhizosphere health (Rudrappa et al., 2008). This approach integrates plant genetics with microbiome ecology, opening opportunities for precision breeding of nematode-resilient cultivars.

7.3. Soil health management and microbiome modulation

Soil health practices reduced tillage, organic amendment, cover cropping, diversified rotations promote microbial diversity and stability, fostering disease-suppressive soils (Zhang et al., 2025; Stirling et al., 2013). Management that increases organic matter and structural complexity supports beneficial fungi and bacteria, while reducing reliance on broad-spectrum pesticides that disrupt microbiomes; organic amendments in particular increase the complexity of the soil food web and enhance nematode mortality relative to fast-release inorganic fertilizers, which instead simplify and degrade it. In rice, for instance, cover crop rotation with ryegrass has been shown to suppress root-knot nematode infection not through direct nematicidal toxicity of root exudates or residues, but by reshaping the composition of the soil microbiota itself, indicating that suppression can be mediated indirectly through microbiome restructuring rather than allelochemical action alone (Zhang et al., 2025). Integrating microbiome-aware soil management with targeted inoculants can enhance RKN suppression.

7.4. Role of organic amendments and bioinputs

Organic amendments (composts, manures, green manures, biochar) and bio inputs (microbial inoculants, biostimulants) can modulate microbiome composition and function (Ansabayeva et al., 2025). Some amendments release nematicidal compounds or stimulate indigenous nematophagous communities well-decomposed composts, for instance, mineralize slowly and release low concentrations of nematicidal breakdown products, while biochar additions have been shown to regulate plant-parasitic nematode populations, although this effect depends strongly on application rate and the specific mechanisms remain incompletely resolved (Nahar et al., 2006). Others improve nutrient status and root growth, indirectly reducing nematode impact. Bioinputs containing *Bacillus*, *Pseudomonas*, *Trichoderma*, *Purpureocillium* and AMF are increasingly

commercialized as bio-nematicides or biofertilizers, representing a rapidly expanding frontier in sustainable crop protection (Ansabayeva et al., 2025).

8. Integration with Sustainable Nematode Management Strategies

8.1. Compatibility with biological control agents (e.g., EPNs, fungi, bacteria)

Microbiome-based strategies should be integrated with other biological control agents such as entomopathogenic nematodes (EPNs), parasitoids and predators targeting nematode vectors or associated pests. Compatibility studies are needed to ensure that introduced microbes do not antagonize EPNs or beneficial insects. Synergistic combinations of PGPR, fungi and EPNs may provide multi-trophic suppression of nematodes and other soilborne pests (Darwish et al., 2025).

8.2. Integration with resistant cultivars

Microbiome-driven defense can complement genetic resistance. Resistant cultivars may recruit more beneficial microbiota or respond more strongly to ISR/SAR induction. Conversely, microbiome engineering can enhance the durability of resistance genes by reducing selection pressure on nematodes. Combining host resistance with disease-suppressive microbiomes offers a layered defence strategy (Elhady et al., 2021)

8.3. Synergy with reduced-risk nematicides and bioformulations

Reduced-risk nematicides (e.g. fluopyram, biologicals, and plant-derived compounds) can be used at lower doses in combination with microbiome-based approaches, minimizing environmental impact while maintaining efficacy (Dahlin et al., 2019). Bioformulations containing microbial consortia and compatible chemistries can exploit synergistic effects (e.g. VOCs plus contact nematicides) and broaden the spectrum of control (Oka et al., 2025).

8.4. Field-level validation and scalability

While many microbiome-mediated effects are demonstrated *in vitro* or in controlled environments, field-level validation is essential. Variability in soil, climate and management can influence performance. Large-scale trials, multi-location studies and long-term monitoring are needed to assess scalability, cost-effectiveness and farmer adoption. Formulation stability, shelf-life and delivery methods must be optimized for practical use (Ayaz et al., 2024)

9. Challenges and Limitations

9.1. Variability in field performance

Microbial inoculants often show inconsistent performance across sites and seasons due to differences in soil properties, native microbiomes, climate and agronomic practices. This variability complicates recommendations and may reduce farmer confidence. Developing predictive models and site- specific formulations is essential to overcome this limitation.

9.2. Microbiome stability and establishment issues

Introduced microbes must establish and persist in the rhizosphere or endosphere to provide lasting benefits. Competition with native communities, predation by protozoa, and environmental stress can limit establishment. Designing resilient SynComs and optimizing application timing and methods are ongoing challenges.

9.3. Environmental and soil-related constraints

Extreme temperatures, drought, salinity and nutrient imbalances can impair microbial activity and plant–microbe interactions. Beneficial taxa may be sensitive to specific conditions, limiting their utility in marginal environments. Tailored microbiome strategies are needed for different agroecological zones and are required to ensure consistent efficiency under diverse field conditions.

9.4. Regulatory and commercialization barriers

Regulatory frameworks for microbial products vary across countries and may be complex, especially for multi-strain consortia. Quality control, biosafety, intellectual property and registration costs can hinder commercialization. Clear guidelines and harmonized regulations would facilitate innovation and deployment.

10. Future Perspectives and Research Directions

10.1. Precision micro-biome engineering

Future research work will focus on precision engineering of microbiomes using systems biology, synthetic biology and ecological modelling. Designing communities with defined functions (nematicidal metabolite production, ISR induction, exudate modulation) and predictable behaviour will enable targeted interventions. Precision SynComs tailored to crop species and agroecological contexts will provide reproducible, scalable biocontrol solutions.

10.2. AI and big data in microbiome prediction

Artificial intelligence and machine learning can integrate multi-omics datasets (metagenomics, transcriptomics, and metabolomics), environmental variables and management practices to predict microbiome composition and function. Such tools can identify key taxa, forecast disease risk and guide microbiome-based recommendations. Predictive analytics will accelerate discovery pipelines and support decision-making in precision agriculture.

10.3. Climate-resilient microbiome strategies

Climate change will alter nematode distributions and plant–microbe interactions. Developing microbiome strategies that remain effective under heat, drought and flooding is critical. Stress-tolerant beneficial microbes

and adaptive management practices will be central to climate-resilient nematode control. Integrated microbiome engineering with climate smart agronomy will ensure long-term sustainability.

10.4. Translating lab findings to field applications

Bridging the gap between laboratory and field requires iterative cycles of discovery, validation and refinement. Co-design with farmers, participatory trials and socio-economic analyses will ensure that microbiome-based technologies are practical, acceptable and impactful. Optimizing formulation stability, delivery methods, and cost-effectiveness will be essential for adopting at scale.

11. CONCLUSIONS

Root-knot nematodes pose a major threat to global crop productivity, and conventional management strategies face significant limitations. The plant microbiome offers a powerful, multifaceted defence system against RKNs, operating through direct antagonism (nematicidal metabolites, enzymes, and parasitism), induced systemic resistance and systemic acquired resistance, and modulation of root architecture and exudation. Beneficial bacteria, fungi, endophytes and AMF form dynamic consortia that enhance plant health, resilience and productivity under nematode pressure.

Microbiome-driven bio defense aligns with principles of sustainable agriculture, reducing reliance on synthetic nematicides, preserving environmental quality and supporting soil health. Integrating microbiome engineering, host-mediated selection, soil management and compatible chemistries can deliver robust, scalable solutions for nematode management.

With continued advances in omics, AI and ecological engineering, microbiome-based strategies are poised to become central components of integrated nematode management. Realizing this potential will require careful field validation, regulatory support and farmer engagement—but the trajectory is clear: harnessing the plant microbiome offers transformative opportunities to protect crops, secure yields and build resilient agroecosystems in the face of evolving nematode threats.

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The authors declare that they have no competing interest

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REFERENCE:

1. Abad, P., Gouzy, J., Aury, J. M., Castagnone-Sereno, P., Danchin, E. G. J., Deleury, E., Perfus-Barbeoch, L., Anthouard, V., Artiguenave, F., Blok, V. C., Caillaud, M. C., Coutinho, P. M., Dasilva, C., De Luca, F., Deau, F., Esquibet, M., Flutre, T., Goldstone, J. V., Hamamouch, N., ... Wincker, P. (2008). Genome sequence of the metazoan plant-parasitic nematode *Meloidogyne incognita*. *Nature Biotechnology*, 26(8), 909–915. <https://doi.org/10.1038/nbt.1482>
2. Adam, M., Heuer, H., & Hallmann, J. (2014). Bacterial antagonists of fungal pathogens also control root-knot nematodes by induced systemic resistance of tomato plants. *PloS one*, 9(2), e90402. <https://doi.org/10.1371/journal.pone.0090402>
3. Aioub, A. A., Elesawy, A. E., & Ammar, E. E. (2022). Plant growth promoting rhizobacteria (PGPR) and their role in plant-parasitic nematodes control: a fresh look at an old issue. *Journal of Plant Diseases and Protection*, 129(6), 1305–1321. <https://doi.org/10.1007/s41348-022-00642-3>
4. Anil, A., Johnson, L. W., Pankaj, & Somvanshi, V. S. (2024). Molecular pathways involved in the interaction of rice plants with rice root-knot nematode *Meloidogyne graminicola*. *Indian Journal of Nematology*, 54(2), 109–120. <https://doi.org/10.5958/0974-4444.2024.00023.4>
5. Ansabayeva, A., Makhambetov, M., Rebouh, N. Y., Abdelkader, M., Saudy, H. S., Hassan, K. M., & Ebrahim, M. (2025). Plant growth-promoting microbes for resilient farming systems: mitigating environmental stressors and boosting crops productivity—a review. *Horticulturae*, 11(3), 260. <https://doi.org/10.3390/horticulturae11030260>
6. Araújo, F. F. D., & Marchesi, G. V. P. (2009). Use of *Bacillus subtilis* in the control of root-knot nematode and the growth promotion in tomato. *Ciência Rural*, 39, 1558–1561. <https://doi.org/10.33448/rsd-v10i6.15209>
7. Ayaz, M., Zhao, J. T., Zhao, W., Chi, Y. K., Ali, Q., Ali, F., & Huang, W. K. (2024). Biocontrol of plant parasitic nematodes by bacteria and fungi: a multi-omics approach for the exploration of novel nematicides in sustainable agriculture. *Frontiers in Microbiology*, 15, 1433716. <https://doi.org/10.3389/fmicb.2024.1433716>

8. Bais, H. P., Weir, T. L., Perry, L. G., Gilroy, S., & Vivanco, J. M. (2006). The role of root exudates in rhizosphere interactions with plants and other organisms. *Annual Review of Plant Biology*, 57, 233–266. <https://doi.org/10.1146/annurev.arplant.57.032905.105159>
9. Benitez, M. S., Ewing, P. M., Osborne, S. L., & Lehman, R. M. (2021). Rhizosphere microbial communities explain positive effects of diverse crop rotations on maize and soybean performance. *Soil Biology and Biochemistry*, 159, 108309. <https://doi.org/10.1016/j.soilbio.2021.108309>
10. Bozbuga, R., Lilley, C. J., Knox, J. P., & Urwin, P. E. (2018). Host-specific signatures of the cell wall changes induced by the plant parasitic nematode, *Meloidogyne incognita*. *Scientific reports*, 8(1), 17302. <https://doi.org/10.1038/s41598-018-35529-7>
11. Chaparro, J. M., Sheflin, A. M., Manter, D. K., & Vivanco, J. M. (2012). Manipulating the soil microbiome to increase soil health and plant fertility. *Biology and Fertility of Soils*, 48(5), 489–499. <https://doi.org/10.1007/s00374-012-0691-4>
12. Choudhary, K., Bishnoi, S. P., Dhayal, R., Chandrawat, B. S., Kumari, M., Gurjar, V., & Gurjar, H. (2023). Effect on Hatching and Mortality of Root-knot Nematode (*Meloidogyne javanica*) by Bio-agents. *Int J Plant Soil Sci*, 35(19), 1728–1735. <https://doi.org/10.9734/ijpss/2023/v35i193721>
13. Compant, S., Samad, A., Faist, H., & Sessitsch, A. (2019). A review on the plant microbiome: ecology, functions, and emerging trends in microbial application. *Journal of advanced research*, 19, 29–37. <https://doi.org/10.1016/j.jare.2019.03.004>
14. Contreras-Cornejo, H. A., Macías-Rodríguez, L., del-Val, E., & Larsen, J. (2018). The root endophytic fungus *Trichoderma atroviride* induces foliar herbivory resistance in maize plants. *Applied Soil Ecology*, 124, 45–53. <https://doi.org/10.1016/j.apsoil.2017.10.004>
15. Dahlin, P., Eder, R., Consoli, E., Krauss, J., & Kiewnick, S. (2019). Integrated control of *Meloidogyne incognita* in tomatoes using *fluopyram* and *Purpureocillium lilacinum* strain 251. *Crop Protection*, 124, 104874. <https://doi.org/10.1016/j.cropro.2019.104874>
16. Darwish, I. A. A., Martins, D. P., Ryan, D., & Kakouli-Duarte, T. (2025). State of the art on the interaction of entomopathogenic nematodes and plant growth-promoting rhizobacteria to innovate a sustainable plant health product. *Crops*, 5(4), 52. <https://doi.org/10.3390/crops5040052>
17. De Kock, K., Matthys, J., & Kyndt, T. (2024). Ros detection and quantification in plant–nematode interactions. In *Plant-Nematode Interactions* (pp. 305–316). New York, NY: Springer US. https://doi.org/10.1007/978-1-0716-3638-1_10
18. Desmedt, W., Kudjordjie, E. N., Chavan, S. N., Desmet, S., Nicolaisen, M., Vanholme, B., & Kyndt, T. (2022). Distinct chemical resistance-inducing stimuli result in common transcriptional, metabolic, and nematode community signatures in rice root and rhizosphere. *Journal of Experimental Botany*, 73(22), 7564–7581. <https://doi.org/10.1093/jxb/erac375>
19. Dong, L., Li, X., Huang, L., Gao, Y., Zhong, L., Zheng, Y., & Zuo, Y. (2014). Lauric acid in crown daisy root exudate potently regulates root-knot nematode chemotaxis and disrupts Mi-flp-18 expression to block infection. *Journal of Experimental Botany*, 65(1), 131–141. <https://doi.org/10.1093/jxb/ert356>
20. Durán, P. (2024). The core microbiota across the green lineage. *Current Opinion in Plant Biology*, 77, 102487. <https://doi.org/10.1016/j.pbi.2023.102487>
21. Elhady, A., Abbasi, S., Safaie, N., & Heuer, H. (2021). Responsiveness of elite cultivars vs. ancestral genotypes of barley to beneficial rhizosphere microbiome, supporting plant defense against root-lesion nematodes. *Frontiers in Plant Science*, 12, 721016. <https://doi.org/10.3389/fpls.2021.721016>
22. Escudero, N., Ferreira, S. R., Lopez-Moya, F., Naranjo-Ortiz, M. A., Marin-Ortiz, A. I., Thornton, C. R., & Lopez-Llorca, L. V. (2016). Chitosan enhances parasitism of *Meloidogyne javanica* eggs by the nematophagous fungus *Pochonia chlamydosporia*. *Fungal biology*, 120(4), 572–585. <https://doi.org/10.1016/j.funbio.2015.12.005>
23. Faizi, S., Fayyaz, S., Bano, S., Yawar Iqbal, E., Siddiqi, H., & Naz, A. (2011). Isolation of nematicidal compounds from *Tagetes patula* L. yellow flowers: Structure–activity relationship studies against cyst nematode *Heterodera* infective stage larvae. *Journal of Agricultural and Food Chemistry*, 59(17), 9080–9093. <https://doi.org/10.1021/jf201611b>
24. Fan, H., Yao, M., Wang, H., Zhao, D., Zhu, X., Wang, Y., & Chen, L. (2020). Isolation and effect of *Trichoderma citrinoviride* Snf1910 for the biological control of root-knot nematode, *Meloidogyne incognita*. *BMC microbiology*, 20(1), 299. <https://doi.org/10.1186/s12866-020-01984-4>
25. Fang, M., Long, W., Sun, J., Wang, A., Chen, L., Cui, Y., & Wei, X. (2023). Toxicity of fungal-derived volatile organic compounds against root-knot nematodes. *Pest Management Science*, 79(12), 5162–5172. <https://doi.org/10.1002/ps.7719>
26. Gao, Z., Zhang, B., Liu, H., Han, J., & Zhang, Y. (2017). Identification of endophytic *Bacillus velezensis* ZSY-1 strain and antifungal activity of its volatile compounds against *Alternaria solani* and *Botrytis cinerea*. *Biological Control*, 105, 27–39. <https://doi.org/10.1016/j.biocontrol.2016.11.007>
27. Giné, A., & Sorribas, F. J. (2017). Effect of plant resistance and BioAct WG (*Purpureocillium lilacinum* strain 251) on *Meloidogyne incognita* in a tomato–cucumber rotation in a greenhouse. *Pest management science*, 73(5), 880–887. <https://doi.org/10.1002/ps.4357>

28. Grabau, Z. J., Sandoval-Ruiz, R., & Liu, C. (2024). Fumigation using 1, 3-dichloropropene manages *Meloidogyne enterolobii* in sweet potato more effectively than fluorinated nematicides. *Plant Disease*, 108(7), 2162-2169. <https://doi.org/10.1094/pdis-12-23-2726-re>
29. Gómez-Lama Cabanás, C., Schilirò, E., Valverde-Corredor, A., & Mercado-Blanco, J. (2014). The biocontrol endophytic bacterium *Pseudomonas fluorescens* PICF7 induces systemic defense responses in aerial tissues upon colonization of olive roots. *Frontiers in microbiology*, 5, 427. <https://doi.org/10.3389/fmicb.2014.00427>
30. Habteweld, A., Kantor, M., Kantor, C., & Handoo, Z. (2024). Understanding the dynamic interactions of root-knot nematodes and their host: Role of plant growth-promoting bacteria and abiotic factors. *Frontiers in Plant Science*, 15, 1377453. <https://doi.org/10.3389/fpls.2024.1377453>
31. Han, M., Han, Y., Liu, X., Li, G., & Li, P. (2025). Rhizosphere microbiomes altered by environmental stresses and agronomic practices: Implications for plant adaptation and soil biogeochemical processes. *Plant Stress*, 101062. <https://doi.org/10.1016/j.stress.2025.101062>
32. Harbort, C. J., et al. (2024). Root exudation and rhizosphere microbial recruitment are influenced by novel plant trait diversity in carrot genotypes. <https://doi.org/10.1016/j.soilbio.2024.109516>
33. Hermosa, R., Viterbo, A., Chet, I., & Monte, E. (2012). Plant-beneficial effects of *Trichoderma* and of its genes. *Microbiology*, 158(1), 17-25. <https://doi.org/10.1099/mic.0.052274-0>
34. Huang, C.-J., Tsay, J.-F., Chang, S.-Y., Yang, H.-P., Wu, W.-S., & Chen, C.-Y. (2012). Dimethyl disulfide is an induced systemic resistance elicitor produced by *Bacillus cereus* C1L. *Pest Management Science*, 68(9), 1306–1310. <https://doi.org/10.1002/ps.3301>
35. Ismail, M., Javed, S., Kazim, M., Razaq, A., Hussain, E., Ali, S., & Choudhary, M. I. (2022). Phenylpropanoids from *Tanacetum baltistanicum* with nematocidal and insecticidal activities. *Chemistry of Natural Compounds*, 58(4), 637-643. <https://doi.org/10.20944/preprints202312.0814.v1>
36. Jung, J., Ahn, S., Kim, D. H., & Riu, M. (2024). Triple interactions for induced systemic resistance in plants. *Frontiers in Plant Science*, 15, 1464710. <https://doi.org/10.3389/fpls.2024.1464710>
37. Kiewnick, S., & Sikora, R. A. (2006). Biological control of the root-knot nematode *Meloidogyne incognita* by *Paecilomyces lilacinus* strain 251. *Biological Control*, 38(2), 179–187. <https://doi.org/10.1016/j.biocontrol.2005.12.006>
38. Kirwa, H. K., Murungi, L. K., Beck, J. J., & Torto, B. (2018). Elicitation of differential responses in the root-knot nematode *Meloidogyne incognita* to tomato root exudate cytokinin, flavonoids, and alkaloids. *Journal of Agricultural and Food Chemistry*, 66(43), 11291-11300. <https://doi.org/10.1021/acs.jafc.8b05101>
39. Krithika, V. P., Shandeep, G., Bellie, A., Banu, J. G., Mannu, J., Suganthi, M., & Mohan, P. (2024). Harnessing nature's arsenal: *Ochrobactrum* bacteria metabolites in the battle against root-knot nematode—Insights from in vitro and molecular docking studies. *Journal of Invertebrate Pathology*, 204, 108114. <https://doi.org/10.1016/j.jip.2024.108114>
40. Kudjordjie, E. N., Santos, S. S., Topalović, O., & Vestergård, M. (2024). Distinct changes in tomato-associated multi-kingdom microbiomes during *Meloidogyne incognita* parasitism. *Environmental Microbiome*, 19(1), 53. <https://doi.org/10.1186/s40793-024-00597-y>
41. Kumar, S. M., Ragupathy, T. V., Dananjeyan, B., Thiagarajan, C., Loganathan, A., & Natarajan, S. (2026). Microbiome-assisted plant breeding: integrating host-microbiome interactions into crop improvement. *Archives of Microbiology*, 208(5), 242. <https://doi.org/10.1007/s00203-026-04795-9>
42. Lamassiaude, N., Courtot, E., Corset, A., Charvet, C. L., & Neveu, C. (2022). Pharmacological characterization of novel heteromeric GluCl subtypes from *Caenorhabditis elegans* and parasitic nematodes. *British Journal of Pharmacology*, 179(6), 1264-1279. <https://doi.org/10.1111/bph.15703>
43. Li, T., Wang, H., Xia, X., Cao, S., Yao, J., & Zhang, L. (2018). Inhibitory effects of components from root exudates of Welsh onion against root-knot nematodes. *PLoS ONE*, 13(7), e0201471. <https://doi.org/10.1371/journal.pone.0201471>
44. Li, Y., Sun, Z., Zhang, J., Wang, X., & Zhang, K. Q. (2023). Volatile organic compounds produced by *Trichoderma* spp. as biocontrol agents against plant-parasitic nematodes: Mechanisms and applications. *Journal of Fungi*, 9(4), 425. <https://doi.org/10.3390/jof9040425>
45. Liang, L. M., Zou, C. G., Xu, J., & Zhang, K. Q. (2019). Signal pathways involved in microbe–nematode interactions provide new insights into the biocontrol of plant-parasitic nematodes. *Philosophical Transactions of the Royal Society B*, 374(1767), 20180317. <https://doi.org/10.1098/rstb.2018.0317>
46. Lifschitz, A., Nava, S., Miró, V., Cantón, C., Alvarez, L., & Lanusse, C. (2024). Macrocyclic lactones and ectoparasites control in livestock: efficacy, drug resistance and therapeutic challenges. *International Journal for Parasitology: Drugs and Drug Resistance*, 26, 100559. <https://doi.org/10.1016/j.ijpddr.2024.100559>
47. Lu, Q., Liu, T., Wang, N., Dou, Z., Wang, K., & Zuo, Y. (2020). Nematicidal effect of methyl palmitate and methyl stearate against *Meloidogyne incognita* in bananas. *Journal of agricultural and food chemistry*, 68(24), 6502-6510. <https://doi.org/10.1021/acs.jafc.0c00218>
48. Lu, Q., Wang, K., Gu, S., Ma, J., Cui, D., Chi, Z., & Zuo, Y. (2026). Siderophore-producing *Bacillus* and free-living nematodes are associated with soil suppressiveness to banana root-knot nematodes. *Nature Communications*, 17(1), 2688-2688. <https://doi.org/10.1038/s41467-026-69647-y>

49. Lu, T., Xuanquan, Z., Jia, M., Yuan, G., Li, J., Liu, Z., & Bai, Y. Rhizosphere Microecological Characteristics Associated with Tobacco Root-Knot Nematode Disease. *Frontiers in Microbiology*, 17, 1874628. <https://doi.org/10.3389/fmicb.2026.1874628>
50. Mantelin, S., Bellafiore, S., & Kyndt, T. (2022). Rooting out the mechanisms of root-knot nematode–plant interactions. *Annual Review of Phytopathology*, 60, 43–67. <https://doi.org/10.1146/annurev-phyto-021621-120943>
51. Martins, S. J., Pasche, J., Silva, H. A. O., Selten, G., Savastano, N., Abreu, L. M., ... & Cernava, T. (2023). The use of synthetic microbial communities to improve plant health. *Phytopathology*®, 113(8), 1369-1379. <https://doi.org/10.1094/phyto-01-23-0016-ia>
52. Martínez-Medina, A., Fernandez, I., Lok, G. B., Pozo, M. J., Pieterse, C. M., & Van Wees, S. C. (2017). Shifting from priming of salicylic acid-to jasmonic acid-regulated defences by *Trichoderma* protects tomato against the root knot nematode *Meloidogyne incognita*. *New phytologist*, 213(3), 1363-1377. <https://doi.org/10.1111/nph.14251>
53. Marin, O., & Kuzmanović, N. (2023). The use of synthetic microbial communities to improve plant health. *Phytopathology*, 113(9). <https://doi.org/10.1094/PHYTO-01-23-0016-IA>
54. Mata, A. S., Cruz, C., Gaspar, J. R., Abrantes, I., Conceição, I. L., Morais, P. V., & Proença, D. N. (2025). Plant growth-promoting bacteria as biological control agents for sustainable agriculture: targeting root-knot nematodes. *Frontiers in Plant Science*, 16, 1567265. <https://doi.org/10.3389/fpls.2025.1567265>
55. Medeiros, H. A. D., Araújo Filho, J. V. D., Freitas, L. G. D., Castillo, P., Rubio, M. B., Hermosa, R., & Monte, E. (2017). Tomato progeny inherit resistance to the nematode *Meloidogyne javanica* linked to plant growth induced by the biocontrol fungus *Trichoderma atroviride*. *Scientific reports*, 7(1), 40216. <https://doi.org/10.1038/srep40216>
56. Migunova, V. D., & Sasanelli, N. (2021). Bacteria as biocontrol tool against phytoparasitic nematodes. *Plants*, 10(2), 389. <https://doi.org/10.3390/plants10020389>
57. Mo, C., & Zhang, L. (2024). Unraveling the Roles of Neuropeptides in the Chemosensation of the Root-Knot Nematode *Meloidogyne javanica*. *International Journal of Molecular Sciences*, 25(12), 6300. <https://doi.org/10.3390/ijms25126300>
58. Molinari, S., Farano, A. C., & Leonetti, P. (2024). Root-knot nematode early infection suppresses immune response and elicits the antioxidant system in tomato. *International Journal of Molecular Sciences*, 25(23), 12602. <https://doi.org/10.3390/ijms252312602>
59. Molinari, S., Farano, A. C., & Leonetti, P. (2024). Root-knot nematode early infection suppresses immune response and elicits the antioxidant system in tomato. *International Journal of Molecular Sciences*, 25(23), 12602. <https://doi.org/10.3390/ijms252312602>
60. Nahar, K., Kyndt, T., De Vleeschauwer, D., Höfte, M., & Gheysen, G. (2011). The jasmonate pathway is a key player in systemically induced defense against root knot nematodes in rice. *Plant physiology*, 157(1), 305-316. <https://doi.org/10.1104/pp.111.177576>
61. Nahar, M. S., Grewal, P. S., Miller, S. A., Stinner, D., Stinner, B. R., Kleinhenz, M. D., ... & Doohan, D. (2006). Differential effects of raw and composted manure on nematode community, and its indicative value for soil microbial, physical and chemical properties. *Applied Soil Ecology*, 34(2-3), 140-151. <https://doi.org/10.1016/j.apsoil.2006.03.011>
62. Niu, J., Liu, P., Liu, Q., Chen, C., Guo, Q., Yin, J., & Jian, H. (2016). Msp40 effector of root-knot nematode manipulates plant immunity to facilitate parasitism. *Scientific reports*, 6(1), 19443. <https://doi.org/10.1038/srep19443>
63. Oka, Y. (2025). Synergistic control of *Meloidogyne* species on agar plates by plant extracts combined with a nematicide or biocontrol agent. *European Journal of Plant Pathology*, 1-16. <https://doi.org/10.1007/s10658-025-03164-4>
64. Parveen, A., Tanaka, K., & Khan, M. (2025). Biocontrol efficacy of *Pochonia chlamydosporia* against root-knot nematode *Meloidogyne javanica* in eggplant and its impact on plant growth. *Scientific Reports*, 15(1), 36990. <https://doi.org/10.1038/s41598-025-99527-2>
65. Pereira, C.G., Varejão, J.O.S., Barros, A.F. et al. Identification and fumigant effects of nematicidal volatile organic compounds produced by nematophagous fungi against root-knot nematodes. *BioControl* 71, 613–625 (2026). <https://doi.org/10.1007/s10526-026-10384-y>
66. Pieterse, C. M., de Jonge, R., & Berendsen, R. L. (2016). The soil-borne supremacy. *Trends in plant science*, 21(3), 171-173. <https://doi.org/10.1016/j.tplants.2016.01.018>
67. Pinto, Y., & Bhatt, A. S. (2024). Sequencing-based analysis of microbiomes. *Nature Reviews Genetics*, 25(12), 829-845. <https://doi.org/10.1038/s41576-024-00746-6>
68. Pires, D., Vicente, C. S., Menéndez, E., Faria, J. M., Rusinque, L., Camacho, M. J., & Inácio, M. L. (2022). The fight against plant-parasitic nematodes: Current status of bacterial and fungal biocontrol agents. *Pathogens*, 11(10), 1178. <https://www.mdpi.com/2076-0817/11/10/1178>
69. Radwan, M. A., Saad, A. S. A., Mesbah, H. A., Ibrahim, H. S., & Khalil, M. S. (2019). Investigating the in vitro and in vivo nematicidal performance of structurally related macrolides against the root-knot nematode, *Meloidogyne incognita*. *Hell. Plant Prot. J.*, 12(1), 24-37. [10.2478/hppj-2019-0005](https://doi.org/10.2478/hppj-2019-0005)

70. Raza, F. B., Vijayaraghavalu, S., Kandasamy, R., & Krishnaswami, V. (2023). Microbiome and the inflammatory pathway in peri-implant health and disease with an updated review on treatment strategies. *Journal of oral biology and craniofacial research*, 13(2), 84-91. 10.1016/j.jobcr.2022.11.005
71. Romão, I. R., do Carmo Gomes, J., Silva, D., & Vilchez, J. I. (2025). The seed microbiota from an application perspective: an underexplored frontier in plant–microbe interactions. *Crop Health*, 3(1), 12. <https://doi.org/10.1007/s44297-025-00051-6>
72. Rubayet, M. T., & Hossain, M. M. (2025). Bio-exploration of plant growth-promoting fungus *Trichoderma* as a potent candidate for plant disease management: An overview. *OnLine Journal of Biological Sciences*, 25(1), 22-52. 10.3844/ojbsci.2025.22.52
73. Rudrappa, T., Czymbek, K. J., Paré, P. W., & Bais, H. P. (2008). Root-secreted malic acid recruits beneficial soil bacteria. *Plant Physiology*, 148(3), 1547–1556. <https://doi.org/10.1104/pp.108.127613>
74. Santoyo, G. (2025). Advances in the Plant Microbiome: Rhizosphere, Endosphere, and Phyllosphere. *Microorganisms*, 13(11), 2581. <https://doi.org/10.3390/microorganisms13112581>
75. Shores, M., Harman, G. E., & Mastouri, F. (2010). Induced systemic resistance and plant responses to fungal biocontrol agents. *Annual review of phytopathology*, 48(1), 21-43. <https://doi.org/10.1146/annurev-phyto-073009-114450>
76. Shrivani, V., Nallusamy, S., Govindasamy, J., Eswaran, K., Iruthayasamy, J., & Annaiyan, S. (2024). Unravelling the potent nematotoxic compounds from *Clonostachys rosea* effective against root knot nematode, *Meloidogyne incognita*-an in-vitro and in-silico approach. *Physiological and Molecular Plant Pathology*, 131, 102279. <https://doi.org/10.1016/j.pmpp.2024.102279>
77. Siddiqui, I. A., & Shaikat, S. S. (2004). Systemic resistance in tomato induced by biocontrol bacteria against the root-knot nematode, *Meloidogyne javanica* is independent of salicylic acid production. *Journal of Phytopathology*, 152(1), 48-54. <https://doi.org/10.1046/j.1439-0434.2003.00800.x>
78. Singh, N. (2020). Emerging problem of guava decline caused by *Meloidogyne enterolobii* and *Fusarium oxysporum* f. sp. *psidii*. *Indian Phytopathology*, 73(2), 373-374. <https://doi.org/10.1007/s42360-020-00198-y>
79. Smus, J. P., Ludlow, E., Dallièr, N., Luedtke, S., Monfort, T., Lilley, C., & Mahajan, S. (2017). Coherent anti-Stokes Raman scattering (CARS) spectroscopy in *Caenorhabditis elegans* and *Globodera pallida*: evidence for an ivermectin-activated decrease in lipid stores. *Pest management science*, 73(12), 2550-2558. <https://doi.org/10.1002/ps.4707>
80. Soulé, S., Huang, K., Mulet, K., Mejias, J., Bazin, J., Truong, N. M., & Quentin, M. (2024). The root-knot nematode effector MiEFF12 targets the host ER quality control system to suppress immune responses and allow parasitism. *Molecular Plant Pathology*, 25(7), e13491. <https://doi.org/10.1111/mpp.13491>
81. Souza, R. M., Oliveira, D. F., Gomes, V. M., Viana, A. J., Silva, G. H., & Machado, A. R. (2023). *Meloidogyne enterolobii*-induced changes in guava root exudates are associated with root rotting caused by *Neocosmospora falciformis*. *Journal of Nematology*, 55(1), 20230055. 10.2478/jofnem-2023-0055
82. Stirling, G. R. (2013). Integration of organic amendments, crop rotation, residue retention and minimum tillage into a subtropical vegetable farming system enhances suppressiveness to root-knot nematode (*Meloidogyne incognita*). *Australasian Plant Pathology*, 42(6), 625-637. <https://doi.org/10.1007/s13313-013-0236-9>
83. Strobel, G. A. (2006). *Muscodor albus* and its biological promise. *Journal of Industrial Microbiology & Biotechnology*, 33(7), 514–522. <https://doi.org/10.1007/s10295-006-0090-7>
84. Sun, T., Hu, C., Zhu, C., Cai, J., Wang, G., Xia, X., & Zhou, J. (2025). HY5 integrates light and electrical signaling to trigger a jasmonate burst for nematode defense in tomato. *Nature Communications*, 16(1), 8750. <https://doi.org/10.1038/s41467-025-63779-3>
85. Talavera-Rubia, M., Vela-Delgado, M. D., & Verdejo-Lucas, S. (2020). Nematicidal efficacy of milbemectin against root-knot nematodes. *Plants*, 9(7), 839. <https://doi.org/10.3390/plants9070839>
86. Tian, T., Gheysen, G., Kyndt, T., Mo, C., Xiao, X., Lv, Y., & Xiao, Y. (2025). Pepper root exudate alleviates cucumber root-knot nematode infection by recruiting a rhizobacterium. *Plant Communications*, 6(1). 10.1016/j.xplc.2024.101139
87. Tian, Z., Zhou, N., Yang, H., Gao, X., Liu, L., Peng, D., & Han, S. (2025). Chemical and biological controls and soil amendments for plant-parasitic nematode management. *New Plant Protection*, 2(4), e70020. <https://doi.org/10.1002/npp2.70020>
88. Topalović, O., Hussain, M., & Heuer, H. (2020). Plants and associated soil microbiota cooperatively suppress plant-parasitic nematodes. *Frontiers in microbiology*, 11, 313. <https://doi.org/10.3389/fmicb.2020.00313>
89. Trivedi, P., Leach, J. E., Tringe, S. G., Sa, T., & Singh, B. K. (2020). Plant–microbiome interactions: from community assembly to plant health. *Nature reviews microbiology*, 18(11), 607-621. <https://doi.org/10.1038/s41579-020-0412-1>
90. Vandenkoornhuys, P., Quaiser, A., Duhamel, M., Le Van, A., & Dufresne, A. (2015). The importance of the microbiome of the plant holobiont. *New Phytologist*, 206(4), 1196-1206. <https://doi.org/10.1111/nph.13312>
91. Vasantha-Srinivasan, P., Park, K. B., Kim, K. Y., Jung, W. J., & Han, Y. S. (2025). The role of *Bacillus* species in the management of plant-parasitic nematodes. *Frontiers in Microbiology*, 15, 1510036. <https://doi.org/10.3389/fmicb.2024.1510036>

92. Vashisth, S., Kumar, P., Chandel, V. G. S., Kumar, R., Verma, S. C., & Chandel, R. S. (2024). Unraveling the enigma of root-knot nematodes: from origins to advanced management strategies in agriculture. *Planta*, 260(2), 36. <https://doi.org/10.1007/s00425-024-04464-5>
93. Veronico, P., Paciolla, C., Pomar, F., De Leonardis, S., García-Ulloa, A., & Melillo, M. T. (2018). Changes in lignin biosynthesis and monomer composition in response to benzothiadiazole and root-knot nematode *Meloidogyne incognita* infection in tomato. *Journal of plant physiology*, 230, 40-50. <https://doi.org/10.1016/j.jplph.2018.07.013>
94. Vos, C. M., Tesfahun, A. N., Panis, B., De Waele, D., & Elsen, A. (2012). Arbuscular mycorrhizal fungi induce systemic resistance in tomato against the sedentary nematode *Meloidogyne incognita* and the migratory nematode *Pratylenchus penetrans*. *Applied Soil Ecology*, 61, 1-6. <https://doi.org/10.1016/j.apsoil.2012.04.007>Get rights and content
95. Wang, C., Masler, E. P., & Rogers, S. T. (2018). Responses of *Heteroderaglycines* and *Meloidogyne incognita* infective juveniles to root tissues, root exudates, and root extracts from three plant species. *Plant Disease*, 102(9), 1733-1740 <https://doi.org/10.1094/PDIS-09-17-1445-RE>
96. Wolstenholme, A. J., & Rogers, A. T. (2005). Glutamate-gated chloride channels and the mode of action of the avermectin/milbemycin anthelmintics. *Parasitology*, 131(S1), S85-S95. <https://doi.org/10.1017/S0031182005008218>
97. Xie, J., Li, S., Mo, C., Xiao, X., Peng, D., Wang, G., & Xiao, Y. (2016). Genome and transcriptome sequences reveal the specific parasitism of the nematophagous *Purpureocillium lilacinum* 36-1. *Frontiers in microbiology*, 7, 1084. <https://doi.org/10.3389/fmicb.2016.01084>
98. Yadav, H., Roberts, P. A., & Lopez-Arredondo, D. (2025). Combating root-knot nematodes (*Meloidogyne* spp.): from molecular mechanisms to resistant crops. *Plants*, 14(9), 1321. <https://doi.org/10.3390/plants14091321>
99. Yan, Y., Mao, Q., Wang, Y., Zhao, J., Fu, Y., Yang, Z., & Ahammed, G. J. (2021). *Trichoderma harzianum* induces resistance to root-knot nematodes by increasing secondary metabolite synthesis and defense-related enzyme activity in *Solanum lycopersicum* L. *Biological Control*, 158, 104609. <https://doi.org/10.1016/j.biocontrol.2021.104609>
100. Yang, G., Zhou, B., Zhang, X., Zhang, Z., Wu, Y., Zhang, Y., & Teng, L. (2016). Effects of tomato root exudates on *Meloidogyne incognita*. *PLoS one*, 11(4), e0154675. <https://doi.org/10.1371/journal.pone.0154675>
101. Yang, J., Liang, L., Li, J., & Zhang, K. Q. (2013). Nematicidal enzymes from microorganisms and their applications. *Applied Microbiology and Biotechnology*, 97(16), 7081-7095. <https://doi.org/10.1007/s00253-013-5045-0>
102. Yang, T., Xin, Y., Liu, T., Li, Z., Liu, X., Wu, Y., & Xiang, M. (2022). Bacterial volatile-mediated suppression of root-knot nematode (*Meloidogyne incognita*). *Plant disease*, 106(5), 1358-1365. <https://doi.org/10.1094/PDIS-06-21-1139-RE>
103. Yao, Y., Wang, L., Zhai, H., Dong, H., Wang, J., Zhao, Z., & Xu, Y. (2025). *Bacillus velezensis* A-27 as a potential biocontrol agent against *Meloidogyne incognita* and effects on rhizosphere communities of celery in field. *Scientific Reports*, 15(1), 1057. <https://doi.org/10.1038/s41598-024-83687-8>
104. Ye, S., Yan, R., Li, X., Lin, Y., Yang, Z., Ma, Y., & Ding, Z. (2022). Biocontrol potential of *Pseudomonas rhodesiae* GC-7 against the root-knot nematode *Meloidogyne graminicola* through both antagonistic effects and induced plant resistance. *Frontiers in microbiology*, 13, 1025727. <https://doi.org/10.3389/fmicb.2022.1025727>
105. Youssar, L., Wernet, V., Hensel, N., Yu, X., Hildebrand, H. G., Schreckenberger, B., & Fischer, R. (2019). Intercellular communication is required for trap formation in the nematode-trapping fungus *Duddingtonia flagrans*. *PLoS Genetics*, 15(3), e1008029. <https://doi.org/10.1371/journal.pgen.1008029>
106. Yu, S., Mao, M., Zhang, H., Song, H., & Sun, Y. (2025). Growth-Promoting Effects and Mechanisms of Synthetic Plant Growth-Promoting Rhizobacteria on Maize Seedlings. *Microorganisms*, 13(11), 2460. <https://doi.org/10.3390/microorganisms13112460>
107. Yue, P., Hu, Q., Zhou, W., Rang, X., & Liu, Y. (2024). Tomato root exudates infected by *Meloidogyne incognita* impact the colonization of nematicidal *Proteus vulgaris*. *Microorganisms*, 12(11), 2188. <https://doi.org/10.3390/microorganisms12112188>
108. Zeng, Y., Wang, Y., Wang, X., Jing, X., Shu, X., Ren, P., & Wang, X. (2025). Arbuscular mycorrhizal fungi as core engineers in synthetic microbial communities: Boosting plant growth and soil health for sustainable agriculture. *Journal of Fungi*, 11(11), 769. <https://doi.org/10.3390/jof11110769>
109. Zhang, H., Guo, D., Lei, Y., Lozano-Torres, J. L., Deng, Y., Xu, J., & Hu, L. (2025). Cover crop rotation suppresses root-knot nematode infection by shaping soil microbiota. *New Phytologist*, 245(1), 363-377. <https://doi.org/10.1111/nph.20220>
110. Zhang, J., Liu, W., Bu, J., Lin, Y., & Bai, Y. (2023). Host genetics regulate the plant microbiome. *Current Opinion in Microbiology*, 72, 102268. <https://doi.org/10.1016/j.mib.2023.102268>
111. Zhao, W., Liang, J., Huang, H., Yang, J., Feng, J., Sun, L., & Wang, S. (2023). Tomato defence against *Meloidogyne incognita* by jasmonic acid-mediated fine-tuning of kaempferol homeostasis. *New Phytologist*, 238(4). <https://doi.org/10.1111/nph.18837>

112. Zheng, F., Fu, Y., Yu, P., Qin, C., Guo, T., Xu, H., & Chen, S. (2024). Flavonoid synthesis is crucial for *Trichoderma asperellum*-induced systemic resistance to root-knot nematodes in tomato plants. *Plant Physiology and Biochemistry*, 212, 108706. <https://doi.org/10.1016/j.plaphy.2024.108706>Get rights and content