Review

Nematicidal Effects of Volatile Organic Compounds from Microorganisms and Plants on Plant-Parasitic Nematodes

Xiaotong Deng, Xin Wang * and Guohong Li *

State Key Laboratory for Conservation and Utilization of Bio-Resources in Yunnan, Key Laboratory for Southwest Microbial Diversity of the Ministry of Education, Yunnan University, Kunming 650032, China; dxiaotongyn@163.com
* Correspondence: xinwang2@ynu.edu.cn (X.W.); ligh@ynu.edu.cn (G.L.)

Abstract: Plant-parasitic nematodes (PPNs) are one of the most destructive plant pathogens worldwide, and controlling them is extremely challenging. Volatile organic compounds (VOCs), which naturally exist in plants and microorganisms, play an important role in the biological control of PPNs and are considered potential substances for the development of commercial nematicides. This paper summarizes the VOCs produced by microorganisms and plants as well as their toxic effects on PPNs. VOCs from 26 microbial strains and 51 plants that are active against nematodes from over the last decade were reviewed. Furthermore, the mechanisms of toxicity of some VOCs against PPNs are also illustrated.

Keywords: volatile organic compounds; plant-parasitic nematodes; nematicidal; microorganism; plant; toxicity

1. Introduction

Nematodes are tiny worms that are some of the most complex and numerous organisms in the world [1]. Nematode species that cause damage to cultivated plant species are called plant-parasitic nematodes (PPNs), and it is difficult to control them [2]. They parasitize a large number of crops all over the world, causing huge economic losses every year. The root-knot nematodes (RKNs), Meloidogyne spp., which can attack almost all cultivated plant species, are some of the most economically damaging PPNs on horticultural and field crops [3]. One of the most abundant RKNs in the world is Meloidogyne incognita, which is capable of infecting a large number of plants species [4]. Meloidogyne javanica is also a highly destructive nematode of Meloidogyne spp. It has been reported to be the major pathogen for many crop plants, including tomatoes, potatoes, peanuts, papayas, and rootstocks [5–7]. In addition, the pine wood nematode (PWN), Bursaphelenchus xylophilus, is the pathogen behind pine wilt disease, which causes serious damage to pine species in many countries [8,9]. In China, B. xylophilus is widely spread and causes billions of dollars of economic losses annually [10].

Chemical nematicides are an important part of control strategies. However, they also have significant disadvantages, such as detrimental effects on human health and the environment. With growing public concern about the toxicity of chemical pesticides and ecological protection, the application of many synthetic pesticides has been limited. In recent years, researchers have begun to find and study natural products that can replace typically more effective chemical pesticides [11,12]. Volatile organic compounds (VOCs), which exist in plants and microorganisms, are considered to be potential substances for the development of commercial nematicides [13]. VOCs cover a wide range of alcohols, aldehydes, ketones, esters, ethers, phenols, alkenes, alkynes, and alkyl compounds [14]. Over the past decade, there has been growing awareness of the importance of VOCs.
In this review, we will summarize the nematicidal activity of VOCs produced by microorganisms and plants against PPNs, including *Meloidogyne* spp. and *B. xylophilus*, as well as investigate the nematicidal mechanisms found in some VOCs.

2. Nematicidal Effects of Volatile Organic Compounds

2.1. Nematicidal Effects of Microbial Volatile Organic Compounds

Many VOCs from different microbial strains have been analyzed to determine their nematicidal activity against *Meloidogyne* spp. and *B. xylophilus* (Table 1).

Table 1. Nematicidal activity of VOCs produced by microorganisms against *Meloidogyne* spp. and *B. xylophilus*.

| Nematodes | Microorganisms | VOCs | References |
|-----------|----------------|------|------------|
| *M. incognita* | Pseudomonas putida 1A00316 | dimethyl disulfide, 2-nonanone, 2-octanone, (Z)-hexen-1-ol acetate, 2-undecanone | [15] |
| | Pseudomonas koreensis T3GI1 | 3-methoxy-2,5-dimethyl pyrazine, 1-undecene, dimethyl disulfide | [16] |
| | Pseudomonas monteilii T8GH4 | 1-undecene, dimethyl disulfide, 2-undecanone | [16] |
| | Comamonas sediminis T13GI2 | 1-undecene, dimethyl disulfide | [16] |
| | Variovorax paradoxus T1GI1 | dimethyl disulfide | [16] |
| | Bacillus atrophaeus CBS656 | dimethyl disulfide, methyl isovalerate, 2-undecanone | [17] |
| | Bacillus cereus Bc-cm103 | dimethyl disulfide, 5-methyl ester butanethioic acid | [18] |
| | Bacillus megaterium YFM3.25 | benzeneacetalddehyde, 2-nonanone, decanal, 2-undecanone, dimethyl disulfide | [19] |
| | Bacillus mycoides R2 | styrene | [20] |
| | Comamonas sediminis T13GI2 | 1-undecene, dimethyl disulfide | [16] |
| | Pseudomonas soli T13GI4 | 1-undecene, dimethyl disulfide | [16] |
| | Variovorax paradoxus T1GI1 | dimethyl disulfide | [16] |
| | Bacillus megaterium YFM3.25 | benzeneacetalddehyde, 2-nonanone, decanal, 2-undecanone, dimethyl disulfide | [19] |
| | Bacillus mycoides R2 | styrene | [20] |
| | Lysinibacillus mangiferahumi M-GX18T | 2-octanol, cyclohexene, 3-chloro-4-fluorobenzaldehyde, dibutyl phthalate, 2-nitro-2-chloropropane, dimethyltrisulfide | [21] |
| | Pantoea polymyxa KM2501-1 | furfural acetone, 2-decanol, 2-undecanone, 2-decanone, 2-nonanol | [22] |
| | Pseudochlorobium saccharolyticum AM180484 | dimethyl disulfide, 5-methylthiobutyrate, acetophenone, ethyl 3,3-dimethylacrylate, nonan-2-one, 1-methoxy-4-methylbenzene | [14] |
| | Proteus hauseri JN092591 | dimethyl disulfide, 5-methylthiobutyrate, nonan-2-one, 1-methoxy-4-methylbenzene, butyl isovalerate | [14] |
| | Wautersiella falsenii AM238607 | dimethyl disulfide, 5-methylthiobutyrate, nonan-2-one, 1-methoxy-4-methylbenzene, butyl isovalerate | [14] |
| | Arthrobacter visnioticus IQ971518 | dimethyl disulfide, 5-methylthiobutyrate, acetophenone, nonan-2-one, 1-methoxy-4-methylbenzene | [14] |
| | Achromobacter xylosoxidans AF411019 | dimethyl disulfide, 5-methylthiobutyrate, acetophenone, nonan-2-one, 1-methoxy-4-methylbenzene | [14] |
| | Virgibacillus dokdonensis MCCC 1A00493 | acetaldehyde, dimethyl disulfide, 4-vinylphenol | [23,24] |
| | Duddingtonia flagrans | cyclohexanamine, cyclohexanone, cyclohexanol | [25] |
| | Fusarium oxysporum 21 | 2-methylbutyl acetate, 3-methylbutyl acetate, ethyl acetate, 2-methylpropyl acetate, caryophyllene | [26,27] |
| | Meloidogyne javanica | 3-methoxy-2,5-dimethyl pyrazine, 1-undecene, dimethyl disulfide | [16] |
| | Pseudomonas koreensis T3GI1 | dimethyl disulfide | [16] |
| | Variovorax paradoxus T1GI1 | 1-undecene, dimethyl disulfide | [16] |
| | Comamonas sediminis T13GI2 | 1-undecene, dimethyl disulfide, 2-undecanone | [16] |
| | Pseudomonas monteilii T8GH4 | 1-undecene, dimethyl disulfide | [16] |
| | Pseudomonas soli T13GI4 | 1-undecene, dimethyl disulfide | [16] |
| | Daldinia cf. concentrica | 3-methyl-1-butanol, (±)-2-methyl-1-butanol, 4-heptanone, isoamyl acetate | [28] |
| | Meloidogyne hapla | 1-octen-3-ol, 3-octanone | [29] |
| | Metarhizium brunneum | dimethyl disulfide, dimethyl trisulfide | [30] |
| | Pseudalteromonas marina H-42 | dimethyl disulfide, dimethyl trisulfide, benzaldehyde, tert-butylamine, 1,8-cineole | [31] |
| | Vibrio atlanticus S-16 | 1,8-cineole | [31] |
| | Annulohypoxylon sp. FPYF3050 | dimethyl disulfide, dimethyl trisulfide, benzaldehyde, tert-butylamine, 1,8-cineole | [31] |
| | Trichoderma sp. YMF 1.00416 | 6-pentyl-2H-pyran-2-one | [32] |

2.1.1. Nematicidal VOCs from Bacteria

Nematicidal VOCs from *Pseudomonas*

VOCs produced by *Pseudomonas putida* 1A00316, isolated from Antarctic soil, have been found to exhibit nematicidal potential against *M. incognita* [15]. From this strain, five compounds (2-octanone, (Z)-hexen-1-ol acetate, 2-undecanone, dimethyl disulfide, and 2-nonanone) have shown direct-contact nematicidal activity, with LC50/48h values of 22.712 mg/L, 32.351 mg/L, 22.872 mg/L, 134.330 mg/L, and 63.320 mg/L, respectively. However, only 2-undecanone was found to have fumigant activity against *M. incognita*. Wolfgang et al. reported the nematicidal activity of *Pseudomonas koreensis* T3GI1, *Pseudomonas monteilii* T8GH4, and *Pseudomonas soli* T13GI4 against *M. incognita* and *M. javan-
The metabolite 1-undecene was found to be one of the main VOCs of *P. monteilii* and *P. soli*, and dimethyl disulfide was found to be the major constituent of all three strains. Furthermore, *P. koreensis* can also produce 3-methoxy-2,5-dimethyl pyrazine, and *P. monteilii* can produce 2-undecanone. Among them, *P. koreensis* was found to have the most significant effect. Although its product, pyrazine, was not as effective as 2-undecanone, it may have an enhancement effect on the nematicidal activity of the total volatiles in *P. koreensis*.

### Nematicidal VOCs from Bacillus

In this study, nematicidal VOCs from *Bacillus* dominated. *Bacillus atrophaeus* GBSC56, derived from plant-growth-promoting rhizobacteria, from the Tibet region of China, was isolated [17]. Among the VOCs produced by GBSC56, dimethyl disulfide, methyl isovalerate, and 2-undecanone exhibited strong nematicidal activity. These three VOCs can induce severe oxidative stress in nematodes, which subsequently caused rapid death. *Bacillus cereus* Bc-cm103 was found to be significantly toxic to *M. incognita* [18]. It can produce nematicidal VOCs, including dimethyl disulfide and S-methyl ester butanethioic acid. *Bacillus megaterium* YMF3.25, as a plant-growth-promoting rhizobacteria, can efficiently and biologically control *M. incognita* via the production of toxic VOCs [19]. Among the VOCs, five compounds, including benzeneacetaldehyde, 2-nonanone, decanal, 2-undecanone, and dimethyl disulfide, showed nematicidal activity against *M. incognita*, and the activity of 2-nonanone and 2-undecanone was even higher. Another plant-growth-promoting bacterium, *Bacillus mycoides* R2, was isolated from tomato rhizosphere soil, which can produce volatile styrene to kill *M. incognita*, and the nematicidal activity of styrene was found to be superior to the nematicides, such as thiacloprid and cadusafos [20].

### Nematicidal VOCs from Other Bacteria

*Lysinibacillus mangiferahumi* M-GX18T, isolated from mango rhizosphere soil, can produce nematicidal VOCs against *M. incognita* [21]. Its active metabolites are 2-octanol, cyclohexene, 3-chloro-4-fluorobenzaldehyde, dibutyl phthalate, 2-nitro-2-chloropropane, dimethachlore, and dimethyl disulfide. VOCs produced by *Paenibacillus polymyxa* KM2501-1 have exhibited contact nematicidal and fumигant activity against *M. incognita* [22]. Among VOCs with contact nematicidal activity, furfuralacetone, 2-nonanone, 4-acetylbenzoic, and 2-decanol acid were the most active, followed by 2-nonanol, 2-undecanone, 2-decanone, and 2-nonanone. Except for 4-acetobenzoic and 2-decanol acid, the other six VOCs had fumigant activity. In addition, furfural acetone has been found to have the highest activity against *M. incognita*, with LC$_{50}$/48h value of 4.44 mg/L. Xu et al. identified five strains that produce VOCs with nematicidal activity against *M. incognita*, namely, *Pseudochrobacter saccharolyticum*, *Wautersiella falsenii*, *Proteus hauseri*, *Arthrobacter nicotianae*, and *Achromobacter xylosoxidans* [14]. All five strains can produce dimethyl disulfide and S-methyl thiobutyrate. Moreover, *P. saccharolyticum* can produce acectophenone, ethyl 3,3-dimethylacrylate, and nonan-2-one; *W. falsenii* can produce nonan-2-one, 1-methoxy-4-methylbenzene, and butyl isovalerate; *P. hauseri* can produce nonan-2-one and 1-methoxy-4-methylbenzene; *A. nicotianae* can produce acectophenone; and *A. xylosoxidans* can produce acectophenone, nonan-2-one, and 1-methoxy-4-methylbenzene. Among these, S-methyl thiobutyrate and nonan-2-one had higher nematicidal activity than the commercially available nematicide dimethyl disulfide. *Virgibacillus dokdonensis* MCCC 1A00493, a deep-sea bacterium, has exhibited significant nematicidal activity against *M. incognita* [23]. Among the VOCs produced by *V. dokdonensis*, acetaldehyde has direct-contact killing, fumigation, and attraction activities, and dimethyl disulfide had direct-contact killing and attraction activities. This indicates that the strain can attract nematodes in order to kill them. Acetaldehyde has been found to be a product of ethanol metabolism in vivo; it has certain toxic effects, and it has been widely reported to be useful as an insect attractant and insecticide [33]. Similar to acetaldehyde, dimethyl disulfide is also an effective component of many insecticides and attractants [34,35]. This compound not only has nematicidal activity against *M. incognita* but also against *B. xylophilus*. Therefore, dimethyl disulfide...
has been widely studied because of its good field application effect on RKNs and some fungal diseases as well as because of its minor effect on soil microbial communities in the environment. In addition, in another study by Huang et al., the volatile nematicidal compound 4-vinylphenol was identified from V. dokdonensis [24].

The nematicidal activity of Comamonas sediminis T13GI2 and Variovorax paradoxus against M. incognita and M. javanica was reported [16]. The metabolite 1-undecene was found to be one of the main VOCs of C. sediminis, and dimethyl disulfide was found to be the major constituent in the two strains. Yu et al. isolated two marine strains, Pseudaoalteromonas marina strain H-42 and Vibrio atlanticus strain S-16 [30]; their VOCs have strong nematicidal activity against B. xylophilus. The main active constituents of P. marina H-42 are dimethyl disulphide and dimethyl trisulphide, while for V. atlanticus S-16 they are dimethyl disulphid, dimethyl trisulphide, benzaldehyde, and tert-butylamine.

2.1.2. Nematicidal VOCs from Fungi

VOCs produced by fungi also have important nematicidal effects. Duddingtonia flagrans is a nematode-trapping fungus that produces three-dimensional adhesive networks to trap nematodes, then uses VOCs to kill them [25]. Three VOCs containing cyclohexanol, cyclohexanone, and cyclohexanamine have shown strong nematicidal activity against M. incognita. Among these, cyclohexylamine had the highest nematicidal activity, followed by cyclohexanone and cyclohexanol. VOCs produced by Fusarium oxysporum strain 21 can kill M. incognita [27]. The compounds 2-methylbutyl acetate, 3-methylbutyl acetate, ethyl acetate, and 2-methylpropyl acetate have been identified as having nematicidal activity. Another study showed that the VOC caryophyllene, from F. oxysporum 21, may be toxic to M. incognita [26].

Daldinia cf. concentrica is an endophytic fungus that can secrete VOCs with nematicidal activity against M. javanica [28]. Interestingly, although the VOCs 3-methyl-1-butanol, (±)-2-methyl-1-butanol, 4-heptanone, and isoamyl acetate each significantly reduces the viability of M. javanica, a synthetic volatile mixture composed of these four compounds can completely kill it in a volumetric ratio of 1:1:2:1. The VOCs produced by Metarhizium brunneum have nematicidal activity against Meloidogyne hapla [29]. The VOCs 1-octen-3-ol and 3-octanone can completely kill M. hapla, at the highest doses tested (20 µL). In addition, over the course of this study, we found that 3-octanone appeared to be more toxic than 1-octen-3-ol.

Annulohypoxylon sp. FPYF3050 is an endophytic fungus isolated from Neolitsea pulchella [31]. The volatile compound produced by this strain, 1,8-Cineole, has strong nematicidal activity, which causes more than 82.9% mortality in B. xylophilus. In addition, this compound may synergize with other metabolites of Annulohypoxylon sp. FPYF3050 to achieve a stronger nematicidal effect than single compounds. Trichoderma is an important biocontrol fungus that produced metabolites that are harmful to nematodes [32]. The volatile compound produced by Trichoderma sp. YMF 1.00416, 6-Pentyl-2H-pyran-2-one, has also been demonstrated to have nematicidal activity against B. xylophilus. The activity of certain Trichoderma metabolites allowing them to be used as biological control agents was attributed, at least in part, to the presence of these active compounds [36].

2.2. Nematicidal Effects of Volatile Organic Compounds from Plants

Nematicidal VOCs from different plants have been summarized in Table 2.

| Nematode       | Plant Sources | Family | VOCs                        | References |
|----------------|---------------|--------|-----------------------------|------------|
| M. incognita   | Agastache rugosa | Lamiaceae | methyleugenol, estragole, eugenol | [37]       |
| M. incognita   | Rosmarinus officinalis | Lamiaceae | 1,8-cineole, camphor, α-pinene | [38]       |
| M. incognita   | Thymus satureioides | Lamiaceae | borneol, thymol            | [38]       |
| M. incognita   | Mentha spicata  | Lamiaceae | carvone                    | [39]       |

Table 2. VOCs produced by plants against Meloidogyne spp. and B. xylophilus.
| Nematode     | Plant Sources  | Family       | VOCs                                                                 | References |
|-------------|----------------|--------------|----------------------------------------------------------------------|------------|
| *M. incognita* | *Mentha pulegium* | Lamiaceae    | menthofuran, pulegone, trans-anethole, carvacrol                      | [39,40]    |
| *M. incognita* | *Origanum vulgare* | Lamiaceae    | carvacrol, thymol, terpinen-4-ol                                       | [1,40]     |
| *M. incognita* | *Origanum dictamnus* | Lamiaceae    | carvacrol, thymol, terpinen-4-ol                                       | [40]       |
| *M. incognita* | *Melissa officinalis* | Lamiaceae    | 1-carvone, trans-anethole, geraniol, eugenol, carvacrol, thymol, terpinen-4-ol | [40]       |
| *M. incognita* | *Mentha piperita* | Lamiaceae    | -                                                                     | [41]       |
| *B. xylophilus* | *Thymus citriodorus* | Lamiaceae    | carvacrol, γ-terpinene, p-cymene                                       | [42]       |
| *B. xylophilus* | *Thymbra capitata* | Lamiaceae    | carvacrol, γ-terpinene, p-cymene                                       | [42]       |
| *B. xylophilus* | *Eucalyptus globulus* | Myrtaceae    | carvacrol, γ-terpinene, p-cymene                                       | [42]       |
| *M. javanica*  | *Tagetes minuta*  | Asteraceae    | 2,3-butanediol, sabinene, eucalyptol, limonene, α-thujene             | [43]       |
| *M. javanica*  | *Eupatorium viscidum* | Asteraceae    | 6-methyl-5-hepten-2-one                                               | [47]       |
| *M. javanica*  | *Artemisia herba-alba* | Asteraceae    | -                                                                     | [44]       |
| *M. javanica*  | *Helianthus annuus* | Asteraceae    | -                                                                     | [45,46]    |
| *M. javanica*  | *Cuminum cyminum* | Apiaceae      | γ-terpinene, p-cymene                                                  | [55]       |
| *M. javanica*  | *Pimpinella anisum* | Apiaceae      | estragole, trans-anethole, carvone                                     | [49]       |
| *M. javanica*  | *Foeniculum vulgare* | Apiaceae      | estragole, trans-anethole, carvone                                     | [49]       |
| *M. javanica*  | *Citrus reticulata* | Rutaceae      | limonene                                                               | [57]       |
| *M. incognita* | *Ruta graveolens L.* | Rutaceae      | 2-undecanone, carvitol, 2-nonanone, 2-decanone                          | [41,50,58] |
| *B. xylophilus* | *Zanthoxylum alatum* | Rutaceae      | linalool, limonene, methyl trans-cinnamate, 1,8-cineole                | [59]       |
| *M. incognita* | *Cinnamomum zeylanicum* | Lauraceae    | (E)-cinnamaldehyde, eugenol                                           | [50,60]    |
| *M. incognita* | *Rhododendron anthropogonoides* | Ericaceae   | benzyl acetone                                                         | [61]       |
| *B. xylophilus* | *Gaultheria fragrantissima* | Ericaceae    | methyl salicylate, ethyl salicylate                                    | [59]       |
| *M. incognita* | *Dysphania ambrosioides* | Amaranthaceae | (Z)-ascaridole, (E)-ascaridole, p-cymene, isoascaridole               | [3,62,63]  |
| *M. incognita* | *Cymbopogon nardus* | Poaceae       | citronellal                                                            | [63]       |
| *B. xylophilus* | *Cymbopogon citratus* | Poaceae       | geranial, neral, ββ-myrcene                                            | [42]       |
Table 2. Cont.

| Nematode   | Plant Sources          | Family       | VOCs                                      | References  |
|------------|------------------------|--------------|-------------------------------------------|-------------|
| M. incognita | Pistacia terebinthus   | Anacardiaceae | γ-eudesmol                                | [49]        |
| M. incognita | Pelargonium asperum    | Geraniaceae  | linalool, citronellol, geraniol           | [41,50]     |
| M. incognita | Melia azedarach        | Meliaceae    | acetic, butyric, hexanoic, furfural, furfural, 5-hydroxymethylfurfural | [64]        |
| M. incognita | Azadirachta indica     | Meliaceae    | methylisothiocyanate, furfural, 2-thiophenecarboxaldehyde | [53]        |
| M. incognita | Capparis spinosa       | Capparaceae  | -                                         | [65]        |
| M. incognita | Passiflora edulis      | Passifloraceae| -                                         | [54]        |
| M. incognita | Bertholletia excelsa   | Lecythidaceae| -                                         | [66]        |
| M. javanica  | Piper nigrum L.        | Piperaceae   | -                                         | [66]        |
| M. javanica  | garlic (Allium sativum)| Amaryllidaceae| diallyl disulfide                         | [67]        |
| M. javanica  | Ailanthus altissima    | Simaroubaceae| (E,E)-2,4-decadienal, (E)-2-decenal, furfural | [68]        |

2.2.1. Nematicidal VOCs from Lamiaceae

The essential oil of Agastache rugosa has shown strong nematicidal activity against M. incognita [37]. The main components of this essential oil are methyleugenol, estragole, and eugenol, and among these three active constituents, both eugenol and methyleugenol have been found to exhibit stronger nematicidal activity against M. incognita than estragole. Avato et al. described the nematicidal activities of Rosmarinus officinalis and Thymus satureioides essential oils [38]. R. officinalis essential oil is rich in 1,8-cineole, camphor, and α-pinene. Borneol and thymol play the major roles in T. satureioides oil.

Caboni et al. reported nematicidal activity of the essential oils from several mint species against M. incognita [39]. The strong nematicidal activity of Mentha spicata may be related to the presence of carvone. The nematicidal activity of Mentha pulegium against M. incognita is attributed to high concentrations of pulegone, a terpene that exhibits considerable activity against M. incognita. In addition, menthofuran in M. pulegium essential oil also exhibits a certain nematicidal effect. Moreover, the nematicidal effect of M. pulegium essential oil on M. incognita was also observed in another report [40]. In this report, the nematicidal activities of the essential oils of Origanum vulgare, Origanum dictamnus, and Melissa officinalis were also studied. The high content of carvacrol, a monoterpenoid phenol with many biological activities, may contribute to the strong nematicidal activity of O. vulgare and O. dictamnus [69–72]. Carvacrol is also present in M. pulegium and M. officinalis. Likewise, the oils of M. pulegium and M. officinalis have been found to contain high pulegone and trans-anethole contents, respectively. Moreover, the essential oils of O. vulgare, O. dictamnus, and M. officinalis contain small amounts of terpinen-4-ol. Other compounds have been found in M. officinalis oil as well, such as L-carvone geraniol and eugenol. Thymol has been found in O. dictamnus and M. officinalis oils. All of these volatiles have nematicidal activity, and activity appears to decrease in the following order: L-carvone, pulegone, trans-anethole, geraniol, eugenol, carvacrol, thymol, and terpinen-4-ol. Besides carvacrol, thymol is also one of the main components of O. vulgare, as reported by Ntalli et al. [1]. In addition, O. vulgare has been found to have significant nematicidal activity against M. javanica [1]. Besides the plants mentioned above, the essential oil of Mentha piperita also has strong nematicidal activity against M. incognita [41]. However, the active substances of this plant’s essential oil require further research.

The volatile compound of Thymus citriodorus has nematicidal activity against M. javanica. Thymol is the main component of T. citriodorus [1]. Barbosa et al. reported the nematicidal activity of essential oils extracted from four plants (Satureja montana, Thymbra capitata, Thymus caespititius, and O. vulgare) against B. xylophilus [42]. Carvacrol, γ-terpinene, and p-cymene are the main components of the essential oils of O. vulgare and S. montana. Carvacrol is also found to be the main component of T. capitata and T. caespititius oils.
2.2.2. Nematicidal VOCs from Asteraceae

Nematicidal VOCs are described from *Artemisia herba-alba*. Thujone and camphor are regarded as the major contributors of nematicidal activity against *M. incognita* in *A. herba-alba* [38]. VOCs produced by sunflower (*Helianthus annuus*) seeds cause high mortality in *M. incognita* [43]. VOCs found in the plant, such as 2,3-butanediol, sabinene, eucalyptol, limonene, and α-thujene have also been reported to be active against *M. incognita* in other studies [53,73,74]. The essential oil of *Artemisia nilagirica* has strong nematicidal activity against *M. incognita* [44].

(ζ)-Ocimenone, the principal component of *Tagetes minuta* essential oil, may play a major role in nematicidal activity against *M. javanica* [45]. Furthermore, another study reported that dihydrotagetone and (Z)β-ocimene, which are also components of the essential oil of *T. minuta*, have certain nematicidal activities against *M. incognita* [46]. The volatile nematicidal component against *M. javanica* of *Eupatorium viscidum* has been found to be 6-methyl-5-hepten-2-one [47]. Sainz et al. studied *Artemisia pedemontana* subsp. *assoana* and showed that its hydrosols have strong nematicidal activity against *M. javanica* [48].

Hydrosols are by-products of distillation and contain highly polar, volatile compounds that dissolve in water and do not persist in essential oils [75]. However, the nematicidal active ingredients in the hydrosols of *A. pedemontana* need to be studied further.

2.2.3. Nematicidal VOCs from Myrtaceae

The essential oil of *Eucalyptus meliodora* has been found to be very active against *M. incognita* [49]. The main nematicidal compound in *E. meliodora* essential oil is benzaldehyde, with an EC$_{50}$/24h value of 9 µg/mL. In addition, the activity of *Eucalyptus globulus* essential oil against *M. incognita* have also been reported [41]. D’Addabbo et al. found that *Eucalyptus citriodora* and *Syzygium aromaticum* had strong nematicidal activities against *M. incognita* [50]. The nematicidal activity of *E. citriodora* essential oil is high, which might be attributed to its main component, citronellal. The essential oil of *S. aromaticum* consists almost entirely of eugenol, which may be the main reason for its nematotoxic activity.

2.2.4. Nematicidal VOCs from Brassicaceae

The root of *Armoracia rusticana* is capable of producing allylisothiocyanate, a volatile compound with nematicidal activity against *M. incognita* [51]. Allylisothiocyanate is one of the isothiocyanates that has been found to have high volatility. Isothiocyanates are general biocides, with activity that is based on irreversible interactions with proteins [76]. For the nematicidal activity of volatiles in *Eruca sativa*, erucin, pentyl isothiocyanate, hexyl isothiocyanate, (E)-2-hexenal, 2-ethylfuran, and methyl thiocyanate have been found to be the most active against *M. incognita* [52]. VOCs from *Brassica juncea* have been reported to be toxic to *M. incognita* [53], which has been found to yield predominantly sulfur-containing compounds, mainly isothiocyanates. *Nasturtium officinale* leaves can emit VOCs to kill *M. incognita* [54]. In particular, 1-octanol occurring in *N. officinale* shows strong nematicidal activity against *M. incognita*. In addition, other compounds in *N. officinale*, such as 2-methyl-1-propanol and 2-ethyl-1-hexanol, can also induce mortality in *M. incognita*. VOCs produced by broccoli (*Brassica oleracea* var. *italica*) shoots have nematicidal activity against *M. incognita* [43]. Among the VOCs in broccoli, dimethyl disulfide and 3-pentanol have strong nematicidal activities.

2.2.5. Nematicidal VOCs from Apiaceae

The essential oil of *Cuminum cyminum* has been found to have nematicidal activity against both *M. incognita* and *M. javanica* [55]. In essential oils extracted from *C. cyminum* seeds, p-cymene and γ-terpinene are the main nematicidal compounds. Ntalli et al. reported the nematicidal activity of the essential oils of *Foeniculum vulgare* and *Pimpinella anisum* against *M. incognita* [49]. The essential oils of *F. vulgare* and *P. anisum* both contain trans-anethole, estragole, and carvone. Besides, *F. vulgare* is also active against *M. javanica* [56].
2.2.6. Nematicidal VOCs from Rutaceae

The essential oil extracted from Citrus reticulata peel and its main component, limonene, have been shown to be effective against M. incognita [57]. The metabolite is also the nematicidal constituent of Citrus sinensis, another species of the genus Citrus [38]. The nematicidal essential oil of Ruta graveolens L. contains 2-undecanone and carvitol. Furthermore, this oil also includes a discrete amount of carvacrol, which may act synergistically with 2-undecanone. More importantly, the chemical is an isomer of thymol, which is highly toxic to M. incognita [38]. In another report, it has been noted that 2-nonanone and 2-decanone are also present in R. graveolens essential oil, and these two compounds, together with 2-undecanone, are the main components of its insecticidal properties [58].

The essential oils of Zanthoxylum alatum has nematicidal activity against B. xylophilus [59]. For Z. alatum oil, methyl trans-cinnamate has the highest nematicidal activity. At a concentration of 0.125–2.0 µg/mL, nematode mortality has been found to be 100%. In addition, the nematicidal activities of linalool, limonene, and 1,8-cineole, which are also the main components in Z. alatum oil, have been reported in other studies [77–80].

2.2.7. Nematicidal VOCs from Other Plants

VOCs from other families, such as Lauraceae, Ericaceae, Amaranthaceae, Poaceae, Anacardiaceae, Geraniaceae, Meliaceae, Capparaceae, Passifloraceae, Lecythidaceae, Piperaceae, Amaryllidaceae, and Simaroubaceae, are also important resources for searching new nematicides.

Eugenol and (E)-cinnamaldehyde are the main components against M. incognita of Cinnamomum zeylanicum (Cinnamomum verum) essential oil [50,60]. Eugenol, as 2-alkyl(oxy)phenol, has good activity against bacteria and insects [81,82]. It has been reported that the aliphatic double bond and phenolic proton of eugenol are essential for its biological activity [83]. The toxicity of (E)-cinnamaldehyde, with respect to nematodes, may be related to its aldehyde structure. It has been reported that (E)-cinnamaldehyde is more active as a nematicide than other cinnamic acids within different functional groups [84,85].

The main nematicidal component against M. incognita in the essential oil of Rhododendron anthopogonoides is benzyl acetone [57]. Interestingly, the nematicidal effect of benzyl acetone seemed to be much stronger than the essential oil, and it has even shown activity twice as strong as the oil. The essential oil of Gaultheria fragrantissima has been found to have good nematicidal activity against B. xylophilus [59]. Methyl salicylate and ethyl salicylate are the most abundant nematicidal ingredients in the essential oil of G. fragrantissima.

Dysphania ambrosioides essential oil has a toxic effect on M. incognita. The main components of the essential oil extracted from the fruits and seeds of D. ambrosioides are (Z)-ascaridole, (E)-ascaridole, and p-cymene [3]. Another study showed that the main components of the essential oil extracted from D. ambrosioides are (Z)-ascaridole, p-cymene, and isoascaridole [62]. All of these compounds have nematicidal activities against M. incognita. Among them, (Z)-ascaridole has been found to be the most active, with an LC₅₀ value of 32.79 µg/mL. Silva et al. screened out two antagonistic species from medicinal plants that are toxic to M. incognita, namely, Cymbopogon nardus and D. ambrosioides [63]. Both plants can emit VOCs that are toxic to M. incognita, with citronellal and ascaridole being their major VOCs, respectively. Furthermore, other VOCs from both species, such as 3-methyl-1-butanol, 2-ethylfuran, 2-hexenal, benzaldehyde, α-terpinene, limonene, γ-terpinene, linalool, decanal, citronellol, geraniol, citronellyl acetate, eugenol, dodecanal, etc., have already been shown to have nematicidal activity. The essential oils extracted from Cymbopogon citratus has nematicidal activity of against B. xylophilus [42]. The essential oils of C. citratus are mainly composed of geraniol, neral and β-mycene.

The essential oils of Pistacia terebinthus has strong nematicidal activity against M. incognita [49]. The main nematicidal compound in P. terebinthus is γ-eudesmol with an EC₅₀/24h value of 50 µg/mL. Pelargonium asperum is active against M. incognita [50]. The essential oil of P. asperum is a complex mixture of terpenes composed of three major
components: linalool, citronellol, and geraniol. All of these compounds have a hydroxyl function and are considered to be critical for nematicidal activity.

*Melia azedarach* has attracted much attention due to its range of biological activity against agricultural pests [64]. *M. azedarach* fruits can produce volatile substances with nematicidal activity against *M. incognita*. Organic acids, such as acetic, butyric, and hexanoic, have nematicidal activity against *M. incognita*. However, aldehydes and alcohols have higher nematicidal effects than organic acids. Furfural, 5-hydroxymethylfurfural, and furfurol have shown strong nematicidal activity. Among these compounds, furfural has exhibited the highest nematicidal fumigant activity with an EC$_{50}$ value of 8.52 µg/mL. VOCs from *Azadirachta indica* has been reported to be toxic to *M. incognita* [53]. Alcohols and esters are the main compounds in *A. indica*.

*Capparis spinosa* can act as an effective natural nematicidal agent against *M. incognita* [65]. Methylisothiocyanate is the main component of *C. spinose*. Moreover, other nematicidal components have also been found in *C. spinose*, such as 2-thiophenecarboxaldehyde and furfural. All three compounds have strong nematicidal effects on *M. incognita*. *Passiflora edulis* seeds can emit VOCs to kill *M. incognita* [54]. The VOCs of Brazil nuts (*Bertholletia excelsa* Bonpl.) and blackpepper (*Piper nigrum* L.) have also been found to inhibit activity by reducing the motility of the nematode, but their active substances have not been reported [66].

The volatile component of garlic (*Allium sativum*) that exhibits the most significant nematicidal activity against *M. javanica* is diallyl disulfide, which is a sulfide [67]. The volatile compounds of *Ailanthus altissima* have nematicidal activity against *M. javanica*. The metabolites (*E,E*)-2,4-decadienal and (*E*)-2-decenal were found to be the dominant nematicidal components of *A. altissima* [68]. Furthermore, there was a small amount of furfural in the extract.

### 3. Nematicidal Mechanisms of Volatile Organic Compounds

VOCs kill nematodes via mechanisms that affect the nervous system [86], surface coat, intestine, pharynx, or other tissues [87]. Some compounds, such as eugenol, have been proposed as the primary mode of action with regard to neurotoxicity. Eugenol, a phytochemical belonging to the 2-alkyl(oxy)phenol, has a good toxic effect on nematodes. The compound may act as an acetylcholinesterase inhibitor that blocks octopamine receptors, thus supporting nematicidal effects based on nervous-system targets [88,89]. Carvone is also a potent acetylcholinesterase inhibitor with significant nematicidal activity. This compound is a monoterpenoid with nematicidal potential that is derived from the disruption of nematode nervous systems [90].

Besides the effects on a nematode’s nervous system, volatile nematicidal compounds can also damage other parts of the worm. The exoskeleton and cuticle of nematodes are elastic in order to protect them. The cuticle consists of cross-linked collagens, insoluble proteins called cuticins, glycoproteins, and lipids. Caboni et al. reported the toxic effects of (*E,E*)-2,4-decadienal, (*E*)-2-decanal, and furfural on *M. javanica* [68]. Indeed, aliphatic aldehydes are relatively reactive compounds. Unsaturated aldehydes, such as (*E,E*)-2,4-decadienal and furfural, react with the cuticle’s amino or thiol group through a Michael addition. This interaction can cause damage to the cuticle and the leakage of internal fluid, which can cause injury to the nematode. Furthermore, the study showed that, after treatment with 2-nonanone and 2-decanone, the pharyngeal tissue of *M. incognita* shrank or even disappeared, and the intestinal tissue became blurred [22]. It indicated that 2-nonanone and 2-decanone can damage the intestine and pharynx of *M. incognita*.

VOCs also kill nematodes by causing oxidative stress. Oxidative stress causes cell death by inducing damage to DNA, proteins, and lipids [17]. The study showed that methyl isovalerate, 2-undecanone, and dimethyl disulfide have strong nematicidal activity against *M. incognita* [17]. This might be due to the fact that these compounds induce ROS production in nematodes and negatively affect antioxidant enzyme activity in *M. incognita*, resulting in severe oxidative stress and internal damage, thus resulting in the nematode’s
rapid death. Kalaiselvi et al. also showed that *A. nilagirica* essential oil may achieve its nematicidal effect by enhancing intracellular ROS production [44].

4. Discussion and Conclusions

This study reviewed VOCs produced by 26 microorganism strains and 51 plants as well as their toxic effects on RKNs and PWN that have been economically harmful to plants over the past decade. Bacteria that can produce VOCs with nematicidal activity are mainly concentrated in the genera *Pseudomonas* and *Bacillus*, and active plants include Lamiaceae, Asteraceae, Myrtaceae, Brassicaceae, Apiaceae, Rutaceae, and other plants. In particular, the aromatic plants of the genera *Brassica*, *Agastache*, *Artemisia*, *Rosmarinus*, *Thymus*, *Foeniculum*, *Pimpinella*, *Cymbopogon*, *Mentha*, *Syringa*, *Ruta*, and *Origanum*, as well as the aromatic trees of the genera *Citrus*, *Eucalyptus*, and *Cinnamomum* have been extensively studied.

Interestingly, microorganisms and plants are generally capable of producing their own unique compounds. Only a few compounds exist in both microorganisms and plants, such as dimethyl disulfide, 2-undecanone, 1,8-cineole, benzaldehyde, 2-decanone, and 2-nonanone. Dimethyl disulfide, an active component in many insecticides, has been found to be an effective nematicide and attractant [23]. This compound, which displays strong nematicidal activity against both RKNs and PWN, can be produced by a variety of bacteria and plants. Both dimethyl disulfide and 2-undecanone induce severe oxidative stress in nematodes, resulting in rapid death.

However, most of these compounds are specific to microorganisms and plants. Among the VOCs produced by microorganisms, many compounds have shown outstanding nematicidal activity against *M. incognita*, such as furfural acetone and 2-decanol. The LC$_{50/48h}$ is 4.44 mg/L for the former and 23.12 mg/L for the latter [22]. These two compounds have been found to have not only contact nematicidal activity and fumigant activity but also certain attractant effects on *M. incognita*. This suggests that these compounds can attract nematodes and then kill them through contact and fumigation.

As plant-specific compounds, furfural, isothiocyanates, carvacrol, and thymol can be produced by a variety of plants, and all show strong nematicidal activity against *Meloidogyne* spp. Ntalli et al. showed that the EC$_{50}$ value of furfural is 8.5 µg/mL [64]. The toxic effects of furfural on nematodes may be attributed to its nucleophilic addition reaction with nematode cuticles, which may lead to the evident cuticle suffering internal damage, followed by the leakage of fluid substances [65]. Isothiocyanates, such as methylisothiocyanate and allylisothiocyanate, have been found to have strong volatility and nematicidal effects. Isothiocyanates are known nematicides that can act as electrophiles to irreversibly interact with proteins, thereby altering protein function [51]. Carvacrol and thymol are the main nematicidal active ingredients in many plants. Both compounds are highly toxic to RKNs and PWN. Lei et al. showed that carvacrol and thymol can interact with a receptor to trigger a signaling cascade that leads to nematode death [42].

VOCs need not act alone; they also have synergism or antagonism between different compounds. Synergism is an effect of different compounds used in combination that is greater than the sum of the individual compounds. Antagonism means a reduction in the biological activity of a mixture of compounds, compared to the activity of each component alone [91]. For example, terpenoids have obvious synergistic effects. According to Ntalli et al., among the essential oils from seven plants indigenous to Greece, the most synergistic terpene pairs are *trans*-anethole/geraniol, *trans*-anethole/eugenol, carvacrol/eugenol, and geraniol/carvacrol [49]. In contrast, besides mixtures with *trans*-anethole, L-carvone mixed with other compounds, such as thymol and eugenol, predominantly exhibits antagonism. In general, the activity of essential oils or the extracts of plants should be related to the content of their main constituents. However, the activity of the mixture is not linearly dependent on the content of the main active components. This may be due to the presence of other compounds in the mixture that have synergism or antagonism with the main components.
All of the VOCs summarized in this paper have the potential to be developed as commercial pesticides. However, further research is needed on their practical application in nematode management and the mechanism of their various toxicities.

**Author Contributions:** Investigation, X.D. and G.L.; Writing—original draft preparation, X.D. and G.L.; Writing—review and editing, X.W. and G.L. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research was funded by the National Natural Science Foundation of China (31860015 and 32160012) and a project from the Department of Science and Technology of Yunnan Province (2020BB050061).

**Institutional Review Board Statement:** Not applicable.

**Informed Consent Statement:** Not applicable.

**Data Availability Statement:** Not applicable.

**Conflicts of Interest:** The authors declare no conflict of interest.

**References**

1. Ntalli, N.G.; Ozalexandridou, E.X.; Kasiotis, K.M.; Samara, M.; Golfinopoulos, S.K. Nematicidal activity and phytochemistry of Greek Lamiaceae species. *Agronomy* 2020, 10, 1119. [CrossRef]
2. Bird, D.M.; Williamson, V.M.; Abad, P.; McCarter, J.; Danchin, E.G.; Castagnone-Sereno, P.; Opperman, C.H. The genomes of root-knot nematodes. *Annu. Rev. Phytopathol.* 2009, 47, 333–351. [CrossRef] [PubMed]
3. Barros, A.F.; Campos, V.P.; de Paula, L.L.; Oliveira, D.F.; de Silva, F.J.; Terra, W.C.; Silva, G.H.; Salimena, J.P. Nematicidal screening of essential oils and potent toxicity of *Dysphania ambrosioides* essential oil against *Meloidogyne incognita* in vitro and in vivo. *J. Phytopathol.* 2019, 167, 380–389. [CrossRef]
4. McCarter, J.P. Molecular approaches toward resistance to plant-parasitic nematodes. *Plant Cell Monogr.* 2008, 15, 239–267.
5. Pradhan, M.A.A.; Rahaman, M.M.; Paul, S.K.; Ahamad, M.U.; Goswami, B.K. Effect of BAU-biofungicide, neem oil and a nematicide on the root-rnot (*Bursaphelenchus xylophilus* Steiner & Buhrer, 1934 (Nickle, 1970) in Spain. *Pathol. Plant.* 2012, 657–664. [CrossRef]
6. Vovlas, N.; Mifsud, D.; Landa, B.B.; Castillo, P. Pathogenicity of the root-knot nematode *Meloidogyne javanica* on potato. *Plant Pathol.* 2005, 54, 657–664. [CrossRef]
7. Robertson, L.; Arcos, S.C.; Escuer, M.; Merino, R.S.; Esparrago, G.; Abelleira, A.; Navas, A. Incidence of the pinewood nematode *Bursaphelenchus xylophilus* Steiner & Buhrer, 1934 (Nickle, 1970) in Spain. *Nematology* 2011, 13, 755–757.
8. Fonseca, L.; Cardoso, J.M.S.; Lopes, A.; Pestana, M.; Abreu, F.; Nunes, N.; Mota, M.; Abrantes, I. The pinewood nematode, *Bursaphelenchus xylophilus*, in Madeira Island. *Helminthologia* 2012, 49, 96–103. [CrossRef]
9. Tan, Q.Q.; Hai, Y.W.; Shu, X.J.; Hong, B.M. Mortality and movement behaviour of *Bursaphelenchus xylophilus* under different dosages of *Copper Sulphate*. *Plant Prot. Sci.* 2013, 49, 98–103. [CrossRef]
10. Chitwood, D.J. Phytochemical based strategies for nematode control. *Annu. Rev. Phytopathol.* 2002, 40, 221–249. [CrossRef] [PubMed]
11. Lee, J.H.; Ma, K.C.; Ko, S.J.; Kang, B.R.; Kim, I.S.; Kim, Y.C. Nematicidal activity of a nonpathogenic biocontrol bacterium, *Pseudomonas chlororaphis* O6. *Curr. Microbiol.* 2011, 62, 746–751. [CrossRef] [PubMed]
12. Campos, V.P.; Pinho, R.S.C.; Freire, E.S. Volatiles produced by interacting microorganisms potentially useful for the control of plant pathogens. *Cienc. Agrotecnol.* 2010, 34, 525–535. [CrossRef]
13. Xu, Y.Y.; Lu, H.; Wang, X.; Zhang, K.Q.; Li, G.H. Effect of volatile organic compounds from bacteria on nematodes. *Chem. Biodivers.* 2015, 12, 1415–1421. [CrossRef]
14. Zhai, Y.L.; Shao, Z.Z.; Cai, M.M.; Zheng, L.Y.; Li, G.Y.; Huang, D.; Cheng, W.L.; Thomashow, L.S.; Weller, D.M.; Yu, Z.N.; et al. Multiple modes of nematode control by volatiles of *Pseudomonas putida* 1A00316 from antarctic soil against *Meloidogyne incognita*. *Front. Microbiol.* 2018, 9, 253. [CrossRef]
15. Wolfgang, A.; Taffner, J.; Guimaraes, R.A.; Coyne, D.; Berg, G. Novel strategies for soil-borne diseases: Exploiting the microbiome and volatile-based mechanisms toward controlling *Meloidogyne*-based disease complexes. *Front. Microbiol.* 2019, 10, 1296. [CrossRef]
16. Ayaz, M.; Ali, Q.; Farzand, A.; Khan, A.R.; Ling, H.; Gao, X.W. Nematicidal volatiles from *Bacillus atrophaeus* GBSC56 promote growth and stimulate induced systemic resistance in tomato against *Meloidogyne incognita*. *Int. J. Mol. Sci.* 2021, 22, 5049. [CrossRef]
17. Yin, N.; Liu, R.; Zhao, J.L.; Khan, R.A.A.; Li, Y.; Ling, J.; Liu, W.; Yang, Y.H.; Xie, B.Y.; Mao, Z.C. Volatile organic compounds of *Bacillus cereus* strain Bc-cm103 exhibit fumigation activity against *Meloidogyne incognita*. *Plant Dis.* 2020, 105, 904–911. [CrossRef]
19. Huang, Y.; Xu, C.K.; Ma, L.; Zhang, K.Q.; Duan, C.Q.; Mo, M.H. Characterisation of volatiles produced by Bacillus megaterium YFM3.25 and their nematocidal activity against Meloidogyne incognita. *Eur. J. Plant Pathol.* 2009, 126, 417–422. [CrossRef]

20. Luo, T.; Hou, S.S.; Yang, L.; Qi, G.F.; Zhao, X.Y. Nematodes avoid and are killed by Bacillus mycoides-produced styrene. *J. Invertebr. Pathol.* 2018, 159, 129–136. [CrossRef]

21. Yang, L.L.; Huang, Y.; Liu, J.; Ma, L.; Mo, M.H.; Li, W.J.; Yang, F.X. Lysinibacillus mangiferaeii sp. nov., a new bacterium producing nematocidal volatiles. *Antonie Van Leeuwenhoek* 2012, 102, 53–59. [CrossRef] [PubMed]

22. Cheng, W.L.; Yang, J.Y.; Nie, Q.Y.; Huang, D.; Yu, C.; Zheng, L.Y.; Cai, M.M.; Thomasshaw, L.S.; Weller, D.M.; Yu, Z.N.; et al. Volatile organic compounds from Paenibacillus polymyxa KM2501-1 control Meloidogyne incognita by multiple strategies. *Sci. Rep.* 2017, 7, 16213. [CrossRef] [PubMed]

23. Huang, D.; Yu, C.; Shao, Z.Z.; Cai, M.M.; Li, G.Y.; Zheng, L.Y.; Yu, Z.N.; Zhang, J.B. Identification and characterization of nematocidal volatile organic compounds from deep-sea *Virgibacillus dokdonensis* MCCC 1A00493. *Molecules* 2020, 25, 744. [CrossRef] [PubMed]

24. Huang, D.; Yu, H.; Chen, W.; Cheng, W.L.; Shao, Z.Z.; Zhang, J.B. Identification and characteristics of 4-vinylphenol from *Virgibacillus dokdonensis* MCCC 1A00493 against *Meloidogyne incognita*. *Acta Microbiol. Sin.* 2022, 62, 346–356.

25. Mei, X.Y.; Wang, X.; Li, G.H. Pathogenicity and volatile nematocidal metabolites from *Duddingtonia flagrans* against *Meloidogyne incognita*. *Microorganisms* 2021, 9, 2268. [CrossRef]

26. Freire, E.S.; Campos, V.P.; Pinho, R.S.C.; Oliveira, D.F.; Faria, M.R.; Pohlit, A.M.; Noberto, N.P.; Rezende, E.L.; Pfennig, L.H.; Silva, J.R.C. Volatile substances produced by *Fusarium oxysporum* from coffee rhizosphere and other microbes affect *Meloidogyne incognita* and *Arthrobacter coniooides*. *J. Nematol.* 2016, 44, 321–328.

27. Terra, W.C.; Campos, V.P.; Martins, S.J.; Costa, L.S.A.S.; da Silva, J.C.P.; Barros, A.F.; Lopez, L.E.; Santos, T.C.N.; Smart, G.; Oliveira, D.F. Volatile organic molecules from *Fusarium oxysporum* strain 21 with nematocidal activity against *Meloidogyne incognita*. *Crop Prot.* 2018, 106, 125–131. [CrossRef]

28. Liarzi, O.; Bucki, P.; Miyara, S.B.; Ezra, D. Bioactive volatiles from an endophytic *Daldinia cf. concentrica* isolate affect the viability of the plant parasitic nematode *Meloidogyne javanica*. *PloS ONE* 2016, 11, e0168437. [CrossRef]

29. Khoo, S.; Eltayef, K.M.; Baxter, I.; Myrta, A.; Bull, J.C.; Butt, T. Volatiles of the entomopathogenic fungus, *Metarhizium brunneum*, attract and kill plant parasitic nematodes. *Biol. Control* 2021, 152, 104472. [CrossRef]

30. Yu, J.; Du, G.C.; Li, R.G.; Li, L.; Li, Z.; Zhou, C.J.; Chen, C.C.; Guo, D.S. Nematicidal activities of bacterial volatiles and components from two marine bacteria, *Pseudoalteromonas marina* KM2501-1 and *Vibrio atlanticus* strain S-16, against the pine wood nematode, *Bursaphelenchus xylophilus*. *Nematology* 2015, 17, 1011–1025. [CrossRef]

31. Li, H.C.; Dou, G.M.; Gao, M.G.; Ren, F.; Li, R.H.; Zhang, X.Y.; Yan, D.H. *Annulohypoxylon* sp. FPY3050 produces volatile organic compounds against the pine wood nematode, *Bursaphelenchus xylophilus*. *Nematology* 2020, 22, 245–255. [CrossRef]

32. Yang, Z.S.; Yu, Z.F.; Lei, L.P.; Xia, Z.Y.; Shao, L.; Zhang, K.Q.; Li, G.H. Nematicidal effect of volatiles produced by *Trichoderma sp.* J. Asia-Pac. Entomol. 2015, 8, 7856–7863. [CrossRef]

33. Parsons, P.A.; Spence, G.E. Acetaldehyde: A low-concentration resource and larval attractant in 3 *Drosophila* species. *Experientia* 1981, 37, 576–577. [CrossRef]

34. Curto, G.; Dongiovanni, C.; Sasaneli, N.; Santori, A.; Myrta, A. Efficacy of dimethyl disulfide (DMDS) in the control of the root-knot nematode *Meloidogyne incognita* and the cyst nematode *Heterodera carotae* on carrot in field condition in Italy. *Acta Hortic.* 2014, 1044, 405–410. [CrossRef]

35. Fritsch, J.; Fouilliet, T.; Charles, P.; Fargier-Puech, P.; Ramponi-Bur, C.; Descamps, S.; Fretay, G.D.; Myrta, A. French experiences with *Daldinia cf. concentrica* in the control of the root-knot nematode *Meloidogyne incognita*. *Plant Soil* 1990, 121, 287–291. [CrossRef]

36. Ghisalberti, E.L.; Narbey, M.J.; Dewan, M.M.; Sivasithamparam, K. Variability among strains of *Virgibacillus dokdonensis*. *Microorganisms* 2015, 9, 2268. [CrossRef]

37. Li, H.Q.; Liu, Q.Z.; Liu, Z.L.; Du, S.S.; Deng, Z.W. Chemical composition and nematocidal activity of essential oil of *Agastache rugosa* against *Meloidogyne incognita*. *Molecules* 2013, 18, 4170–4180. [CrossRef]

38. Avato, P.; Laquale, S.; Argentieri, M.P.; Lamiri, A.; Radici, V.; D’Addabbo, T. Nematicidal activity of essential oils from aromatic plants of Morocco. *J. Pest Sci.* 2017, 90, 711–722. [CrossRef]

39. Caboni, P.; Saba, M.; Tocco, G.; Casu, L.; Murgia, A.; Maxia, A.; Menkissoglou-Spiroudi, U.; Ntalli, N. Nematicidal activity of mint aqueous extracts against the root-knot nematode *Meloidogyne incognita*. *J. Agric.* 2013, 61, 9784–9788. [CrossRef]

40. Ntalli, N.G.; Ferrari, F.; Giannakou, I.; Menkissoglou-Spiroudi, U. Phytochemistry and nematocidal activity of the essential oils from 8 Greek Lamiaceae aromatic plants and 13 terpene components. *J. Agric.* 2010, 58, 7856–7863. [CrossRef]

41. Laquale, S.; Candido, V.; Avato, P.; Argentieri, M.P.; D’Addabbo, T. Essential oils as soil biofumigants for the control of the root-knot nematode *Meloidogyne incognita* on tomato. *Ann. Appl. Biol.* 2015, 167, 217–224. [CrossRef]

42. Barbosa, P.; Lima, A.S.; Vieira, P.; Dias, L.S.; Tinoco, M.T.; Barroso, J.G.; Figueiredo, A.C.; Mota, M. Nematicidal activity of essential oils and volatiles derived from *Portuguese aromatic flora* against the pine wood nematode, *Bursaphelenchus xylophilus*. *J. Nematol.* 2010, 42, 8–16. [PubMed]

43. Silva, J.C.P.; Campos, V.P.; Barros, A.F.; Pedroso, M.P.; Terra, W.C.; Lopez, L.E.; de Souza, J.T. Plant volatiles reduce the viability of the root-knot nematode *Meloidogyne incognita* either directly or when retained in water. *Plant Dis.* 2018, 102, 2170–2179. [CrossRef] [PubMed]
44. Kalaiselvi, D.; Mohankumar, A.; Shanmugam, G.; Thiruppathi, G.; Nivitha, S.; Sundararaj, P. Altitude-related changes in the phytochemical profile of essential oils extracted from Artemisia nilagirica and their nematicidal activity against Meloidogyne incognita. *Ind. Crops Prod.* **2019**, *139*, 111472. [CrossRef]

45. Massuh, Y.; Cruz-Estrada, A.; Gonzalez-Coloma, A.; Ojeda, M.S.; Zygaldo, J.A.; Andrés, M.F. Nematicidal activity of the essential oil of three varieties of Tagetes minuta from Argentina. *Nat. Prod. Commun.* **2017**, *12*, 705–707. [CrossRef]

46. Adekunle, O.K.; Acharya, R.; Singh, B. Toxicity of pure compounds isolated from Tagetes minuta oil to Meloidogyne incognita. *Australas. Plant Dis. Notes* **2007**, *2*, 101–104. [CrossRef]

47. Sosa, M.E.; Lancellle, H.G.; Tonn, C.E.; Andres, M.F.; Gonzalez-Coloma, A. Insecticidal and nematicidal essential oils from Argentinean Eupatorium and Baccharis spp. *Biochem. Syst. Ecol.* **2012**, *43*, 132–138. [CrossRef]

48. Sainz, P.; Andres, M.F.; Martinez-Diaz, R.A.; Baien, M.; Navarro-Rocha, J.; Diaz, C.E.; Gonzalez-Coloma, A. Chemical composition and biological activities of Artemisia pedemontana subsp. assoana essential oils and hydrilate. *Biomolecules* **2019**, *9*, 558.

49. Ntalli, N.G.; Ferrari, F.; Giannakou, I.; Menkissoglou-Spiroudi, U. Synergistic and antagonistic interactions of terpenes against Meloidogyne incognita and the nematicidal activity of essential oils from seven plants indigenous to Greece. *Pest Manag. Sci.* **2011**, *67*, 341–351. [CrossRef]

50. D’Addabbo, T.; Argentieri, M.P.; Laquale, S.; Candido, V.; Avato, P. Relationship between chemical composition and nematicidal activity of different essential oils. *Plants* **2020**, *9*, 1546. [CrossRef]

51. Aissani, N.; Urgeghe, P.P.; Oplos, C.; Saba, M.; Tocco, G.; Petretto, G.L.; Elokh, K.; Menkissoglou-Spiroudi, U.; Ntalli, N.; Caboni, P. Nematicidal activity of the volatilome of *Eruca sativa* leaves and passion fruit (*Passiflora edulis*) seeds against Meloidogyne incognita. *J. Agric. Food Chem.* **2015**, *63*, 6120–6125. [CrossRef] [PubMed]

52. Aissani, N.; Urgeghe, P.P.; Oplos, C.; Saba, M.; Tocco, G.; Petretto, G.L.; Elokh, K.; Menkissoglou-Spiroudi, U.; Ntalli, N.; Caboni, P. Nematicidal activity of the volatilome of *Eruca sativa* leaves and passion fruit (*Passiflora edulis*) seeds against Meloidogyne incognita. *J. Agric. Food Chem.* **2015**, *63*, 1413–1421. [CrossRef] [PubMed]

53. Barros, A.F.; Campos, V.P.; da Silva, J.C.P.; Pedroso, L.A.; Silva, F.D.J.; da Silva, J.C.P.; de Oliveira, D.F.; Silva, G.H. The role of organic compounds emitted by *Brassica juncea* (L.) Gaertn. against *Bursaphelenchus xylophilus* and the nematicidal activity of *Meloidogyne javanica* against *B. juncea*. *J. Agric. Food Chem.* **2020**, *69*, 229–238. [CrossRef]

54. Silva, M.F.; Campos, V.P.; Barros, A.F.; Terra, W.C.; Pedroso, M.P.; Gomes, V.A.; Ribeiro, C.R.; Silva, F.J. Volatile emissions of watercress (*Nasturtium officinale*) and their nematicidal activity against *Meloidogyne incognita*. *J. Agric. Food Chem.* **2015**, *63*, 7345–7351. [CrossRef] [PubMed]

55. Goyal, L.; Kaushal, S.; Dhillon, N.K.; Heena. Nematicidal potential of *Citrus reticulata* peel essential oil, isolated major compound and its derivatives against *Meloidogyne incognita*. *Arch. Phytopathol. Plant Prot.* **2021**, *54*, 449–467. [CrossRef]

56. da Silva, F.G.E.; Mendes, F.R.d.S.; Assunção, J.C.D.C.; Santiago, G.M.P.; Bezerra, M.A.X.; Barbosa, F.G.; Mafezoli, J.; Rocha, R.R. Seasonal variation, larvicidal and nematicidal activities of the lef essential oil of *Ruta graveolens* L. *J. Essent. Oil Res.* **2015**, *26*, 204–209. [CrossRef]

57. Pardavella, I.; Daferera, D.; Tsilois, T.; SKiada, P.; Giannakou, I. The use of essential oil and hydroalcohol extracted from *Cuminum cyminum seeds for the control of Meloidogyne incognita* and *Meloidogyne javanica*. *Plants* **2020**, *10*, 46. [CrossRef] [PubMed]

58. Sousa, R.M.O.F.; Rosa, J.S.; Silva, C.A.; Almeida, M.T.M.; Novo, M.T.; Cunha, A.C.; Fernandes-Ferreira, M. Larvicidal, molluscicidal and nematicidal activities of essential oils and compounds from *Foeniculum vulgare*. *J. Pest Sci.* **2015**, *88*, 413–426. [CrossRef]

59. Goyal, L.; Kaushal, S.; Dhillon, N.K.; Heena. Nematicidal potential of *Citrus reticulata* peel essential oil, isolated major compound and its derivatives against *Meloidogyne incognita*. *Arch. Phytopathol. Plant Prot.* **2021**, *54*, 449–467. [CrossRef]

60. Silva, F.G.E.; Mendes, F.R.d.S.; Assunção, J.C.D.C.; Santiago, G.M.P.; Bezerra, M.A.X.; Barbosa, F.G.; Mafezoli, J.; Rocha, R.R. Seasonal variation, larvicidal and nematicidal activities of the lef essential oil of *Ruta graveolens* L. *J. Essent. Oil Res*. **2014**, *26*, 204–209. [CrossRef]

61. Kim, J.; Seo, S.-M.; Park, I.-K. Nematicidal activity of *Meloidogyne incognita* C. *J. Agric. Food Chem.* **2015**, *63*, 54

62. Silva, M.F.; Campos, V.P.; da Silva, J.C.P.; Pedroso, M.P.; Medeiros, F.H.V.; Pozza, E.A.; Reale, A.L. Nematicidal activity of volatile organic compounds emitted by *Brassica juncea*, *Azadirachta indica*, *Canavalia ensiformis*, *Mucuna pruriens* and *Cajanus cajan* against *Meloidogyne incognita*. *Appl. Soil Ecol.* **2014**, *80*, 34–43. [CrossRef]

63. Silva, M.F.; Campos, V.P.; Barros, A.F.; Terra, W.C.; Pedroso, M.P.; Gomes, V.A.; Ribeiro, C.R.; Silva, F.J. Volatile emissions of *Eruca sativa* (*Passiflora edulis*) seeds against *Meloidogyne incognita*. *Pest Manag. Sci.* **2020**, *76*, 1413–1421. [CrossRef] [PubMed]

64. D’Addabbo, T.; Argentieri, M.P.; Laquale, S.; Candido, V.; Avato, P. Relationship between chemical composition and nematicidal activity of different essential oils. *Plants* **2020**, *9*, 1546. [CrossRef]

65. Barros, A.F.; Campos, V.P.; de Paula, L.L.; Pedroso, L.A.; Silva, F.D.J.; da Silva, J.C.P.; de Oliveira, D.F.; Silva, G.H. The role of *Cinnamomum zeylanicum* essential oil, (*E*)-cinnamaldehyde and (*E*)-cinnamaldehyde oxime in the control of *Meloidogyne incognita*. *J. Phytopathol.* **2021**, *169*, 229–238. [CrossRef]

66. Bai, C.Q.; Bai, C.Q.; Liu, Q.Z.; Du, S.S.; Liu, Z.L. Nematicidal activity of the essential oil of *Rhododendron anthopogonoides* aerial parts and its constituent compounds against *Meloidogyne incognita*. *Z. Fur Nat.* **2013**, *68*, 307–312.

67. Anastasiadis, I.; Kimbaris, A.C.; Kornpi, M.; Polissiou, M.G.; Karanastasi, E. The effect of a garlic essential oil component and entomopathogenic nematodes on the suppression of *Meloidogyne javanica* on tomato. *Hell. Plant Prot. J.* **2011**, *4*, 21–24.
Ailanthus altissima against Meloidogyne javanica. J. Agric. Food Chem. 2012, 60, 1146–1151. [CrossRef]

69. Baser, K.H.C. Biological and pharmacological activities of carvacrol and carvacrol bearing essential oils. Curr. Pharm. Des. 2008, 14, 3106–3119. [CrossRef]

70. Oka, Y.; Nacar, S.; Putievsky, E.; Ravid, U.; Yaniv, Z.; Spiegel, Y. Nematicidal activity of essential oils and their components against the root-knot nematode. Phytopathology 2000, 90, 710–715. [CrossRef]

71. Trabace, L.; Zotti, M.; Morgese, M.G.; Tucci, P.; Colaianna, M.; Schiavone, S.; Avato, P.; Cuomo, V. Estrous cycle affects the neurochemical and neurobehavioral profile of carvacrol-treated female rats. Toxicol. Appl. Pharmacol. 2011, 255, 169–175. [CrossRef] [PubMed]

72. Zotti, M.; Colaianna, M.; Morgese, M.G.; Tucci, P.; Schiavone, S.; Avato, P.; Trabace, L. Carvacrol: From ancient flavoring to modern biopharmaceutical agent. Molecules 2013, 18, 6161–6172. [CrossRef] [PubMed]

73. Geng, C.; Nie, X.T.; Tang, Z.Z.; Zhang, Y.Y.; Lin, J.; Sun, M.; Peng, D.H. DS-1 has nematicidal activity and degrades multiple intestinal-associated nematode proteins. Molecules 2013, 18, 375–386. [CrossRef] [PubMed]

74. Silva, W.R.J.; Machado, A.R.T.; Campos, V.A.C.; Zeri, A.C.M.; Campos, V.P.; Oliveira, D.F. Volatile organic compounds for the control of Meloidogyne exigua in Coffea arabica. Trop. Plant Pathol. 2013, 38, 375–386. [CrossRef]

75. Wąs-Bytkowska, A.; Sienkiewicz, M.; Stobiecka, A.; Maciąg, A.; Szoka, U.; Karna, E. Chemical composition and biological activity of Abies alba and A. koraiensis seed and cone essential oils and characterization of their seed hydrolates. Chem. Biodivers. 2015, 12, 407–418. [CrossRef] [PubMed]

76. Silva, W.R.J.; Machado, A.R.T.; Campos, V.A.C.; Zeri, A.C.M.; Campos, V.P.; Oliveira, D.F. Volatile organic compounds for the control of Meloidogyne exigua in Coffea arabica. Trop. Plant Pathol. 2013, 38, 375–386. [CrossRef] [PubMed]

77. Choi, I.H.; Kim, J.; Shin, S.C.; Park, I.K. Nematicidal activity of monoterpenoids against the pine wood nematode (Bursaphelenchus xylophilus). Russ. J. Nematol. 2007, 15, 35–40.

78. Kim, J.; Seo, S.M.; Lee, S.G.; Shin, S.C.; Park, I.K. Nematicidal activity of plant essential oils and components from coriander (Coriandrum sativum), oriental sweetgum (Liquidambar orientalis), and valerian (Valeriana wallichii) essential oils against pine wood nematode (Bursaphelenchus xylophilus). J. Agric. Food Chem. 2008, 56, 7316–7320. [CrossRef]

79. Park, I.K.; Kim, J.; Lee, S.G.; Shin, S.C. Nematicidal activity of plant essential oils and components from ajo (Trachyspermum ammi), allspice (Pimenta dioica), and litsea (Litsea cubeba) essential oils against pine wood nematode (Bursaphelenchus xylophilus). J. Agric. Food Chem. 2008, 56, 7316–7320. [CrossRef]

80. Choi, I.H.; Park, J.Y.; Shin, S.C.; Park, I.K. Nematicidal activity of medicinal plant extracts and two cinnamates isolated from Kaempferia galanga L. (Proh Hom) against the pine wood nematode, Bursaphelenchus xylophilus. Nematology 2006, 8, 359–365. [CrossRef]

81. Mahizan, N.A.; Yang, S.K.; Moo, C.L.; Song, A.A.L.; Chong, C.M.; Chong, C.W.; Abushelaibi, A.; Lim, S.H.E.; Lai, K.S. Terpene derivatives as a potential agent against antimicrobial resistance (AMR) pathogens. Molecules 2019, 24, 2631. [CrossRef] [PubMed]

82. Huang, Y.; Ho, S.H.; Lee, H.C.; Yap, Y.L. Insecticidal properties of eugenol, isoeugenol and methyleugenol and their effects on intestinal-associated nematode proteins. Sci. Rep. 2016, 6, 375–386. [CrossRef] [PubMed]

83. Barbosa, J.D.F.; Silva, V.B.; Alves, P.B.; Gumina, G.; Santos, R.L.C.; Sousa, D.P.; Cavalcanti, S.C.H. Structure-activity relationships of eugenol derivatives against Aedes aegypti (Diptera: Culicidae) larvae. Pest Manag. Sci. 2012, 68, 1478–1483. [CrossRef] [PubMed]

84. Kong, J.O.; Lee, S.M.; Moon, Y.S.; Lee, S.G.; Ahn, Y.J. Nematicidal activity of cassia and cinnamon oil compounds and related compounds toward Bursaphelenchus xylophilus (Nematoda: Parasitaphelenchidae). J. Nematol. 2007, 39, 31–36.

85. Wang, Z.Q.; Kim, H.K.; Tao, W.Q.; Mo, W.; Young-Joon, A.J. Contact and fumigant toxicity of cinnamaldehyde and cinnamic acid and related compounds to Deratophagoides farinae and Dermatophagoides pteronyssinus (Acari: Pyroglyphidae). J. Med. Entomol. 2011, 48, 366–371. [CrossRef]

86. Warnock, N.D.; Wilson, L.; Patton, C.; Fleming, C.C.; Maule, A.G.; Dalzell, J.J. Nematode neuropeptides as transgenic nematicides. PLoS Pathog. 2017, 13, e1006237. [CrossRef]

87. Geng, C.; Nie, X.T.; Tang, Z.Z.; Zhang, Y.Y.; Lin, J.; Sun, M.; Peng, D.H. DS-1 has nematicidal activity and degrades multiple intestinal-associated nematode proteins. Sci. Rep. 2016, 6, 25012. [CrossRef]

88. Kostyukovsky, M.; Rafaeli, A.; Gileadi, C.; Demchenko, N.; Shaaya, E. Activation of octopaminergic receptors by essential oil derivatives from ancient flavoring to modern biopharmaceutical agent. Molecules 2013, 18, 6161–6172. [CrossRef] [PubMed]

89. Oka, Y.; Nacar, S.; Putievsky, E.; Ravid, U.; Yaniv, Z.; Spiegel, Y. Nematicidal activity of essential oils and their components against the root-knot nematode. Phytopathology 2000, 90, 710–715. [CrossRef]

90. Trabace, L.; Zotti, M.; Morgese, M.G.; Tucci, P.; Colaianna, M.; Schiavone, S.; Avato, P.; Cuomo, V. Estrous cycle affects the neurochemical and neurobehavioral profile of carvacrol-treated female rats. Toxicol. Appl. Pharmacol. 2011, 255, 169–175. [CrossRef] [PubMed]