Volatile compounds as potential bio-fumigants against plant-parasitic nematodes – a mini review

Hung Xuan Bui* and Johan A. Desaeger
Department of Entomology and Nematology, Gulf Coast Research and Education Center, University of Florida, Wimauma, FL, 33598.
*E-mail: hungbui@ufl.edu
This paper was edited by Guiping Yan.
Received for publication July 16, 2020.

Plant-parasitic nematodes (PPNs) are one of the major constraints to crop production, and especially in high-value vegetable and fruit crops, they can cause significant economic yield loss, estimated to be more than US$100 billion annually (Bernard et al., 2017). Chemical soil fumigants have been in use for more than a century now, and remain the standard practice in many crops, especially fruits and vegetables. Although many of the early fumigants have been banned, the ones that have managed to stay, such as 1,3-dichloropropene, metam, and chloropicrin, are still considered to be the most effective products for the control of PPNs (De Cal et al., 2005; Desaeger et al., 2017; Rosskopf et al., 2005). However, environmental and safety concerns are putting more and more pressure on these products. Also, the evidence is growing of their adverse effect on beneficial soil organisms and the rapid resurgence of soilborne pathogens, including PPNs. Effects of VCs on plants, and soilborne pathogens such as bacteria and fungi have been reviewed elsewhere (Kai et al., 2009, 2016; Schulz-Bohm et al., 2017). Here, we summarize the recent studies of VCs that focused on PPNs as well as the challenges and knowledge gaps that remain in the future application of VCs as potential bio-fumigants for nematode management in the field.

What are volatile compounds?
Volatile compounds (VCs) are typically small, lipophilic, odorous, and low molecular mass compounds that...
can be evaporated and diffused aboveground and belowground through gas- and water-filled pores in soil and rhizosphere environments (Effmert et al., 2012; Insam and Seewald, 2010; Vespermann et al., 2007). These VCs are considered as the products of secondary metabolisms in plants and microorganisms such as bacteria and fungi (Dudareva et al., 2013; Schulz-Bohm et al., 2017; Vivaldo et al., 2017). The emission of VCs from plants and microorganisms depends on various factors such as the growth stage, nutrient availability, temperature, oxygen availability, pH, and soil moisture content (Insam and Seewald, 2010). VCs are classified into different chemical classes such as alkenes, alcohols, ketones, benzenoids, pyrazines, sulfides, and terpenes which have either beneficial or harmful effects on other organisms (Schmidt et al., 2015; Vivaldo et al., 2017).

**Plant volatile compounds against plant-parasitic nematodes**

Plant VCs that are well-known as bio-fumigants for the control of PPNs are glucosinolates which emit isothiocyanates (ITCs) as VCs under the process of biodegradation. ITCs are also the active ingredient of chemical fumigants such as metam. Plants belonging to the families Brassicaceae, Capparaceae, and Caricaceae all produce glucosinolates, and many genera within these plant families have been studied for their nematicidal effects on PPNs (Kruger et al., 2013; Monfort et al., 2007) (Table 1). Following maceration and incorporation, glucosinolates will be hydrolyzed to release ITCs which have broad-spectrum biological activities, against many soilborne pathogens and PPNs (Matthiesen et al., 2004; Schroeder and MacGuidwin, 2010). Several studies have shown the potential of these plants to control PPNs such as *Meloidogyne incognita*, *M. javanica*, *Heterodera schachtii*, *Pratylenchus neglectus*, *Paratrichodorus allius*, and *Globodera pallida* (Lord et al., 2011; Potter et al., 1998; Thierfelder and Friedt, 1995). More than 200 glucosinolates were identified from 3,500 Brassica species and each Brassica species can contain various types and amounts of glucosinolates (Clarke, 2010). Additionally, more than 120 glucosinolates were identified from at least 500 non-Brassica plants (Kruger et al., 2013). The use of Brassica and non-Brassica plants as biofumigation crops can be through maceration and incorporation of plant parts into the soil as green manure, through the use of seed meal, or as poor-host winter or summer cover crops (Hafez and Sundararaj, 2009; Rahman and Somers, 2005; Smith et al., 2004). Biofumigation is usually not as effective as chemical fumigation and biofumigant crops can also be good hosts to some of the target PPNs (Daryanto et al., 2018; Grabau et al., 2017; Monfort et al., 2007). The cost of biofumigation is still high and often not economically practical for farmers to apply (Clay et al., 2020; Dutta et al., 2019). There are excellent review articles of using Brassica plants as biofumigation to control PPNs that readers can find in the literature (Brennan et al., 2020; Dutta et al., 2019).

Recently, many other plant VCs have been shown to have potential for controlling PPNs. Dimethyl disulfide and 3-pentanol, selected from the broccoli volatilome, were able to reduce the mobility of *M. incognita* in vitro and gall incidence and egg production on tomato in planta (da Silva et al., 2019; Silva et al., 2018). Interestingly, the dry macerates of citronella, black pepper, and broccoli worked more effectively than the aqueous filtered macerates (da Silva et al., 2019). Phenol, 4-methylphenol, γ-decalactone, and skatole emitted by castor bean cake inhibited egg hatching and mobility and caused mortality to second-stage juveniles (J2s) of *M. incognita*. Also, *M. incognita* J2s exposed to these VCs showed reduced infectivity and reproduction on tomato (Pedroso et al., 2019). 2-methyl-1-butanol, 3-methyl-1-butanol, phenyl-ethylalcohol, benzene-1-ethyl-4-methoxy (p-ethylanisole), and 4-ethyl-1,2-dimethoxybenzene are the main VCs emitted from cottonseed meal and immobilized 95 to 100% of *M. incognita* J2s after 20 days of exposure and reduced gall formation and eggs on tomato in a greenhouse trial (Estupiñan-López et al., 2017). (Z)-3-hexenyl acetate, (Z)-3-hexen-1-ol and erucin selected from ru cola (*Eruca sativa*) volatilome killed *M. incognita* J2s in an in vitro test (Aïssani et al., 2015).

The VCs ascaridole and citronella, emitted from two medicinal plants citronella grass (Cymbopogon nardus) and Mexican tea (*Dysphania ambrosioides*), immobilized 46 to 79% of *M. incognita* J2s in vitro and reduced 19 to 37% of gall formation and 80% of eggs on tomato under greenhouse conditions (de Freitas Silva et al., 2020; Silva et al., 2020). Seeds of papaya fruit (*Carica papaya*) emitted VCs that killed 80% of *M. incognita* J2s in vitro and reduced root galls and nematode eggs by 70%. VCs from papaya seed were identified as vinyl acetate and phenylacetaldehyde (Gomes et al., 2020). Certainly, these results indicate that many plants can produce VCs that have nematicidal activity, and probably many more remain to be identified.

**Fungal volatile compounds against plant-parasitic nematodes**

Several fungal VCs have been evaluated against PPNs, mostly *Meloidogyne* spp. (Table 2). Non-pathogenic
Table 1. Overview of studies investigating the effect of plant volatile compounds on different plant-parasitic nematodes.

| Volatile compound producers | Identified volatile compounds | Experiment conditions | Target plant-parasitic nematodes | References |
|-----------------------------|------------------------------|-----------------------|----------------------------------|------------|
| Brassica                    | Glucosinolates and isothiocyanates | Field biofumigation   | *Meloidogyne incognita*, *M. javanica*, *Heterodera schachtii*, *Pratylenchus neglectus*, *Paratrichodorus allius* | Thierfelder and Friedt (1995), Potter et al. (1998), Lord et al. (2011) |
| White mustard (*Sinapis alba*) | Methyl sulfide, dimethyl disulfide | Field biofumigation   | *Tylenchulus semipenetrans* | Wang et al. (2009) |
| Brassica leaf               | 2-propenyl glucosinolate       | Field biofumigation   | *Globodera pallida* | Lord et al. (2011) |
| *Brassica juncea*, *Azadirachta indica*, *Canavalia ensiformis*, *Mucuna pruriens*, and *Cajanus cajan* | Alcohols and esters and sulfur containing compounds (mainly isothiocyanates) | In vitro and greenhouse | *M. incognita* | Barros et al. (2014) |
| Camellia seed cake          | 18 compounds were identified   | In vitro             | *M. javanica* | Yang et al. (2015) |
| *Eruca sativa*              | (Z)-3-hexenyl acetate, (Z)-3-hexen-1-ol and erucin | In vitro             | *M. incognita* | Aissani et al. (2015) |
| Cottonseed meal             | 2-methyl-1-butanol, 3-methyl-1-butanol, phenyl-ethylalcohol, benzene-1-ethyl-4methoxy (p-ethylanisole), and 4-ethyl-1,2-dimethoxybenzene | In vitro and greenhouse | *M. incognita* | Estupiñan-López et al. (2017) |
| Castor bean cake            | Phenol, 4-methylphenol, γ-decalactone, and skatole | In vitro and greenhouse | *M. incognita* | Pedroso et al. (2019) |
| Citronella (*Cymbopogon nardus* L.) or black pepper (*Piper nigrum* L.) leaves, broccoli shoots (*Brassica oleracea* L.) and Brazil nuts (*Bertholletia excelsa* Bonpl.) | Dimethyl disulfide and 3-pentanol | In vitro and greenhouse | *M. incognita* | Silva et al. (2018), da Silva et al. (2019) |
| Watercress (*Nasturtium officinale*) leaves and passion fruit (*Passiflora edulis*) seeds | 26 and 12 compounds were identified. 1-octanol had strong nematicidal activity | In vitro and greenhouse | *M. incognita* | Silva et al. (2020) |
| Seeds of papaya fruit (*Carica papaya*) | Vinyl acetate, phenylacetaldehyde and benzylacetoniitrile | In vitro and greenhouse | *M. incognita* | Gomes et al. (2020) |
| *Cymbopogon nardus* and *Dysphania ambrosioides* | Ascaridole and citronellal | In vitro and greenhouse | *M. incognita* | de Freitas Silva et al. (2020) |
Table 2. Overview of studies investigating the effect of fungal volatile compounds on different plant-parasitic nematodes.

| Volatile compound producers | Identified volatile compounds | Experiment conditions | Target plant-parasitic nematodes | References |
|-----------------------------|-------------------------------|----------------------|---------------------------------|------------|
| *Muscodor albus*            | Unidentified                  | In vitro             | *Meloidogyne chitwoodi*, *M. hapla*, *Paratrichodorus allius*, and *P. penetrans* | Riga et al. (2008) |
| *Trichoderma sp.* YMF 1.00416 | *1β*-vinylcyclopentane-1α,3α-diol, 6-pentyl-2H-pyran-2-one and 4-(2-hydroxyethyl) phenol | In vitro             | *Bursaphelenchus xylophilus* | Yang et al. (2012) |
| *Fusarium oxysporum* and *Fusarium solani* | Dioctyl disulfide (2-propyldecan-1-ol or 1-(2-hydroxyethoxy) tridecane); caryophyllene; 4-methyl-2,6-di-tert-butylphenol; and acoradiene | In vitro and greenhouse | *M. incognita* | Freire et al. (2012) |
| *Fusarium oxysporum*        | Unidentified                  | In vitro             | *M. exigua*                     | Costa et al. (2015) |
| Endophytic fungus *Daldinia cf. concentrica* | 3-methyl-1-butanol, (±)-2-methyl-1-butanol, 4-heptanone, and isoamyl acetate, | In vitro and greenhouse | *M. javanica*                   | Liarzi et al. (2016) |
| *Epicoccum nigrum* and *Schizophyllum commune* | Alcohols, esters, terpenes, and ketones | In vitro and greenhouse | *M. incognita*                   | Pimenta et al. (2017) |
| *Fusarium oxysporum* strain 21 | More than 28 volatile organic compounds were identified. | In vitro and greenhouse | *M. incognita*                   | Terra et al. (2017) |
| *Fusarium oxysporum* strain 21 | 2-methylbutyl acetate, 3-methylbutyl acetate, ethyl acetate, and 2-methylpropyl acetate | In vitro and greenhouse | *M. incognita*                   | Terra et al. (2018) |
| *Fusarium oxysporum* and *Fusarium solani* | 23 compounds belong to esters, alcohols, phenols, aldehydes, carboxylic acids and sesquiterpenes | In vitro and greenhouse | *M. incognita*                   | Estupiñan-López et al. (2018) |

*Fusarium oxysporum* not causing disease to plants have been used as biocontrol agents due to their suppression of plant pathogens such as *Fusarium wilt* (*Fusarium oxysporum*) and *Verticillium wilt* (*Verticillium dahliae*) on a wide host range including various vegetables, fruit, and ornamental trees (Mulero-Aparicio et al., 2019; Sajeena et al., 2020). Until now, VCs emitted from *Fusarium* spp. have been the most extensively studied. Among 35 fungi isolated from the coffee plant rhizosphere, including from *Meloidogyne exigua* eggs and egg masses on coffee roots, *Fusarium oxysporum* isolates 20a and 21 and an *F. solani* isolate caused 88 to 96% *M. incognita* J2 mortality. Also, *M. incognita* J2s lost their infectivity when exposed to *F. oxysporum* isolate 21 VCs which were identified as dioctyl disulfide; caryophyllene; 4-methyl-2,6-di-tert-butylphenol; and acoradiene (Freire et al., 2012). Another *F. oxysporum* isolate 26
isolated from *M. exigua* egg masses caused 94% immobility and 27% mortality to *M. exigua* J2s in vitro. However, the VCs were not identified in this study (Costa et al., 2015). In the studies of Terra et al. (2017, 2018), *Fusarium oxysporum* strain 21 was used to test the VCs effectiveness against *M. incognita*. The results indicated that VCs from *Fusarium oxysporum* strain 21 immobilized 100% of *M. incognita* J2s and reduced the infectivity of *M. incognita* J2s and reproduction by 70 and 65%, respectively. More than 28 VCs were identified in which 2-methylbutyl acetate, 3-methylbutyl acetate, ethyl acetate, and 2-methylpropyl acetate killed 80 to 100% of *M. incognita* J2s. Also, 3-methylbutyl acetate and ethyl acetate inhibited 90% of *M. incognita* egg hatching (Terra et al., 2017). However, only 2-methylbutyl acetate reduced gall formation by 22% compared to the control. Estupiñán-López et al. (2018) showed that VCs emitted from *F. oxysporum* isolate F63 and *F. solani* isolate F12 isolated from *M. paranaensis* egg masses caused 100% and 40 to 70% of immobility to *M. incognita* J2s in vitro at 25°C in the dark for six days, respectively. More than 50% of gall and egg reduction has been observed when *M. incognita* J2s were exposed to water containing fungal VCs prior to inoculation to tomato plants.

*Trichoderma* spp. are well-known as biocontrol agents of many soilborne pathogens and have been studied as biocontrol agents of PPNs as well (Reino et al., 2008; Sharon et al., 2011). However, little is known about VCs from *Trichoderma* spp. VCs from the unidentified *Trichoderma* sp. YMF 1.00416 isolated from soil in Yunnan, China were tested against *Bursaphelenchus xylophilus* in vitro, where 41.53% of *B. xylophilus* were killed (Yang et al., 2012). 1β-vinylcyclopentane-1α,3α-diol, 6-pentyl-2H-pyran-2-one and 4-(2-hydroxyethyl) phenol were identified as the main VCs from *Trichoderma* sp. YMF 1.00416. Among that, 6-pentyl-2H-pyran-2-one was toxic to *B. xylophilus* in 48 hr at 200 mg/L.

The VCs emitted from the endophytic fungus, *Muscodor albus*, isolated from cinnamon tree (*Cinnamomum zeylanicum*) caused more than 80% mortality to J2s of *M. chitwoodi*, *Paratrichodorus allius*, and *Pratylenchus penetrans* after 72 hr of exposure in vitro (Riga et al., 2008). VCs emitted from the endophytic fungus *Daldinia concentrica* (*Xylariaceae*) have shown the ability to antagonize various fungal pathogens (Liarzi et al., 2016). Volatile compounds from *Daldinia cf. concentrica* isolated from an olive tree (*Olea europaea* L) in Israel also reduced viability of *M. javanica* J2s by 67%. A mixture of 3-methyl-1-butanol, (±)-2-methyl-1-butanol, 4-heptanone, and isoamyl acetate (1:1:2:1 ratio) based on the VCs emitted from *Daldinia cf. concentrica* demonstrated a 99% reduction of *M. javanica* J2s viability and 87% inhibition of egg hatching. Soil application of this mixture showed a reduction in root galls and egg reproduction on tomato in a greenhouse trial (Liarzi et al., 2016). Another study showed that 28 fungal isolates from decaying wood released toxic VCs that immobilized from 77 to 100% of *M. incognita* J2s (Pimenta et al., 2017). Isolated fungi included *Epicoccum nigrum*, *Schizophyllum commune*, *Pestalotiopsis* sp., *Phanaerochaete chrysosporium*, *Nigrospora* sp., and *Lasiodiplodia* sp. and 20 VCs were identified, including alcohols, esters, terpenes, and ketones.

### Bacterial volatile compounds against plant-parasitic nematodes

A wide diversity of bacterial VCs have been investigated for the suppression of plant pathogens (Audrain et al., 2015; Bennett et al., 2012). However, few studies focused on managing PPNs (Table 3). Gu et al. (2007) investigated VCs of 200 bacterial isolates affecting *B. xylophilus*. Of these, seven isolates had a negative effect on *B. xylophilus* mobility within 24 hr. Among the 20 identified VCs, phenol, 2-octanol, benzaldehyde, benzeneacetaldehyde, decanal, 2-nonanone, 2-undecanone, cyclohexene, and dimethyl disulfide had nematicidal activity on *B. xylophilus*. Similarly, Huang et al. (2010) showed that VCs from *Bacillus megaterium* YFM3.25 inhibited egg hatching and killed *M. incognita* J2s after 24 hr of exposure. Also, these VCs reduced gall formation and egg mass production in a dose-dependent manner. Five bacterial isolates *Pseudochrobactrum saccharolyticum*, *Wautersiella falsenii*, *Proteus hauseri*, *Arthrobacter nicotianae*, and *Achromobacter xylosidans* emitted VCs that were toxic to *M. incognita* in vitro within 24 hr. Of the VC identified in these bacterial isolates, S-methyl thiobutyrate, butyl isovalerate, ethyl 3,3-dimethylacrylate, and 1-methoxy-4-methylbenzene showed more than 90% nematicidal activity against *M. incognita* (Xu et al., 2015). VCs from *Pseudomonas putida* BP25 were tested against *Radopholus similis* and showed more than 92% mortality (Agisha et al. 2019; Sheoran et al., 2015). Many VCs were identified such as 1-undecene; disulfide dimethyl; pyrazine, methyl-pyrazine, 2,5-dimethyl; isoamyl alcohol; pyrazine, and methyl; dimethyl trisulfide. but the effect of the individual VCs on *Radopholus similis* was not tested. Cheng et al. (2017) also tested the adverse effect of VCs from *Paenibacillus polymyxa* KM 2501 on *M. incognita*. This study showed that
Table 3. Overview of studies investigating the effect of bacterial volatile compounds on different plant-parasitic nematodes.

| Volatile compound producers | Identified volatile compounds | Experiment conditions | Target plant-parasitic nematodes | References |
|-----------------------------|------------------------------|-----------------------|----------------------------------|------------|
| Bacillus simplex, B. subtilis, B. weihenstephanensis, Stenotrophomonas maltophilia and Serratia marcescens | Terpineol, benzeneethanol, propanone, phenyl ethanone and nonane | In vitro | B. xylophilus | Gu et al. (2007) |
| Bacillus megaterium YFM3.25 | Benzeneacetaldehyde, 2-nonanone, decanal, 2-undecanone and dimethyl disulphide, phenyl ethanone, nonane, phenol, 3,5-dimethoxytoluene, 2,3-dimethyl-butanedinitrile and 1-thenyl-4-methoxy-benzene | In vitro and greenhouse | M. incognita | Huang et al. (2010) |
| Pseudomonas putida, Microbacterium sp., Bacillus methylotrophicus, Bacillus pumilus and Bacillus pumilus | Unidentified | In vitro | M. exigua | Costa et al. (2015) |
| Pseudomonas putida BP25 | As 1-Undecene; Disulfide dimethyl; Pyrazine, methyl-Pyrazine, 2,5-dimethyl-; Isoamyl alcohol; Pyrazine, methyl-; Dimethyl trisulfide | In vitro | Radopholus similis | Sheoran et al. (2015), Agisha et al. (2019) |
| Pseudochrobactrum saccharolyticum, Wautersiella falsenii, Proteus hauseri, Arthrobacter nicotianae, and Achromobacter xylosidans | Acetophenone, S-methyl thiobutyrate, dimethyl disulfide, ethyl 3,3-dimethylacrylate, nonan-2 one, 1-methoxy-4-methylbenzene, and butyl isovalerate | In vitro | M. incognita | Xu et al. (2015) |
| Paenibacillus polymyxa KM 2501 | Acetone, 2-heptanone, benzaldehyde, 2-nonanone, 2-nonanol, cyclopentasiloxane, decamethyl-, 11-dodeceny-2-one, 2-decanone, 2-decanol, 4-acetylbenzoic acid, furfural acetone, 2-undecanone, Acetic acid, [bis[(trimethylsilyl)oxy] phosphinyl]-, trimethylsilyl ester, 2-undecanol | In vitro | M. incognita | Cheng et al. (2017) |
the most active VCs to control *M. incognita* J2s were furfural acetone, 2-undecanol, 4-acetylbenzoic, and 2-decanol acid. Zhai et al. (2018) showed that VCs from *Pseudomonas putida* 1A00316 killed almost 100% of *M. incognita* J2s after 72 hr of exposure. From the VC profiles, dimethyl disulfide, 1-undecene, 2-nonanone, 2-octanone, (Z)-hexen-1-ol acetate, 2-undecanone, and 1-(ethenyloxy)-octadecane all inhibited egg hatching of *M. incognita*, and dimethyl disulfide, 2-nonanone, 2-octanone, (Z)-hexen-1-ol acetate, and 2-undecanone also showed nematicidal activity against *M. incognita* J2s. In another report, VCs emitted from *Bacillus* sp., *Paenibacillus* sp. and *Xanthomonas* sp. isolated from soil in a rice field caused more than 99% mortality of *M. graminicola* J2s in vitro and reduced gall incidence and egg production on rice in a greenhouse trial (Bui et al., 2020). However, VC identification from these bacterial isolates was not conducted in this study.

### The gap of knowledge and challenges

There is no standard procedure for testing the effects of VCs on PPNs in vitro. Each study has developed its own device where VCs were kept in closed conditions together with PPNs (two- or three-compartment petri dish, microtube in a vial, or microtube in a closed box). Each design has contributed a valuable test system to the ‘proof of concept’ of the potential use of VCs as bio-fumigants. However, the results might be different when VCs from one source are tested in different designs. Up to now, most of the studies used a two- or three-compartment petri dish for testing the microbial VCs in vitro (Kai et al., 2016). The advantages of this experimental design are simple, inexpensive, and separating the VC emitters and receivers. However, this design also created non-natural conditions that alternated the metabolisms of the tested microorganisms (Kai et al., 2016). For example, the high concentration of CO\(_2\) accumulation, 10 times higher than the ambient concentration (20°C, 84 μmol m\(^{-2}\)s\(^{-1}\) light, 16 h/8 h light/darkness), was the most obvious observation in this design (Kai and Piechulla, 2009). Therefore, standardizing in vitro testing conditions to evaluate the efficacy of VCs is needed. Also, many of the studies did not look at the recovery of nematodes, where following the exposure of VCs, the PPNs are removed from the exposure of VCs and their recovery in the absence of VCs is observed. Also, whether the efficacy is due to an individual VC or a blend of VCs, is often not known.

It is also very important to establish whether VCs are phytotoxic or not. Many researchers have shown that VCs from different microorganisms can actually promote plant growth (Hung et al., 2013; Lee et al., 2014; Nieto-Jacobo et al., 2017; Park et al., 2015; Ryu et al., 2003; Tahir et al., 2017), whereas other studies have shown that VCs from various microorganisms can cause phytotoxicity (Blom et al., 2011; Hung et al., 2013; Lee et al., 2014; Vespermann et al., 2007; Wenke et al., 2012). Recently, Bui et al. (2019) indicated that bacterial VCs inhibited rice germination in vitro but not *in planta*, probably because the concentration of VCs was higher in in vitro conditions than in *in planta* conditions. This obviously applies to nematicidal efficacy as well, as in vitro studies typically employ much higher concentrations than *in planta* studies. Therefore, it is important to keep in mind that in vitro studies, no matter how promising, only indicate potential, and by no means will guarantee that a certain compound will be efficacious in a greenhouse or field. Also, VCs that are phytotoxic are not necessarily bad and may have potential as
herbicidal soil fumigants, as long as they are applied sufficiently long before the crop is planted.

Although VCs from plants and microorganisms may constitute a more sustainable approach and reduce the use of synthetic chemical pesticides, potential adverse effects of VCs on human health, the environment and the soil ecosystem also need to be addressed, as biological products are not by definition safer than chemical products. For instance, Bahlai et al. (2010) showed that organic approved insecticides in Canada (Superior 70 oil® (UAP) and BotaniGard® (Laverlam)) had more adverse effects on natural enemies (Asian lady beetle Harmonia axyridis and insidious flower bug Orius insidiosus) in the laboratory and field conditions than novel synthetic insecticides. However, as plants and microorganisms have been co-existing with humans and emitting VCs for millions of years, it is more likely that VCs emitted from plants and microorganisms are safe for human health, the environment, and the soil ecosystem. For instance, the effects of VCs emitted from the fungus Muscodor albus on human health and the environment were studied and no harmful potential was detected (Tilocca et al., 2020).

The mechanisms of VC emission from microorganisms are not clearly understood yet, but some have suggested that VCs are waste products in the microbial lifecycle (Schulz-Bohm et al., 2017). Cheng et al. (2016) and Ossowicki et al. (2017) demonstrated that the production of VCs was triggered by the GaC-A/GaC-S two-component regulatory system in bacteria. New biotechnology techniques such as gene editing may help to better understand the mechanisms of VC emission, and potentially to manipulate microbes to more efficiently release beneficial VCs.

Microbial VCs have also been reported to induce plant resistance to pathogens (He et al., 2006; Huang et al., 2012; Kottbo et al., 2015; Lee et al., 2012; Naznin et al., 2014; Park et al., 2013; Raza et al., 2016). In these studies, the mechanism of induced resistance by microbial VCs involves salicylic acid or jasmonic acid/ethylene signaling pathways, similar to the mechanisms of induced resistance by plant growth-promoting microbes in dicot and monocot plants (Balmer et al., 2013; Pieterse et al., 2014). Nonetheless, the exact mechanisms of VCs inducing plant resistance, or their nematicidal mode of action, against PPNs are still unknown. Cheng et al. (2017) suggested that VCs could kill PPNs by affecting the nervous system, surface coat, intestine, pharynx, or other tissues of PPNs. Likely, different VCs have different modes of action as well, and while certain VCs may be nematode-specific, other VCs like isothiocyanates (ITCs), which are produced by glucosinolate-containing plants, are identical to chemical fumigants like metam, and have a broad-spectrum biocidal activity, with a multi-site mode of action.

Currently, several VCs have been shown to be able to control PPNs in the laboratory and sometimes greenhouse conditions. However, field application of VCs is still in its infancy (Farag et al., 2013), and only a few studies have demonstrated success in applying VCs to induce plant resistance against bacterial pathogens and insects on cucumber and pepper under field conditions (Choi et al., 2014; Song and Ryu, 2013). Even if efficacy can be demonstrated in the field, many hurdles remain, not in the least the need to produce or synthesize commercial and cost-effective quantities of VCs. In addition, there will also be a need for technology and equipment to apply VCs, similar to the equipment that is currently used to apply chemical fumigants.

Conclusions

Evidence is growing that plant and microbial volatile compounds have potential as a more environmentally friendly and ecosystem sustainable alternative to chemical soil fumigants. An increasing number of VCs emitted from plants and microorganisms are studied and have shown nematicidal activity in vitro and in greenhouse conditions. Field studies are still few and far between, and also the mechanisms of VC emission as well as their effects on host plants, plant-parasitic nematodes, the ecosystem, the environment, and human health are still not well-understood. While we do not claim to have covered all current knowledge, we hope that this review of VCs with regard to PPNs will help to stimulate more research into their use as a potential alternative source of soil fumigants.

References

Agisha, V. N., Kumar, A., Eapen, S. J., Sheoran, N. and Suseelabhai, R. 2019. Broad-spectrum antimicrobial activity of volatile organic compounds from endophytic Pseudomonas putida BP25 against diverse plant pathogens. Biocontrol Science and Technology 29:1069–89.

Aissani, N., Urgeghe, P. P., Oplos, C., Saba, M., Tocco, G., Petretto, G. L., Eloh, K., Menkissoglu-Spiroudi, U., Ntalli, N. and Caboni, P. 2015. Nematicidal activity of the volatilome of Eruca sativa on Meloidogyne incognita. Journal of Agricultural and Food Chemistry 63:6120–5.
Audrain, B., Farag, M. A., Ryu, C. M. and Ghigo, J. M. 2015. Role of bacterial volatile compounds in bacterial biocontrol. FEMS Microbiology Reviews 39:222–33.

Bahrai, C. A., Xue, Y., McCreary, C. M., Schaafsma, A. W. and Hallett, R. H. 2010. Choosing organic pesticides over synthetic pesticides may not effectively mitigate environmental risk in soybeans. PLoS ONE 5:e11250, available at: https://doi.org/10.1371/journal.pone.0011250.

Balmer, D., Planchamp, C. and Mauch-Mani, B. 2013. On the move: induced resistance in monocots. Journal of Experimental Botany 64:1249–61.

Barros, A. F., Campos, V. P., da Silva, J. C. P., Pedroso, M. P., Medeiros, F. H. V., Pozza, E. A. and Reale, A. L. 2014. Nematicidal activity of volatile organic compounds emitted by Brassica juncea, Azadirachta indica, Canavalia ensiformis, Mucuna pruriens and Cajanus cajan against Meloidogyne incognita. Applied Soil Ecology 80:34–43.

Bennett, J. W., Hung, R., Lee, S. and Padhi, S. 2012. “18 Fungal and bacterial volatile organic compounds: an overview and their role as ecological signaling agents”, In Hock, B. (Ed.), Fungal Associations. The Mycota (A comprehensive treatise on fungi as experimental systems for basic and applied research), vol 9 Springer, Berlin and Heidelberg, pp. 373–93.

Bernard, G. C., Egnin, M. and Bonsi, C. 2017. “The impact of plant-parasitic nematodes on agriculture and methods of control”, In Manjur, S. A. and Mahamood, M. (Eds), Nematology-concepts, Diagnosis and Control IntechOpen, London, pp. 121–51, doi: 10.5772/intechopen.68958.

Blom, D., Fabbri, C., Eberl, L. and Weisskopf, L. 2011. Volatile-mediated killing of Arabidopsis thaliana by bacteria is mainly due to hydrogen cyanide. Applied and Environmental Microbiology 77:1000–8.

Brennan, R. J. B., Glaze-Corroran, S., Robert, W. I. C. K. and Hashemi, M. 2020. Biofumigation: an alternative strategy for the control of plant parasitic nematodes. Journal of Integrative Agriculture 19:1680–90.

Bui, H. X., Hadil, B. A., Oliva, R. and Schroeder, N. E. 2020. Beneficial bacterial volatile compounds for the control of root-knot nematode and bacterial leaf blight on rice. Crop Protection 135:104792, available at: https://doi.org/10.1016/j.cropro.2019.04.016.

Cheng, W., Yang, J., Nie, Q., Huang, D., Yu, C., Zheng, L., Cai, M., Thomashow, L. S., Weller, D. M., Yu, Z. and Zhang, J. 2017. Volatile organic compounds from Paenibacillus polymyxa KM2501-1 control Meloidogyne incognita by multiple strategies. Scientific Reports 7:1–11.

Cheng, X., Cordovez, V., Etalo, D. W., van der Voort, M. and Raaijmakers, J. M. 2016. Role of the GacS sensor kinase in the regulation of volatile production by plant growth-promoting Pseudomonas fluorescens SBW25. Frontiers in Plant Science 7:1706, doi: 10.3389/fpls.2016.01706.

Choi, H. K., Song, G. C., Yi, H. S. and Ryu, C. M. 2014. Field evaluation of the bacterial volatile derivative 3-pentanol in priming for induced resistance in pepper. Journal of Chemical Ecology 40:882–92.

Clarke, D. B. 2010. Glucosinolates, structures and analysis in food. Analytical Methods 2:310–25.

Clay, L., Perkins, K., Motallebi, M., Plastina, A. and Farmaha, B. S. 2020. The perceived benefits, challenges, and environmental effects of cover crop implementation in South Carolina. Agriculture 10:372, available at: https://doi.org/10.3390/agriculture10090372.

Costa, L. S. A. S., Campos, V. P., Terra, W. C. and Pfennling, L. H. 2015. Microbiota from Meloidogyne exigua egg masses and evidence for the effect of volatiles on infective juvenile survival. Nematology 17:715–24.

da Silva, J. C. P., Campos, V. P., Barros, A. F., Pedroso, L. A., de Freitas Silva, M., de Souza, J. T., Pedroso, M. P. and de Medeiros, F. H. V. 2019. Performance of volatiles emitted from different plant species against juveniles and eggs of Meloidogyne incognita. Crop Protection 116:196–203, available at: https://doi.org/10.1016/j.cropro.2018.11.006.

Dangi, S. R., Tirado-Corbalá, R., Gerik, J. and Hanson, B. D. 2017. Effect of long-term continuous fumigation on soil microbial communities. Agronomy 7:37.

Daryanto, S., Fu, B., Wang, L., Jacinthe, P. A. and Zhao, W. 2018. Quantitative synthesis on the ecosystem services of cover crops. Earth-Science Reviews 185:357–73.

De Cal, A., Martinez-Treceno, A., Salto, T., López-Aranda, J. M. and Melgarejo, P. 2005. Effect of chemical fumigation on soil fungal communities in Spanish strawberry nurseries. Applied Soil Ecology 28:47–56.

de Freitas Silva, M., Campos, V. P., Barros, A. F., da Silva, J. C. P., Pedroso, M. P., de Jesus Silva, F., Gomes, V. A. and Justino, J. C. 2020. Medicinal plant volatiles applied against the root-knot nematode Meloidogyne incognita. Crop Protection 130:105057, available at: https://doi.org/10.1016/j.cropro.2019.105057.

Deseaeger, J., Dickson, D. W. and Locascio, S. J. 2017. Methyl bromide alternatives for control of root-knot nematode (Meloidogyne spp.) in tomato production in Florida. Journal of Nematology 49:140–9.

Dudareva, N., Klempien, A., Muhlemann, K. J. and Kaplan, I. 2013. Biosynthesis, function and metabolic engineering of plant volatile organic compounds. New Phytologist 198:16–32.

Dutta, T. K., Khan, M. R. and Phani, V. 2019. Plant-parasitic nematode management via biofumigation using brassica and non-brassica plants: current status and future prospects. Current Plant Biology 17:17–32.

Effmer, U., Kalderás, J., Warnke, R. and Piechulla, B. 2012. Volatile mediated interactions between bacteria and fungi in the soil. Journal of Chemical Ecology 38:665–703.

Estupiñan-López, L., Campos, V. P., da Silva Júnior, J. C., Pedroso, M. P., Terra, W. C., da Silva, J. C. P. and...
Volatile compounds and biocontrol: Bui and Desaeger

de Paula, L. L. 2018. Volatile compounds produced by Fusarium spp. isolated from Meloidogyne paranaensis egg masses and corticous root tissues from coffee crops are toxic to Meloidogyne incognita. Tropical Plant Pathology 43:183–93.

Estupiñan-López, L., Campos, V. P., Silva, A. P., Barros, A. F., Pedroso, M. P., Silva, J. C. and Terra, W. C. 2017. Volatile organic compounds from cottonseed meal are toxic to Meloidogyne incognita. Tropical Plant Pathology 42:443–50.

Farag, M. A., Zhang, H. and Ryu, C. M. 2013. Dynamic chemical communication between plants and bacteria through airborne signals: induced resistance by bacterial volatiles. Journal of Chemical Ecology 39:1007–18.

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. and Silva, J. R. C. 2012. Volatile substances produced by Fusarium oxysporum from coffee rhizosphere and other microbes affect Meloidogyne incognita and Arthrobotrys conoides. Journal of Nematology 44:321–8.

Gomes, V. A., Campos, V. P., da Silva, J. C. P., de Jesus Silva, F., de Freitas Silva, M. and Pedroso, M. P. 2020. Activity of papaya seeds (Carica papaya) against Meloidogyne incognita as a soil biofumigant. Journal of Pest Science 93:783–92.

Grabau, Z. J., Maung, Z. T. Z., Noyes, D. C., Baas, D. G., Werling, B. P., Brainard, D. C. and Melakeberhan, H. 2017. Effects of cover crops on Pratylenchus penetrans and the nematode community in carrot production. Journal of Nematology 49:114–23.

Gu, Y. Q., Mo, M. H., Zhou, J. P., Zou, C. S. and Zhang, K. Q. 2007. Evaluation and identification of potential organic nematicidal volatiles from soil bacteria. Soil Biology and Biochemistry 39:2567–75.

Hafez, S. L. and Sundararaj, P. 2009. Evaluation of suppressive effect of trap crops on Heterodera schachtii and Meloidogyne chitwoodi under greenhouse conditions. Nematologia Mediterranea. 37:245-8.

He, P. Q., Tian, L., Chen, K. S., Hao, L. H. and Li, G. Y. 2006. Induction of volatile organic compounds of Lycopersicon esculentum Mill. and its resistance to Botrytis cinerea Pers. by burdock oligosaccharide. Journal of Integrative Plant Biology 48:550–7.

Huang, C. J., Tsay, J. F., Chang, S. Y., Yang, H. P., Wu, W. S. and Chen, C. Y. 2012. Dimethyl disulfide is an induced systemic resistance elicitor produced by Bacillus cereus C1L. Pest Management Science 68:1306–10.

Huang, Y., Xu, C., Ma, L., Zhang, K., Duan, C. and Mo, M. 2010. Characterisation of volatiles produced from Bacillus megaterium YFM3. 25 and their nematocidal activity against Meloidogyne incognita. European Journal of Plant Pathology 126:417–22.

Hung, R., Lee, S. and Bennett, J. W. 2013. Arabidopsis thaliana as a model system for testing the effect of Trichoderma volatile organic compounds. Fungal Ecology 6:19–26.

Insam, H. and Seewald, M. S. 2010. Volatile organic compounds (VOCs) in soils. Biology and Fertility of Soils 46:199–213.

Kai, M. and Piechulla, B. 2009. Plant growth promotion due to rhizobacterial volatiles – an effect of CO2? FEBS letters 583:3473–7.

Kai, M., Effmert, U. and Piechulla, B. 2016. Bacterial-plant-interactions: approaches to unravel the biological function of bacterial volatiles in the rhizosphere. Frontiers in Microbiology 7:108, available at: https://doi.org/10.3389/fmicb.2016.00108.

Kai, M., Haustein, M., Molina, F., Petri, A., Scholz, B. and Piechulla, B. 2009. Bacterial volatiles and their action potential. Applied Microbiology and Biotechnology 81:1001–12.

Kottb, M., Gigolashvili, T., Großkinsky, D. K. and Piechulla, B. 2015. Trichoderma volatiles effecting Arabidopsis: from inhibition to protection against phytopathogenic fungi. Frontiers in Microbiology 6:995, available at: https://doi.org/10.3389/fmicb.2015.00995.

Kruger, D. H. M., Fourie, J. C. and Malan, A. P. 2013. Cover crops with biofumigation properties for the suppression of plant-parasitic nematodes: a review. South African Journal of Enology and Viticulture 34:287–95.

Lee, B., Farag, M. A., Park, H. B., Kloepper, J. W., Lee, S. H. and Ryu, C. M. 2012. Induced resistance by a long-chain bacterial volatile: elicitation of plant systemic defense by a C13 volatile produced by Paenibacillus polymyxa. PLoS ONE 7:e48744, available at: https://doi.org/10.1371/journal.pone.0048744.

Lee, S., Hung, R., Schink, A., Mauro, J. and Bennett, J. W. 2014. Arabidopsis thaliana for testing the phytotoxicity of volatile organic compounds. Plant Growth Regulation 74:177–86.

Liarzi, O., Bucki, P., Miyara, S. B. and Ezra, D. 2016. Bioactive volatiles from an endophytic Deladinia cf. concentrica isolate affect the viability of the plant parasitic nematode Meloidogyne javanica. PLoS ONE 11:e0168437, available at: https://doi.org/10.1371/journal.pone.0168437.

Lord, J. S., Lazzeri, L., Atkinson, H. J. and Urwin, P. E. 2011. Biofumigation for control of pale potato cyst nematodes: activity of brassica leaf extracts and green manures on Globodera pallida in vitro and in soil. Journal of Agricultural and Food Chemistry 59:7882–90.

Martin, F. N. 2003. Development of alternative strategies for management of soilborne pathogens currently controlled with methyl bromide. Annual Review of Phytopathology 41:325–50.

Matthiessen, J. N., Warton, B. and Shackleton, M. A. 2004. The importance of plant maceration and water addition in achieving high Brassica-derived isothiocyanate levels in soil. Agroindustria 3:277, available at: http://hdl.handle.net/102.100.100/189079?index=1.

Mazzola, M., Hewavitharana, S. S. and Strauss, S. L. 2015. Brassica seed meal soil amendments transform
the rhizosphere microbiome and improve apple production through resistance to pathogen reinfestation. Phytopathology 105:460–9.

Monfort, W. S., Csinos, A. S., Desaeger, J., Seebold, K., Webster, T. M. and Díaz-Perez, J. C. 2007. Evaluating Brassica species as an alternative control measure for root-knot nematode (M. incognita) in Georgia vegetable plasticulture. Crop Protection 26:1359–68.

Mulero-Aparicio, A., Agustí-Brisach, C., Varo, Á., López-Escudero, F. J. and Trapero, A. 2019. A non-pathogenic strain of Fusarium oxysporum as a potential biocontrol agent against Verticillium wilt of olive. Biological Control 139:104045, available at: https://doi.org/10.1016/j.biocontrol.2019.104045.

Naznin, H. A., Kiyohara, D., Kimura, M., Miyazawa, M., Shimizu, M. and Hyakumachi, M. 2014. Systemic resistance induced by volatile organic compounds emitted by plant growth-promoting fungi in Arabidopsis thaliana. PLoS ONE 9:e86882, available at: doi.org/10.1371/journal.pone.0086882.

Nieto-Jacobo, M. F., Steyaert, J. M., Salazar-Badillo, F. B., Nguyen, D. V., Rostás, M., Braithwaite, M., De Souza, J. T., Jimenez-Bremont, J. F., Ohkura, M., Stewart, A. and Mendoza-Mendoza, A. 2017. Environmental growth conditions of Trichoderma spp. affects indole acetic acid derivatives, volatile organic compounds, and plant growth promotion. Frontiers in Plant Science 8:102, doi: 10.3389/fpls.2017.00102.

Ossowicki, A., Jafra, S. and Garbeva, P. 2017. The antimicrobial volatile power of the rhizospheric isolate Pseudomonas donghuensis P482. PLoS ONE 12:e0174362, doi: 10.1371/journal.pone.0174362.

Park, H. B., Lee, B., Kloepper, J. W. and Ryu, C. M. 2013. One shot-two pathogens blocked: Exposure of Arabidopsis to hexadecane, a long chain volatile organic compound, confers induced resistance against both Pectobacterium carotovorum and Pseudomonas syringae. Plant Signaling and Behavior 24619:1, doi: 10.4161/psb.24619.

Park, Y. S., Dutta, S., Ann, M., Raaijmakers, J. M. and Park, K. 2015. Promotion of plant growth by Pseudomonas fluorescens strain SS101 via novel volatile organic compounds. Biochemical and Biophysical Research Communications 461:361–5.

Pedroso, L. A., Campos, V. P., Pedroso, M. P., Barros, A. F., Freire, E. S. and Resende, F. M. 2019. Volatile organic compounds produced by castor bean cake incorporated into the soil exhibit toxic activity against Meloidogyne incognita. Pest Management Science 75:476–83.

Pieterse, C. M., Zamioudis, C., Berendse, R. L., Weller, D. M., Van Wees, S. C. and Bakker, P. A. 2014. Induced systemic resistance by beneficial microbes. Annual Review of Phytopathology 52:347–75.

Pimenta, L., Ferreira, M. A., Pedroso, M. P. and Campos, V. P. 2017. Wood-associated fungi produce volatile organic compounds toxic to root-knot nematode. Scientia Agricola 74:303–10.

Potter, M. J., Davies, K. and Rathjen, A. J. 1998. Suppressive impact of glucosinolates in Brassica vegetative tissues on root lesion nematode Pratylenchus neglectus. Journal of Chemical Ecology 24:67–80.

Rahman, L. and Somers, T. 2005. Suppression of root-knot nematode (Meloidogyne javanica) after incorporation of Indian mustard cv. Nemfix as green manure and seed meal in vineyards. Australasian Plant Pathology 34:77–83.

Raupach, G. S. and Kloepper, J. W. 2000. Biocontrol of cucumber diseases in the field by plant growth-promoting rhizobacteria with and without methyl bromide fumigation. Plant Disease 84:1073–5.

Raza, W., Wang, J., Wu, Y., Ling, N., Wei, Z., Huang, Q. and Shen, Q. 2016. Effects of volatile organic compounds produced by Bacillus amyloliquefaciens on the growth and virulence traits of tomato bacterial wilt pathogen Ralstonia solanacearum. Applied Microbiology and Biotechnology 100:7639–50.

Reino, J. L., Guerrero, R. F., Hernández-Galán, R. and Collado, I. G. 2008. Secondary metabolites from species of the biocontrol agent Trichoderma. Phytochemistry Reviews 7:89–123.

Riga, E., Lacey, L. A. and Guerra, N. 2008. Muscodor albus, a potential biocontrol agent against plant-parasitic nematodes of economically important vegetable crops in Washington State. Biological Control 46:380–5.

Rosskopf, E. N., Chellemi, D. O., Kokalis-Burelle, N. and Church, G. T. 2005. Alternatives to methyl bromide: A Florida perspective. Plant Health Progress 6:19, doi: 10.1094/APSnetFeature/2005-0605.

Ryu, C. M., Farag, M. A., Hu, C. H., Reddy, M. S., Wei, H. X., Paré, P. W. and Kloepper, J. W. 2003. Bacterial volatiles promote growth in Arabidopsis. Proceedings of the National Academy of Sciences 100:4927–32.

Sajeena, A., Nair, D. S. and Sreepavan, K. 2020. Non-pathogenic Fusarium oxysporum as a biocontrol agent. Indian Phytopathology 73:177–83.

Sánchez-Moreno, S., Jiménez, L., Alonso-Prados, J. L. and García-Baudin, J. M. 2010. Nematodes as indicators of fumigant effects on soil food webs in straw-berry crops in Southern Spain. Ecological Indicators 10:148–56.

Schmidt, R., Cordovez, V., De Boer, W., Raaijmakers, J. and Garbeva, P. 2015. Volatile affairs in microbial interactions. The ISME Journal 9:2329–35.

Schroeder, N. E. and MacGuidwin, A. E. 2010. Mortality and behavior in Heterodera glycines juveniles following exposure to isothiocyanate compounds. Journal of Nematology 42:194–200.

Schulz-Bohm, K., Martín-Sánchez, L. and Garbeva, P. 2017. Microbial volatiles: small molecules with an important role in plant-microbe interactions and ecological relevance. Journal of Nematology 51:1–13.
role in intra-and inter-kingdom interactions. Frontiers in Microbiology 8:2484, available at: https://doi.org/10.3389/fmicb.2017.02484.

Sharon, E., Chet, I. and Spiegel, Y. 2011. “Trichoderma as a biological control agent”, In Davies, K. and Spiegel, Y. (Eds), Biological Control of Plant-parasitic Nematodes: Progress in Biological Control, Vol. 11 Springer, Dordrecht, pp. 183–201.

Sheoran, N., Nadakakath, A. V., Munjal, V., Kundu, A., Subaharan, K., Venugopal, V., Rajamma, S., Eapen, S. J. and Kumar, A. 2015. Genetic analysis of plant endophytic Pseudomonas putida BP25 and chemoprofiling of its antimicrobial volatile organic compounds. Microbiological Research 173:66–78.

Silva, J. C. P., Campos, V. P., Barros, A. F., Pedroso, M. P., Terra, W. C., Lopez, L. E. and de Souza, J. T. 2018. Plant volatiles reduce the viability of the root-knot nematode Meloidogyne incognita either directly or when retained in water. Plant Disease 102:2170–9.

Silva, M. F., Campos, V. P., Barros, A. F., Terra, W. C., Pedroso, M. P., Gomes, V. A., Ribeiro, C. R. and Silva, F. J. 2020. Volatile emissions of watercress (Nasturtium officinale) leaves and passion fruit (Passiflora edulis) seeds against Meloidogyne incognita. Pest Management Science 76:1413–21.

Smith, H. J., Gray, F. A. and Koch, D. W. 2004. Reproduction of Heterodera schachtii Schmidt on resistant mustard, radish, and sugar beet cultivars. Journal of Nematology 36:123–30.

Song, G. C. and Ryu, C. M. 2013. Two volatile organic compounds trigger plant self-defense against a bacterial pathogen and a sucking insect in cucumber under open field conditions. International Journal of Molecular Sciences 14:9803–19.

Tahir, H. A., Gu, Q., Wu, H., Raza, W., Hanif, A., Wu, L., Colman, M. V. and Gao, X. 2017. Plant growth promotion by volatile organic compounds produced by Bacillus subtilis SYST2. Frontiers in Microbiology 8:171, available at: https://doi.org/10.3389/fmicb.2017.00171.

Terra, W. C., Campos, V. P., Pedroso, M. P., da Costa, A. L., Freire, E. S., de Pinto, I. P., da Silva, J. C. P., Lopez, L. E. and Santos, T. C. N. 2017. Volatile molecules of Fusarium oxysporum strain 21 are retained in water and control Meloidogyne incognita. Biological Control 112:34–40.

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., Smant, G. and Oliveira, D. F. 2018. Volatile organic molecules from Fusarium oxysporum strain 21 with nematicidal activity against Meloidogyne incognita. Crop Protection 106:125–31.

Thierfelder, A. and Friedt, W. 1995. Development of novel rapeseed varieties (Brassica napus) resistant against beet cyst nematodes (Heterodera schachtii). Organising Committee of the Ninth International Rapeseed Conference Cambridge, ed. Ninth International Rapeseed Congress (GCIRC), Cambridge, pp. 1208–1210.

Tilocca, B., Cao, A. and Migheli, Q. 2020. “Scent of a Killer: microbial volatilome and its role in the biological control of plant pathogens”, Frontiers in Microbiology, 11:41, doi: 10.3389/fmicb.2020.00041.

Vespermann, A., Kai, M. and Pechulla, B. 2007. Rhizobacterial volatiles affect the growth of fungi and Arabidopsis thaliana. Applied and Environmental Microbiology 73:5639–41.

Vivaldo, G., Masi, E., Taiti, C., Caldarelli, G. and Mancuso, S. 2017. The network of plants volatile organic compounds. Scientific Reports 7:1–18.

Wang, D., Rosen, C., Kinkel, L., Cao, A., Tharayil, N. and Gerik, J. 2009. Production of methyl sulfide and dimethyl disulfide from soil-incorporated plant materials and implications for controlling soilborne pathogens. Plant and Soil 324:185–97.

Watson, T. T., Nelson, L. M., Neilsen, D., Neilsen, G. H. and Forge, T. A. 2017. Soil amendments influence Pratylenchus penetrans populations, beneficial rhizosphere microorganisms, and growth of newly planted sweet cherry. Applied Soil Ecology 117:212–20.

Xu, Y. Y., Lu, H., Wang, X., Zhang, K. Q. and Li, G. H. 2015. Effect of volatile organic compounds from bacteria on nematodes. Chemistry and Biodiversity 12:1415–21.

Yang, X., Wang, X., Wang, K., Su, L., Li, H., Li, R. and Shen, Q. 2015. The nematicidal effect of Camellia seed cake on root-knot nematode Meloidogyne javanica of banana. PloS ONE 10:e0119700, available at: https://doi.org/10.1371/journal.pone.0119700.

Yang, Z., Yu, Z., Lei, L., Xia, Z., Shao, L., Zhang, K. and Li, G. 2012. Nematicidal effect of volatiles produced by Trichoderma sp. Journal of Asia-Pacific Entomology 15:647–50.

Zhai, Y., Shao, Z., Cai, M., Zheng, L., Li, G., Huang, D., Cheng, W., Thomashow, L. S., Weller, D. M., Yu, Z. and Zhang, J. 2018. Multiple modes of nematode control by volatiles of Pseudomonas putida 1A00316 from Antarctic soil against Meloidogyne incognita. Frontiers in Microbiology 9:253, doi: 10.3389/fmicb.2018.00253.