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Microbial Biomolecules: Illuminating the Hidden Arsenal against Plant Parasitic Nematodes

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ABSTRACT: Plant parasitic nematodes (PPNs) pose significant threats to global agriculture, causing annual losses exceeding USD 150 billion. Chemical nematicides, once the primary method for PPN control, are now restricted due to environmental and health concerns. Consequently, there is a pressing need for eco-friendly alternatives. Biological agents, particularly botanical nematicides and microbial volatile organic compounds (VOCs), have emerged as promising solutions. VOCs, produced by bacteria and fungi, have garnered attention for their effectiveness against PPNs. These compounds, with diverse chemical compositions, exhibit various modes of action, including fumigant toxicity, repellent activity, and inhibition of egg hatching. Notably, *Bacillus* and *Pseudomonas* species have shown significant nematicidal activity through VOC emission. Additionally, fungal VOCs, particularly those from *Fusarium* and *Trichoderma* spp., have demonstrated efficacy against PPNs. Molecular docking studies have highlighted specific compounds, such as benzoic acid and dimethyl disulfide, as effective against nematode protein targets. Integrating *in vitro* assays with computational analyses offers insights into the mechanisms underlying VOC-mediated nematode control. However, further research is needed to validate VOC efficacy under field conditions and elucidate their molecular impact on nematodes. This review provides a comprehensive overview of the current research on bacterial and fungal VOCs and their potential applications in PPN management, highlighting the need for continued investigation to develop sustainable solutions for nematode control.

Keywords: Biocontrol agents, microbial volatile organic compounds, molecular docking, nematicidal activity, plant parasitic nematodes

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INTRODUCTION

Plant parasitic nematodes (PPNs) hold significant economic importance due to their capacity to inflict severe harm on crop yields (Lu *et al.*, 2017; Poveda *et al.*, 2020). Research indicates that there are more than 4100 species of PPNs, resulting in annual agricultural losses exceeding USD 150 billion (Kyndt *et al.*, 2014). For the past 50 years, chemical nematicides have been employed in managing PPNs. However, their overuse has resulted in detrimental effects on the environment and posed threats to human health (Abdel-Rahman *et al.*, 2013). Consequently, certain chemical nematicides are now restricted in developed nations due to concerns regarding toxicity, tolerance, and environmental persistence (Riga *et al.*, 2011). Notably, the use of chemicals is increasingly discouraged, primarily due to these aforementioned issues. For instance, bromomethane, a potent soil fumigant, has been banned due to its ozone-depleting properties (Whorton *et al.*, 1983). Similarly, dibromochloropropane, an organochlorine nematicide, has been prohibited due to its carcinogenic effects, such as the development of adenocarcinomas (Hasan *et al.*, 2020). Hence, there is a demand for environmental-friendly and efficient alternatives to chemical nematicides. It is, therefore, imperative to seek alternatives for chemical nematode control and to devise safe and efficient application methods.

Recently, the favoured options for managing root-knot nematodes (RKNs) involve biological agents. Among these, botanical nematicides - nematicidal compounds emitted from either plants or microorganisms, have garnered growing attention due to their notable effectiveness and environmental-friendly attributes. Nematodes dwelling in soil encounter a diverse array of microorganisms (Rajaofera *et al.*, 2019), among which nematophagous bacteria and fungi emerge as the most promising contenders for controlling RKNs. Various bacterial species spanning across genera like *Bacillus, Pseudomonas*, and *Pasteuria* have demonstrated antagonistic effects against RKNs. In contrast, fungi harmful to RKNs are frequently isolated from the phyla Ascomycota, Basidiomycota, Zygomycota, and Chytridiomycota (Hung *et al.*, 2015; Li *et al.*, 2015). In the realm of microbial metabolites, volatile organic compounds (VOCs) have recently garnered significant research interest owing to their efficacy in combating RKNs (Yin *et al.*, 2021). Furthermore, utilizing VOCs in agricultural settings could offer both economic feasibility and reduce toxicity to humans compared to conventional nematicides (Lin *et al.*, 2021). Organic compounds with boiling points ranging from 50 to 260°C are regarded as VOC. Many VOCs exhibit toxicity to humans and can pose environmental risks (Berenjian *et al.*, 2012). Microorganisms can synthesize a variety of volatile substances known as microbial VOCs (MVOCs) with low boiling points and small molecular masses (averaging around 300 Da) (Veselova *et al.*, 2019). MVOCs have been observed to influence plant and microbial growth, induce systemic resistance in plants, impact insects, nematodes, and other organisms, and serve as attractants or repellents (Veselova *et al.*, 2019). Bacterial volatiles are typically characterized by alkenes, alcohols, ketones, terpenes, benzenoids, pyrazines, acids, and esters; while alcohols, benzenoids, aldehydes, alkenes, acids, esters, and ketones dominate fungal volatiles. Most microbial volatiles are generated as a result of primary and secondary metabolism, mainly through the oxidation of glucose and its intermediates (Morath *et al.*, 2012; Schmidt *et al.*, 2015). The main function of MVOCs lies in the interaction between microorganisms, typically between bacteria and fungi in a reciprocal manner (Schmidt *et al.*, 2016). These interactions often involve MVOCs exerting antagonistic effects with antifungal activity (such as caryophyllene, hydrogen cyanide, 1-undecen, dimethyl disulfide, dimethyl trisulphide, S-methyl thioacetate, and benzonitrile) or antibacterial properties (including γ-butyrolactones, albaflavenone, dihydro-β-agarofuran, 1-undecene, methanthiol, and dimethyl disulfide). However, these compounds may also facilitate beneficial communication between physically separated microorganisms, playing a crucial role in microbial interactions (Schmidt *et al.*, 2015).

Microorganisms residing in soil or the rhizosphere can release diverse VOCs such as alcohols, ketones, aldehydes, lipids, terpenes, and organic acids through various biosynthetic pathways (Campos *et al.*, 2010). These VOCs can exert antagonist effects on competitive species or act as signalling molecules involved in inter-species communication, even across different kingdoms. For instance, studies have demonstrated that *Bacillus cereus* strain Bc-cm103 exhibited nematicidal activity against *Meloidogyne incognita* through VOC emission (Yin *et al.*, 2021), while *Pseudomonas putida* strain 1A00316 produced dimethyl disulfide (DMDS), 2-nonanone, 2-octane, (Z)-hexen-1-ol acetate, and 2-undecanone, which reduced the viability of *M. incognita* (Zhai *et al.*, 2018).

This review paper provides a comprehensive overview of the current status of and recent advancements in identifying fungal and bacterial VOCs and their potential applications in PPN management.

BACTERIAL VOLATILES FOR THE MANAGEMENT OF PPNs

Numerous reports have demonstrated the toxicity of microbial VOCs to RKNs. These VOCs can impact nematodes through various mechanisms, serving as contact nematicides, fumigants, repellents, attractants, or inhibitors of egg hatching. The subsequent text briefly outlines some of these reports.

Several studies have demonstrated the nematicidal properties of bioactive molecules from *Bacillus* spp. For instance, VOCs emitted by *Bacillus megaterium* YFM3.25 were found to hinder egg hatching and reduce infection by *M. incognita* in pot experiments. Among the 17 VOCs identified, compounds such as 2-nonanone, 2-undecanone, decanal, dimethyl disulfide, and benzeneacetaldehyde showed fumigant toxicity against *M. incognita* juveniles and eggs (Huang *et al.*, 2010). Similarly, *Bacillus atrophaeus* GBSC56 emitted methyl isovalerate, 2-undecanone, and dimethyl disulfide, which exhibited potent nematicidal activity against *M. incognita* (Ayaz *et al.*, 2021). Additionally, *B. cereus* Bc-cm103 displayed repellent activity against *M. incognita* J2, and VOCs from this strain, primarily dimethyl disulfide and S-methyl ester butanethioic acid, exhibited fumigant toxicity to *M. incognita* J2 and reduced root gall numbers in cucumber plants in pot tests (Yin *et al.*, 2021). *Bacillus aryabhattai* MCCC 1K02966 emitted dimethyl disulfide, methyl thioacetate, 1-butanol, and pentane, with methyl thioacetate showing strong contact and fumigant toxicity, as well as repellent activity against *M. incognita* (Chen *et al.*, 2021). Moreover, *Bacillus altitudinis* AMCC 1040 emitted eight VOCs, including acetic acid, octanoic acid, 2-methyl-butanoic acid, 3-methyl-butanoic acid, 2,3-butanedione, and 2-isopropoxy ethylamine, which exhibited nematicidal activity against *M. incognita* (Zhou *et al.*, 2022).

Arun *et al.* (2023) reported that Picoxystrobin and 3-Deoxy-d-mannonic acid from *B. cereus* could serve as promising novel nematostatic compounds against rice root-knot nematode, *M. graminicola*. Shandeep *et al.* (2024) revealed the LC_{50} concentration of 2,1,3 benzothiadiazole (52.17 ìg/mL), 2 hexen-1-ol (84.37 ìg/mL) and heptanoic acid (141.93 ìg/mL) against guava root-knot nematode, *Meloidogyne enterolobii*. Furthermore, molecular docking studies proved that the bacterial biomolecules benzoic acid, 4-cyanophenyl 4-butyl benzoate, trifluoroacetophenone, 6,12-dinaphthylindolo[3,2-b] carbazole, 3-phenyl-1,2,4-triazolin-5-one had a predominant effect over protein targets of *M. enterolobii*.

Paenibacillus polymyxa KM2501-1 exhibited significant efficacy against *M. incognita*, causing mortality rates of 87.6 and 82.6 per cent under both *in vitro* and *in planta* conditions, respectively. Eleven VOCs were identified from *P. polymyxa* KM2501-1, with furfural acetone and 2-decanol demonstrating the ability to attract *M. incognita* and subsequently eliminate the nematode through fumigant or contact nematicidal actions (Cheng *et al.*, 2017). VOCs produced by *Virgibacillus dokdonensis* MCCC 1A00493 exhibited diverse activities against *M. incognita*. Acetaldehyde functioned as an attractant, contact nematicide, and fumigant, while ethylbenzene acted as an attractant and 2-butanone as a repellent (Huang *et al.*, 2020). *Pseudomonas putida* strain 1A00316, isolated from Antarctic soil, released a range of VOCs including 2-nonanone, 2-octanone, 2-undecanone, dimethyl disulfide, (Z)-hexen-1-ol acetate, 1-undecene, and 1-(ethenyloxy)-octadecane. Among these compounds, 2-nonanone, 2-octanone, 2-undecanone, dimethyl disulfide, and (Z)-hexen-1-ol acetate exhibited contact nematicidal effects against *M. incognita*, while only 2-undecanone displayed fumigant activity. Additionally, all seven VOCs inhibited egg hatching and acted as repellents to *M. incognita* J2 in Petri plate experiments (Zhai *et al.*, 2018).

A total of 53 VOCs were identified from five bacterial species, including *Pseudochrobactrum saccharolyticum, Wautersiella falsenii, Proteus hauseri, Arthrobacter nicotianae,* and *Achromobacter xylosoxidans*. Notably, S-methyl thiobutyrate, dimethyl disulfide, acetophenone, 2-nonanone, butyl isovalerate, ethyl 3,3-dimethylacrylate, and 1-methoxy-4-methylbenzene demonstrated significant nematicidal activity against both *C. elegans* and *M. incognita* in Petri plate experiments, with S-methyl thiobutyrate being the most potent VOC (Xu *et al*., 2015). *Ochrobactrum pseudogrignonense* NC1 exhibited significant inhibition of *M. incognita* in both Petri plate and greenhouse trials, with dimethyl disulfide and benzaldehyde being the main VOCs responsible for the nematicidal activity against *M. incognita* emitted by NC1 (Xu *et al*., 2015).

In addition to *M. incognita*, microbial fumigant toxicity to other *Meloidogyne* species has been addressed in some reports. VOCs emitted by three bacterial strains (*Bacillus* sp., *Paenibacillus* sp., and *Xanthomonas* sp.) were found to be toxic to the rice RKN *Meloidogyne graminicola* in both *in vitro* and *in planta* studies (Bui *et al*., 2020). *In vitro* treatment with *P. putida, Microbacterium* sp., *Bacillus methylotrophicus*, and *Bacillus pumilus* led to significant mortality of *Meloidogyne exigua* through VOC release (Costa *et al*., 2015). Furthermore, *Variovorax paradoxus*, *Comamonas sediminis*, *Pseudomonas soli*, *Pseudomonas koreensis*, and two strains of *Pseudomonas monteilii* demonstrated nematicidal activity, exerting potent effects on *M. javanica* via VOC production (Wolfgang *et al*., 2019). Dimethyl disulfide stands out as the most frequently identified among microbial VOCs. Recognizing its broad-spectrum toxicity against pests, dimethyl disulfide was registered by Arkema as a pesticide named Paladin in 2012 (Wolfgang *et al*., 2019).

MODE OF ACTION OF BACTERIAL VOCs AGAINST NEMATODES

VOCs are believed to eliminate nematodes by affecting various aspects of their physiology, including the intestine, nervous system, surface coat, pharynx, or other tissues (Geng *et al*., 2016; Wanrock *et al*., 2017). According to a recent study, VOCs induce rapid nematode death by triggering severe oxidative stress (Ayaz *et al*., 2021). However, the specific molecular mechanisms underlying the nematicidal properties of VOCs remain poorly understood, with only a few exceptions. One extensively studied VOC, dimethyl disulfide, acts by inhibiting the enzyme cytochrome oxidase, thus disrupting the mitochondrial respiration of the pests (Gómez-Tenorio *et al*., 2015).

Additionally, bacterial VOCs have been shown to modulate key genes involved in different signalling pathways that stimulate plant growth and induce systemic resistance against phytopathogens. For instance, methyl isovalerate and 2-undecanone have been found to enhance antioxidant enzyme activity in plant roots infested with *M. incognita*, promoting both plant growth and induced systemic resistance (Ayaz *et al*., 2021). The impact of bacterial VOCs on plant morphology and physiology is further discussed in a recent review article (Sharifi *et al*., 2018).

FUNGAL VOCS AGAINST NEMATODES

Several fungal volatile compounds (VCs) have been assessed for their efficacy against PPNs, primarily targeting *Meloidogyne* spp. Non-pathogenic strains of *Fusarium oxysporum*, which do not cause plant disease, have been utilized as biocontrol agents due to their ability to suppress pathogens such as Fusarium wilt (*Fusarium oxysporum*) and *Verticillium* wilt (*Verticillium dahliae*) across a wide range of hosts, including various vegetables, fruits, and ornamental trees (Sajeena *et al*., 2020). *Fusarium* spp. has been the focus of extensive research regarding emitted VOCs. Among 35 fungi isolated from the rhizosphere of coffee plants, including those found in *Meloidogyne exigua* eggs and egg masses on coffee roots, isolates 20a and 21 of *Fusarium oxysporum*, as well as an isolate of *F. solani*, caused mortality rates of 88 to 96 per cent in *M. incognita* J2. Additionally, exposure to VOCs from *Fusarium oxysporum* isolate 21 led to the loss of infectivity in *M. incognita* J2. These VOCs were identified as dioctyl disulfide, caryophyllene, 4-methyl-2,6-di-tert-butylphenol, and acoradiene (Freire *et al*., 2012).

Another isolate of *Fusarium oxysporum*, designated as isolate 26 and obtained from *M. exigua* egg masses, induced 94 per cent immobility and 27 per cent mortality in *M. exigua* J2 under laboratory conditions. However, the specific volatile compounds responsible for these effects were not identified in the study conducted by Costa *et al*. (2015). In the investigations by Terra *et al.* (2018), *Fusarium oxysporum* strain 21 was utilized to assess the efficacy of its emitted volatile compounds against *M. incognita*. The findings revealed that the volatile compounds from *Fusarium oxysporum* strain 21 immobilized 100 per cent of *M. incognita* J2 and decreased the infectivity and reproduction of *M. incognita* J2 by 70 and 65 per cent, respectively. More than 28 volatile compounds were identified, among which 2-methylbutyl acetate, 3-methylbutyl acetate, ethyl acetate, and 2-methylpropyl acetate eradicated 80 to 100 per cent of *M. incognita* J2. Additionally, 3-methylbutyl acetate and ethyl acetate inhibited 90 per cent of *M. incognita* egg hatching (Terra *et al*., 2017). However, only 2-methylbutyl acetate reduced gall formation by 22 per cent compared to the control. Estupiñan-López *et al.* (2017) demonstrated that volatile compounds emitted by *Fusarium oxysporum* isolate F63 and *Fusarium solani* isolate F12, isolated from *Meloidogyne paranaensis* egg masses, caused 100 per cent and 40 to 70 per cent immobility in *M. incognita* J2 under laboratory conditions at 25°C in the absence of light for six days, respectively. When *M. incognita* J2 was exposed to water containing fungal volatile compounds before inoculation onto tomato plants, an over 50 per cent reduction in galls and eggs was observed.

Trichoderma spp. are renowned for their role as biocontrol agents against various soil-borne pathogens, including PPNs, although there is limited knowledge regarding the VOCs they produce (Reino *et al*., 2008; Sharon *et al*., 2011). VOCs emitted by an unidentified *Trichoderma* sp. strain, YMF 1.00416, isolated from soil in Yunnan, China, were assessed for their effects on *Bursaphelenchus xylophilus* in laboratory conditions, resulting in the mortality of 41.53 per cent of the nematodes (Yang *et al*., 2012). The main volatile compounds identified from *Trichoderma* sp. YMF 1.00416 were 1β-vinylcyclopentane-1α ,3α-diol, 6-pentyl-2H-pyran-2-one, and 4-(2-hydroxyethyl) phenol. Notably, 6-pentyl-2H-pyran-2-one exhibited toxicity against *B. xylophilus* within 48 hrs at a concentration of 200 mg/L.

CONCLUSION

Due to growing concerns regarding the adverse effects of synthetic nematicides, there has been a notable upsurge in interest in developing sustainable alternatives to control root-knot nematodes. Numerous studies have highlighted microorganisms as a promising reservoir for identifying potentially beneficial VOCs for RKN management. While a significant portion of the evidence originates from laboratory tests, a subset has been derived from greenhouse-based *in planta* experiments. Nonetheless, extensive research is warranted to validate the efficacy of VOCs against RKNs in field settings. Exploring the molecular-level impact of VOCs on nematodes remains relatively uncommon. Given the diverse chemical composition of VOCs, it is plausible that each type operates through distinct mechanisms. Addressing this inquiry is not only academically intriguing but also pivotal for advancing VOCs as potential agents for nematode management in the future.

CONFLICT OF INTEREST

The authors report no conflict of interest.

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