Bacterial Volatile Organic Compounds in Root-Knot Nematodes Control

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Plant-parasitic nematodes (PPNs) constitute the most damaging group of plant pathogens. Plant infections by root-knot nematodes (RKNs) alone could cause approximately 5% of global crop loss. Nematodes in soil are exposed to a diversity of microorganisms, of which nematophagous bacteria and fungi represent the most promising candidates to control RKNs. Bacterial species of a range of genera, such as *Bacillus*, *Pseudomonas*, and *Pasteuria*, were observed to exhibit antagonistic activity against RKNs, while the fungi that were detrimental to RKNs were commonly isolated from the phylum *Ascomycota*, *Basidiomycota*, *Zygomycota*, and *Chytridiomycota*. With regard to microbial metabolites, volatile organic compounds (VOCs) have attracted research attention in recent years due to their efficacy in killing RKNs. Additionally, the application of VOCs in agricultural practice could be both economically affordable and less toxic to humans than conventional nematicides.

Keywords: melanoma cells ; melanogenesis ; signaling pathways ; plant extracts

1. Root-Knot Nematodes (RKNs)

Life Cycle

Many economically important crops are hosts of RKNs, including tomato, potato, corn, soybean, maize, oats, wheat, and cotton [1][2][3]. The economic loss caused by RKNs has been estimated at USD 78 billion annually worldwide, accounting for half of the total loss due to PPNs [4]. Although the genus *Meloidogyne* consists of about 100 species [5], *M. incognita*, *M. arenaria*, *M. javanica*, and *M. hapla* are the four major species that infect more than 2000 plant species, particularly underground plant organs [1][6][7][8].

The life span of RKNs is about three to six weeks with a cycle comprising embryo, juvenile (J1, J2, J3, and J4), and adult stages [1]. RKNs reproduce via diverse mechanisms but mostly by parthenogenesis. The eggs of RKNs are laid in gelatinous masses in the soil or plant residues. The worms hatch as second-stage juveniles (J2), and they immediately move toward the roots of plant hosts, attack the elongation zone, and migrate to the root tip [9][10]. When they reach the apical meristem region, they transmigrate to the developing vascular cylinder, triggering the formation of giant cells, which serve as nutrient sinks to support the growth of the nematode. The juveniles then become sedentary and undergo three more molts before they turn into adults [11][12]. In the adult stage, the worm-shaped males move out of the plant root, but the sedentary females continuously develop into pear-shaped females. Afterward, the female adults begin laying eggs (more than 1000 eggs per female) on the external surface of the root [1][13][14].

Genome

The whole genome of mitotic obligate parthenogenetic *M. incognita* was determined to be approximately 86 Mb, which contains 19,212 protein-coding genes, while that of meiotic facultative parthenogenetic *M. hapla* was about 54 Mb, containing 14,700 protein-coding genes [15][16]. Lately, the gene numbers of *M. arenaria*, *M. javanica*, and *M. incognita* were predicted to be 30,308, 26,917, and 24,714, respectively [17]. These genomes share some common features but with their own characteristics. One of the features shared by *M. incognita* and *M. hapla* is the possession of genes encoding distinct plant-cell-wall-degrading enzymes. A phylogenetic analysis suggested that these genes, which are absent in animals, were probably obtained via horizontal gene transfer from fungi or bacteria [18]. Since these enzymes are also present in some other PPNs of the order *Tylenchida*, the acquisition of these genes might occur earlier in an ancestor of *Tylenchida* during evolution, which supported the progress of their capability to parasitize plants [12][19][20].

The most notable differences between *M. incognita* and *M. hapla* are their genome structure and reproduction mode. *M. hapla* has an ordinary genome structure of diploid sexual species, while *M. incognita* is a hypotriploid with a proportion of

one genome present in a second copy. Furthermore, *M. hapla* reproduces with meiosis, whereas *M. incognita* reproduces without meiosis and fusion of gametes.

2. Control Strategies for RKNs

2.1. Physical Control Strategies

Nematodes are highly vulnerable before they penetrate the host plant's roots. Therefore, targeting PPNs at their vulnerable stages could be effective. For instance, increasing soil temperatures above 40 °C by solarization is an effective way to reduce the number of nematodes in soil [3]. Moisture is another critical factor for the survival of nematodes. It has been highlighted that an insufficient amount of water in the soil would affect nematodes' ability to move toward their host roots [21][22]. Flooding represents an opposite strategy to control nematodes in soils. Many PPNs are intolerant to oxygen starvation; therefore, flooding can kill nematodes by limiting their supply of oxygen. Similar effects were observed when nematodes were stored in deep water in a laboratory. To be effective in the field, the duration of anaerobiosis must be long enough to kill the nematodes. However, flooding may not be practicable for every agricultural practice. Taking into consideration the threat of global climate change, flooding would not be a good option to control PPNs. In brief, physical control strategies are less effective than conventional chemical control strategies, although the cost of physical control strategies is relatively lower [23].

2.2. Chemical Control Strategies

Using synthetic chemicals with the features of fumigants or nematicides to control PPNs was a common method applied in agriculture in the previous half-century [24][25]. For example, methyl bromide and dibromochloropropane were intensively used as soil fumigants due to their effectiveness. However, they are highly toxic chemicals causing acute respiratory toxicity and neurotoxicity via inhalation [26][27][28][29]. Exposure to the dibromochloropropane that had accumulated in the soil was found to influence men's fertility and was linked to certain human cancers [30][31][32]. Therefore, its use in agriculture was banned in 1979. In addition, methyl bromide is a strong ozone-depleting substance. The use of methyl bromide in fumigation was banned globally after 2015 under the directive of the Montreal Protocol, except for quarantine and pre-shipment treatments [33][34]. Recently, a couple of less environmentally toxic chemicals have been suggested as alternatives to methyl bromide [23][35][36][37]. However, they have not yet been registered for use in agriculture [38][39]. Nevertheless, farmers need more reliable, eco-friendly, and low-cost approaches for sustainable agriculture.

2.3. Biological Control Strategies

Biological control refers to the suppression of a pest population, or the pest's harmful impact, by using living organisms (natural enemies) or their metabolites [40][41]. Because biological control imitates the competition among species in nature, it is generally thought to be more environmentally friendly than chemical control. The strategies of biological control can be classified into conservation, importation, and augmentation according to the source of the deployed organisms [42]. The conservation strategy is carried out to maintain the existing natural enemies in an environment; the importation strategy is carried out to introduce exotic enemies of the pests where they do not occur naturally; and the augmentation strategy is carried out to release reared natural enemies periodically into the habitat where the pests occur [43][44].

An organism (or its metabolites) that reduces the density of the pest population is defined as a biological control agent (BCA). An ideal BCA should exert its effects by multiple mechanisms without producing harmful substances to humans and the environment [45]. Bacteria from a wide range of genera have demonstrated the capability to control RKNs [46][47]. The common genera include *Achromobacter*, *Arthrobacter*, *Bacillus*, *Burkholderia*, *Pasteuria*, *Pseudomonas*, *Rhizobium*, and *Serratia*. The beneficial effects come from mechanisms such as parasitism, niche competition, the induction of plant systemic resistance, and the production of antagonistic substances (antibiotics, toxins, enzymes, VOCs, etc.) [46][48][49].

3. Volatile Organic Compounds (VOCs)

VOCs are carbon-based, low-molecular-weight compounds that have high vapor pressure and easily evaporate at room temperature [50][51][52]. VOCs emitted by microorganisms are capable of controlling plant-parasitic fungi, insects, bacteria, and nematodes [53]. Therefore, microbial VOCs are suitable to apply to different agricultural systems with relatively low concentrations compared to agrochemicals, and supplemental spray or drench is not essential for the application of VOCs [45][54][55][56]. Microbial VOCs are diverse in terms of their chemical structures. They can be alcohols, ketones, hydrocarbons, terpenes, fatty acids, or heteroatom-containing compounds [57]. A vast number of microbial VOCs are archived in the mVOC 2.0 database, in which more than 2000 VOCs from approximately 1000 different microorganisms are categorized based on chemical structures, mass spectra, and microbial emitters [58][59].

3.1. Biocontrol of RKNs with Bacterial VOCs

The toxicity of microbial VOCs to RKNs has been shown in numerous reports. A VOC could affect nematodes by acting as a contact nematicide, fumigant, repellent, or attractant. It could also suppress the hatching of eggs. Some of these reports are briefly described in the following text. The frequently discovered VOCs and their reported functions are summarized in **Table 1**.

Table 1. In vitro activity of bacterial VOCs on *Meloidogyne incognita*.

VOC	Emitter	Effects on J2s				
		Contact Toxicity	Fumigant Activity			Egg Hatching Suppression
			Fatal	Attractant	Repellent	
Acetaldehyde	*Virgibacillus dokdonensis* MCCC 1A00493 [60]	[60]	[60]	[60]		[60]
Acetic acid	*Bacillus altitudinis* AMCC 1040 [61]	[61]				
Acetone	*Paenibacillus polymyxa* KM2501-1 [62]			[62]		
Acetophenone	*Pseudochrobactrum saccharolyticum* [63] *Arthrobacter nicotianae* [63] *Achromobacter xylosoxidans* [63]		[63]			
4-acetylbenzoic	*Paenibacillus polymyxa* KM2501-1 [62]	[62]				
Benzaldehyde	*Ochrobactrum pseudogrignonense* NC1 [64]	[64]				
Benzeneacetaldehyde	*Bacillus megaterium* YMF3.25 [65]		[65]			[65]
2,3-Butanedione	*Bacillus altitudinis* AMCC 1040 [61]	[61]				
2-butanone	*Virgibacillus dokdonensis* MCCC 1A00493 [60]				[60]	
Butyl isovalerate	*Wautersiella falsenii* [63]		[63]			
Decanal	*Bacillus megaterium* YMF3.25 [65]		[65]			[65]
2-decanol	*Paenibacillus polymyxa* KM2501-1 [62]	[62]	[62]	[62]		
2-decanone	*Paenibacillus polymyxa* KM2501-1 [62]	[62]	[62]			
Dimethyl disulfide	*Pseudochrobactrum saccharolyticum* [63] *Wautersiella falsenii* [63] *Proteus hauseri* [63] *Arthrobacter nicotianae* [63] *Achromobacter xylosoxidans* [63] *Bacillus megaterium* YMF3.25 [65] *Bacillus atrophaeus* GBSC56 [66] *Ochrobactrum pseudogrignonense* NC1 [64] *Virgibacillus dokdonensis* MCCC 1A00493 [60] *Pseudomonas putida* 1A00316 [67] *Bacillus cereus* Bc-cm103 [68] *Bacillus aryabhattai* MCCC 1K02966 [39]	[60][64][66][67]	[63][65]	[60]	[67]	[65][67]

VOC	Emitter	Effects on J2s				
		Contact Toxicity	Fumigant Activity			Egg Hatching Suppression
			Fatal	Attractant	Repellent	
1-(ethenyloxy)-octadecane	*Pseudomonas putida* 1A00316 [67]				[67]	[67]
Ethylbenzene	*Virgibacillus dokdonensis* MCCC 1A00493 [60]			[60]		
Ethyl 3,3-dimethylacrylate	*Pseudochrobactrum saccharolyticum* [63]		[63]			
Furfural acetone	*Paenibacillus polymyxa* KM2501-1 [62]	[62]	[62]	[62]		
(Z)-hexen-1-ol acetate	*Pseudomonas putida* 1A00316 [67]	[67]			[67]	[67]
2-Isopropoxy ethylamine	*Bacillus altitudinis* AMCC 1040 [61]	[61]				
1-methoxy-4-methylbenzene	*Wautersiella falsenii* [63] *Proteus hauseri* [63] *Achromobacter xylosoxidans* [63]		[63]			
2-Methyl-butanoic acid	*Bacillus altitudinis* AMCC 1040 [61]	[61]				
3-Methyl-butanoic acid	*Bacillus altitudinis* AMCC 1040 [61]	[61]				
Methyl isovalerate	*Bacillus atrophaeus* GBSC56 [66]	[66]				
Methyl thioacetate	*Bacillus aryabhattai* MCCC 1K02966 [39]	[39]	[39]		[39]	[39]
S-methyl thiobutyrate	*Pseudochrobactrum saccharolyticum* [63] *Wautersiella falsenii* [63] *Proteus hauseri* [63] *Arthrobacter nicotianae* [63] *Achromobacter xylosoxidans* [63]		[63]			
2-nonanol	*Paenibacillus polymyxa* KM2501-1 [62]	[62]	[62]			
2-nonanone	*Pseudochrobactrum saccharolyticum* [63] *Wautersiella falsenii* [63] *Proteus hauseri* [63] *Achromobacter xylosoxidans* [63] *Bacillus megaterium* YMF3.25 [65] *Paenibacillus polymyxa* KM2501-1 [62] *Pseudomonas putida* 1A00316 [67]	[62][67]	[63][65]		[67]	[65][67]
Octanoic acid	*Bacillus altitudinis* AMCC 1040 [61]	[61]				
2-octanone	*Pseudomonas putida* 1A00316 [67]	[67]			[67]	[67]
2-undecanol	*Paenibacillus polymyxa* KM2501-1 [62]	[62]	[62]			

VOC	Emitter	Effects on J2s				
		Contact Toxicity	Fumigant Activity			Egg Hatching Suppression
			Fatal	Attractant	Repellent	
2-undecanone	*Bacillus megaterium* YMF3.25 [65] *Bacillus atrophaeus* GBSC56 [66] *Pseudomonas putida* 1A00316 [67] *Paenibacillus polymyxa* KM2501-1 [62]	[62][66][67]	[62][65][67]		[62][67]	[65][67]
1-undecene	*Pseudomonas putida* 1A00316 [67]				[67]	[67]

In total, 53 VOCs were identified from five bacteria, namely, *Pseudochrobactrum saccharolyticum*, *Wautersiella falsenii*, *Proteus hauseri*, *Arthrobacter nicotianae*, and *Achromobacter xylosoxidans*. Among the VOCs, S-methyl thiobutyrate, dimethyl disulfide, acetophenone, 2-nonanone, butyl isovalerate, ethyl 3,3-dimethylacrylate, and 1-methoxy-4-methylbenzene, exhibited significant nematicidal activity against both *C. elegans* and *M. incognita* in Petri plate experiments. Moreover, S-methyl thiobutyrate was the most active VOC [63]. *Ochrobactrum pseudogrignonense* NC1 significantly inhibited *M. incognita* in Petri plate and greenhouse trials. The main VOCs emitted by NC1, namely, dimethyl disulfide and benzaldehyde, also had nematicidal activity against *M. incognita* [64].

3.2. Mechanism of Action of Bacterial VOCs

It is thought that VOCs may destroy nematodes by targeting the intestine, nervous system, surface coat, pharynx, or other tissues [62][69][70]. A recent study has claimed that VOCs cause rapid death by inducing severe oxidative stress in nematodes [66]. However, the detailed molecular mechanisms underlying the nematicidal activity of VOCs are poorly understood, with a few exceptions. A well-studied VOC, dimethyl disulfide, exerts its toxicity by blocking the activity of the enzyme cytochrome oxidase, consequently stopping the mitochondrial respiration of the pests [71].

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