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MARSCHNER REVIEW

Root-emitted volatile organic compounds: can they mediate belowground plant-plant interactions?

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Abstract

Background Aboveground, plants release volatile organic compounds (VOCs) that act as chemical signals between neighbouring plants. It is now well documented that VOCs emitted by the roots in the plant rhizosphere also play important ecological roles in the soil ecosystem, notably in plant defence because they are involved in interactions between plants, phytophagous pests and organisms of the third trophic level. The roles played by root-emitted VOCs in between- and within-plant signalling, however, are still poorly documented in the scientific literature.

Scope Given that (1) plants release volatile cues mediating plant-plant interactions aboveground, (2) roots can detect the chemical signals originating from their neighbours, and (3) roots release VOCs involved in biotic interactions belowground, the aim of this paper is to discuss the roles of VOCs in between- and within-plant signalling belowground. We also highlight the technical challenges associated with the analysis of root-emitted VOCs and the design of experiments targeting volatile-mediated root-root interactions.

Conclusions We conclude that root-root interactions mediated by volatile cues deserve more research attention and that both the analytical tools and methods developed to study the ecological roles played by VOCs in interplant signalling aboveground can be adapted to focus on the roles played by root-emitted VOCs in between- and within-plant signalling.

Keywords Plant-plant signalling · Volatile organic compounds (VOCs) · Plant root volatile emission · Rhizosphere · Root-root interactions

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Introduction

In nature, plants continuously interact with other living organisms that share their environment, notably via the synthesis and release of volatile organic compounds (VOCs). VOCs can be produced by various plant organs

(leaves, flowers, fruits and roots) and have been shown to be key mediators in biotic interactions both aboveground and belowground (Dudareva et al. 2006; Peñuelas et al. 2014) (Fig. 1). VOCs produced by plants aboveground are dominated by four chemical families originating from the following biosynthetic pathways: terpenoids (mevalonic acid [MVA] and methylerythritol phosphate [MEP] pathways); fatty acid derivatives (lipoxygenase [LOX] pathway); benzenoid and phenylpropanoid compounds (shikimic acid pathway); and amino acid derivatives (Maffei 2010; Baldwin 2010; Dudareva et al. 2013). These compounds are low molecular weight molecules that can be emitted either constitutively (e.g., floral volatiles attracting pollinators) or in response to biotic (Dudareva et al. 2006; Unsicker et al. 2009; Rasmann et al. 2012; Dudareva et al. 2013) or abiotic stress (Gouinguené and Turlings 2002; Loreto and Schnitzler 2010). Because they can be toxic for plant pathogens (Holopainen 2004; Matsui et al. 2006) and are able to repel insect herbivores (De Moraes et al. 2001), these compounds can act in direct plant defences against pests. In addition, because they are able to attract organisms of the third trophic level (parasitoids, entompathogenic nematodes, etc.) both aboveground (Turlings et al. 1990; De Moraes et al. 1998) and belowground (Rasmann et al. 2005), they are also involved in indirect plant defences. Once released into the air surrounding a plant, VOCs can be perceived by other parts of the same plant (Heil and Silva Bueno 2007; Frost et al. 2007) or by proximate neighbours that eavesdrop on the volatile signals emitted by a damaged plant (Karban et al. 2000). In response to the volatile blends released by emitters, receivers can start expressing genes and synthesise secondary metabolites involved in plant defences (Shulaev et al. 1997; Arimura et al. 2000a; Sugimoto et al. 2014) or can prime their defences against pests (Engelberth et al. 2004; Ton et al. 2006; Heil and Kost 2006), suggesting that VOCs play key roles in mediating within- and between-plant signalling aboveground (Heil and Ton 2008; Heil and Karban 2010) (Fig. 2).

As plants growing next to each other compete for light aboveground and for heterogeneously distributed resources (water and nutrients) belowground, they use specific signals to detect the presence of neighbours and adjust their growth accordingly. Aboveground, both the variations in red/far-red and blue light levels in the plant's canopy detected by photoreceptors (phytochromes and cryptochromes) (Ballaré 1999) and the volatile compounds emitted by plants in the atmosphere

(Ninkovic 2003; Pierik et al. 2003) are signals that enable plants to detect the presence of proximate neighbours. With regard to the use of volatile cues, it has been shown that tobacco plants must be able to perceive the phytohormone ethylene in order to develop a shade-avoidance phenotype (Pierik et al. 2003), and that barley plants allocated significantly more biomass to their roots when they were exposed to the volatiles emitted by undamaged conspecifics belonging to another cultivar (Ninkovic 2003). In addition, airborne volatile blends can help parasitic plants (*Cuscuta pentagona* Engelm.) to select and locate a suitable host (Runyon et al. 2006).

Belowground, root systems can exchange carbon and defence-related signals through common mycorrhizal networks (Simard et al. 1997; Song et al. 2010; Johnson and Gilbert 2015). Plants also release a wide array of molecules via root exudation in the rhizosphere that play numerous roles, particularly in plant nutrition and biotic interactions between plant roots and soil organisms (Bertin et al. 2003; Walker et al. 2003; Haichar et al. 2014; Zhang et al. 2015). Depending on their size, these molecules can be divided into two classes of compounds: low molecular weight (amino acids, organic acids, sugars, phenolics and various other secondary metabolites) and high molecular weight (polysaccharides and proteins) exudates (Walker et al. 2003; Haichar et al. 2014). Once released by plant roots into the rhizosphere, some of these molecules can have negative (phytotoxins, autoinhibition, development of associations with parasitic plants) or positive effects (resistance to herbivores and root detection) on neighbouring plants and can affect plant growth directly (production of phytotoxins) or indirectly (alteration of soil chemistry, microbial populations and nutrient availability) (Inderjit and Weiner 2001; Perry et al. 2007; Weston et al. 2012; Zeng 2014). It is now well documented that roots are able to synthesise and release volatile compounds in the rhizosphere and that VOC-mediated interactions also occur belowground between plant roots and soil organisms (Wenke et al. 2010; Peñuelas et al. 2014). Most studies of belowground VOC-mediated biotic interactions, however, have focused on interactions between plants and organisms of higher trophic levels (herbivorous insects, entompathogenic nematodes, etc.) (Rasmann et al. 2012; Peñuelas et al. 2014) and only a few research papers have dealt with VOC-mediated plant-plant interactions belowground (Ens et al. 2009; Jassbi et al. 2010; Rasmann et al. 2012) (Fig. 2). This is surprising because

Fig. 1 Overview of the bitrophic and tritrophic interactions mediated by VOCs emitted by plants above and below the soil surface. Plant VOCs can have antimicrobial/antifungal properties against phytopathogens (1). Aboveground, floral and fruit VOCs are known to attract pollinators and seed dispersers. In addition, VOCs emitted by attacked leaves can attract/repel plant pests and attract the natural enemies of the attacking herbivores. Belowground, root VOCs can attract plant pests (insect herbivores and parasitic nematodes) and organisms of the third trophic level that will prey on/feed on herbivores (entomopathogenic nematodes [EPNs], parasitoids/predators). +, attraction; −, repellence; solid arrows, VOC emission; red arrows, interactions between plants and phytophagous pests; blue arrows, interactions between plants and organisms of the third trophic level; dashed arrows, feed on/prey on (Drawing: Ir Carolina Levicek)
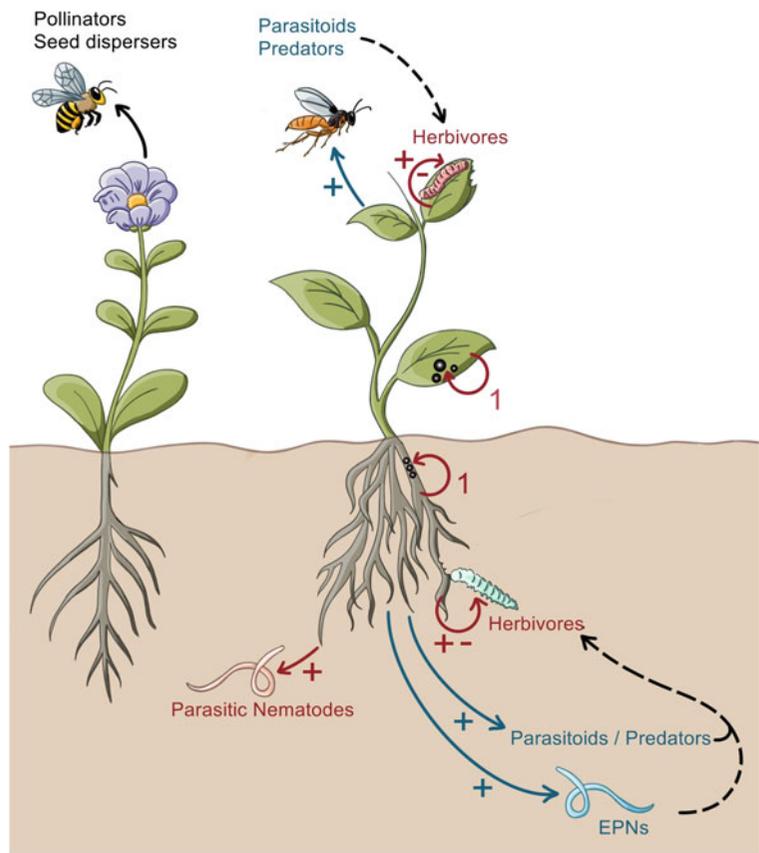
known root-emitted VOC classes, such as terpenes and C_6-volatiles derived from the LOX pathway emitted by damaged plant leaves, have been shown to induce physiological and molecular responses in neighbouring plants (Bate and Rothstein 1998; Arimura et al. 2000a, 2001; Ton et al. 2006).

Given that (1) plants emit volatile cues involved in plant-plant signalling aboveground, (2) roots can detect the chemical signals originating from their neighbours, and (3) roots release VOCs mediating belowground biotic interactions, the objective of this review paper is to discuss the roles of VOCs in belowground plant-plant interactions and highlight the technical challenges associated with the analysis of root-emitted VOCs and the design of experiments for studying VOC-mediated root-root interactions.

VOCs play important ecological roles in plant-plant interactions aboveground

The roles played by VOCs emitted by aboveground plant organs in biotic interactions between neighbouring plants have been extensively reviewed (Dicke and Bruin 2001; Farmer 2001; Heil and Karban 2010; Arimura et al. 2010; Holopainen and Blande 2012; Karban et al. 2014b). Briefly, the emission of an airborne volatile cue by insect-attacked or mechanically damaged trees changing the leaf chemistry of undamaged neighbours was first hypothesized in 1983 in two independent reports (Baldwin and Schultz 1983; Rhoades 1983). Two years later, the controversial debate on 'talking trees' opened with criticisms of the statistical flaws in Baldwin and Schultz's study, as well as the existence of an alternative explanation for Rhoades' results (Fowler and Lawton 1985; Bruin et al. 1995). Since 1983, numerous experiments performed under laboratory and field conditions have shown that VOCs emitted by damaged or undamaged aboveground plant parts of monocotyledonous and dicotyledonous plant species play important roles in interactions between neighbouring plants (Heil and Karban 2010; Karban et al. 2014b) or between different parts of the same plant (Karban et al. 2006; Heil and Silva Bueno 2007; Frost et al. 2007; Park et al. 2007) (Fig. 2). Volatile compounds
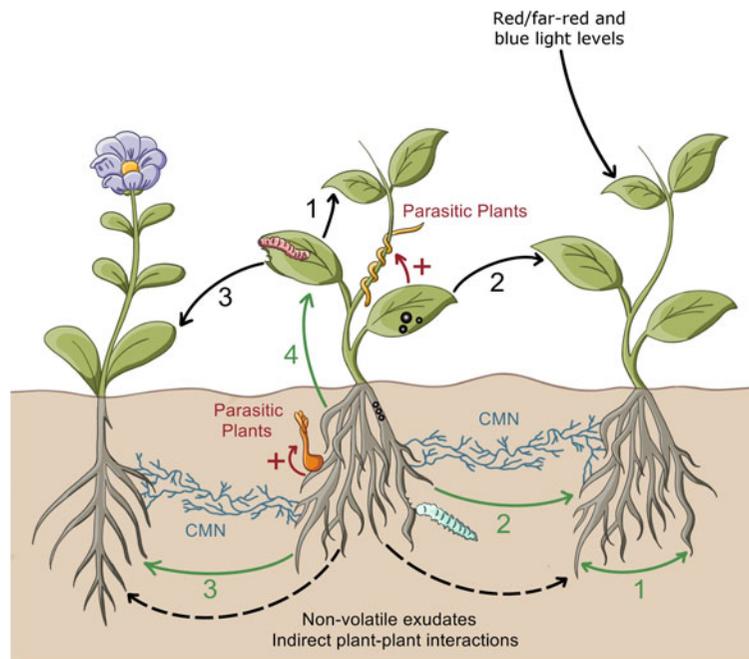
Fig. 2 Overview of the known and potential mechanisms mediating plant-plant interactions above and below the soil surface. Aboveground, both the variations in red/far-red and blue light levels in the plant's canopy and the volatile compounds emitted by plants in the atmosphere enable plants to detect the presence of neighbours. Laboratory and field experiments have also shown that VOCs are involved in within-plant and between-plant signalling aboveground. Belowground, plant-plant interactions mediated by non-volatile exudates, the transport of compounds through common mycorrhizal networks (CMN), and indirect plant-plant interactions (alteration of soil chemistry, microbial populations and nutrient availability) have also been reported in the literature. The green arrows refer to plant-plant interactions mediated by root VOCs. 1, within-plant signalling (shoot-shoot or root-root); 2, intraspecific between-plant signalling (shoot-shoot or root-root); 3, interspecific between-plant signalling (shoot-shoot or root-root); 4, within-plant root-shoot signalling; +, attraction of parasitic plants; solid and labelled arrows, VOC emission (Drawing: Ir Carolina Levicek)

emitted by conspecifics or originating from individuals belonging to another plant species have been shown to promote the induction of direct and indirect defences in undamaged neighbouring plants (Dicke et al. 2003; Heil and Karban 2010), thus increasing their resistance to insect herbivores (Karban et al. 2000; Tscharntke et al. 2001; Karban et al. 2003, 2004; Rodriguez-Saona et al. 2009) or phytopathogens (Shulaev et al. 1997; Yi et al. 2009; Girón-Calva et al. 2012). Volatiles emitted by mechanically damaged or herbivore-attacked plants have also been shown to be able to prime neighbouring plants or parts of the same plant for faster and greater responsiveness to subsequent mechanical stress or herbivore attack, enabling the receiver plants to respond more efficiently when they are attacked (Engelberth et al. 2004; Ton et al. 2006; Heil and Kost 2006; Frost et al. 2007, 2008b; Li et al. 2012; Erb et al. 2015).

With regard to the induction of direct defences, volatile-induced changes reported to date in receiver plants include the transcriptional regulation of genes (Farmer et al. 1992; Shulaev et al. 1997; Bate and Rothstein 1998; Arimura et al. 2000a, b, 2001, 2002; Paschold et al. 2006; Godard et al. 2008), and the production of defensive proteins (Farmer and Ryan 1990; Karban et al. 2000; Tscharntke et al. 2001) and phytohormones (ethylene, jasmonic and salicylic acids) (Shulaev et al. 1997; Arimura et al. 2002; Engelberth et al. 2004; Rodriguez-Saona et al. 2009). Interestingly, VOCs emitted by an insect-damaged plant can also be taken from the air and transformed by an undamaged neighbour into a defensive secondary metabolite that will reduce the effect of insect pests feeding on the exposed plants. For instance, it has been shown that undamaged tomato plants are able to produce a defensive glycoside ([Z]-hex-3-enyl-vicianoside) derived from (Z)-hex-3-en-1-ol emitted by conspecifics infested with *Spodoptera litura* larvae (Sugimoto et al. 2014). Indirect defence mechanisms promoted by volatile cues include the emission of VOCs (Birkett et al. 2000; Farag

and Paré 2002; Engelberth et al. 2004; Choh et al. 2004; Ruther and Kleier 2005; Yan and Wang 2006; Wenda-Piesik et al. 2010) and the secretion of extra floral nectar (Kost and Heil 2006; Choh and Takabayashi 2006; Heil and Silva Bueno 2007; Li et al. 2012) leading to the attraction of insects of the third trophic level.

In addition to plant defences, volatile cues emitted by damaged leaves can inhibit the germination of neighbours, thus affecting the plant community structure (Karban 2007). After plant establishment, volatile compounds released by undamaged plants can also be used for the detection of competing neighbours (Ninkovic 2003; Pierik et al. 2003; Kegge et al. 2015). Volatile compounds released by undamaged plants also affect the attractiveness of neighbours to insect herbivores and insect natural enemies. Fewer aphids (Pettersson et al. 1999; Glinwood et al. 2004; Ninkovic et al. 2009) and more aphid natural enemies (ladybirds and parasitoids) (Ninkovic and Pettersson 2003; Glinwood et al. 2009) have been reported to be attracted to barley plants exposed to the volatiles emitted by undamaged weeds [*Cirsium* spp., *Chenopodium album* L.] or conspecifics (for reviews, see Ahman and Ninkovic 2010; Glinwood 2010; Ninkovic 2010; Glinwood et al. 2011).

Volatile signals being rapidly diluted in the atmosphere, the distance at which VOC-mediated interactions can occur is often short, thus making the leaves closest to the emitter more likely to perceive VOCs. It is very likely that these leaves belong to the emitter or, for plant species with limited dispersal, to genetically related neighbours (Heil and Karban 2010; Heil and Adame-Álvarez 2010). In addition to a role in direct (repulsion of herbivores) and indirect (attraction of insect predators) plant defences, kin selection (i.e., the selection of genetically related plants) has been highlighted as a possible ecological role of VOCs emitted aboveground by plants damaged by herbivores (Heil and Karban 2010; Karban et al. 2011). This hypothesis is supported by experiments showing that sagebrush (*Artemisia tridentata* Nutt.) plants were less damaged by herbivores when they received volatile cues emitted by genetically identical ramets (Karban and Shiojiri 2009) or by conspecifics belonging to the same chemotype (Karban et al. 2014a). Because VOCs can move from the site of attack faster than long distance signals transported via vascular connections and are able to prime undamaged parts of a plant (Heil and Silva Bueno 2007; Frost et al. 2007; Rodriguez-Saona et al. 2009), they are also particularly well-suited candidates for long

distance signalling between different parts of the same plant ('within-plant signalling') and can act synergistically with vascular signals to systemically induce costly defence mechanisms in distal plant organs (Frost et al. 2008a; Heil and Ton 2008; Karban et al. 2011).

Plants can detect root-emitted chemical signals originating from their neighbours

Plant roots can release molecules in the soil that will negatively affect the germination and/or growth of neighbours (Bertin et al. 2003; Perry et al. 2007). The observation that one plant can influence its neighbours through the emission of secondary metabolites is referred to as 'allelopathy' (*allelon* = mutual and *pathos* = suffering or feeling). In 1996, the International Allelopathy Society defined allelopathy as 'any process involving secondary metabolites produced by plants, microorganisms, viruses, and fungi that influence the growth and development of agricultural and biological systems (excluding animals), including positive and negative effects' (Koocheki et al. 2013). This definition has been criticized because of its broad nature covering all chemical interactions that a plant can have with its neighbours. In addition, although 'allelopathy' refers to both the negative and positive effects of one plant on another, many scientists use the term preferentially when describing the negative effects associated with the emission of secondary metabolites (Inderjit and Weiner 2001; Inderjit and Duke 2003; Field et al. 2006). There are many examples of negative plant-plant interactions mediated by root exudates in the scientific literature, particularly in relation to exotic plant invasion (Callaway and Aschehoug 2000; Callaway and Ridenour 2004) and crop-weed interactions in agricultural systems (de Albuquerque et al. 2011), but an exhaustive listing is beyond the scope of this paper (for reviews, see Perry et al. 2007; Koocheki et al. 2013).

Positive intraspecific plant-plant interactions have been demonstrated in *Vicia faba* L. (Chamberlain et al. 2001; Guerrieri et al. 2002) and *Phaseolus lunatus* L. (Dicke and Dijkman 2001). Guerrieri et al. (2002) observed that the parasitoid *Aphidius ervi* Haliday was more attracted to uninfested *V. faba* plants that were potted with plants infested by aphids (*Acyrthosiphon pisum* [Harris]) or were placed in a hydroponic solution that had previously been used for the growth of infested *V. faba* plants. Similarly, Dicke and Dijkman (2001) observed that uninfested lima bean plants became more

attractive to the predatory mite *Phytoseiulus persimilis* Athias-Henriot when they were incubated in a volume of distilled water that had previously contained the roots of a lima bean plant infested with spider mites (*Tetranychus urticae* Koch). In split-root experiments, it has been demonstrated that unstressed plants (*Pisum sativum* L., *Cynodon dactylon* [L.] Pers., *Digitaria sanguinalis* [L.] Scop. and *Stenotaphrum secundatum* [Walter] O. Kuntze) are able to perceive water soluble stress cues released by the roots of their drought-stressed neighbour. In addition, the unstressed receiver plants were able to propagate the signal, causing neighbouring plants to close their stomata, as stressed plants do (Falik et al. 2011, 2012). Recently, it has been reported that root exudates can also influence the flowering timing of neighbours (Falik et al. 2014). Using *Brassica rapa* L., Falik et al. (2014) showed that plants produced under short-day conditions and treated with soil leachates collected from plants produced under long-day conditions reduce the biomass allocation to vegetative organs and accelerate the flowering process compared with plants produced under short-day conditions and exposed to soil leachates collected from short-day plants.

When growing in the soil, plant roots can detect the presence of neighbours, differentiate self from non-self roots, and sense the degree of genetic relatedness between different root parts (kin recognition) (Callaway 2002; de Kroon 2007; Chen et al. 2012; Faget et al. 2013; Depuydt 2014). Self/non-self recognition has been documented for various plant species including *Ambrosia dumosa* Payne and *Larrea tridentata* Cov. (Mahall and Callaway 1991), soybean (*Glycine max* [L.] Merrill) (Gersani et al. 2001), rice (*Oryza sativa* L.) (Fang et al. 2013), pea (*P. sativum*) (Falik et al. 2003), buffalo grass (*Buchloe dactyloides*) (Gruntman and Novoplansky 2004), hevea (*Hevea brasiliensis* Müll. Arg), corn (*Zea mays* L.) (Gonkhamdee et al. 2010) and *Hieracium pilosella* L. (Schmid et al. 2015). Depending on the plant species, at least two kinds of root behaviour have been observed when two plant individuals share the same volume of soil: (1) avoidance of self competition and enhanced root development in response to competition with a non-self neighbour (Gersani et al. 2001; Falik et al. 2003; Gruntman and Novoplansky 2004) or (2) segregation and avoidance of roots belonging to competitors (Mahall and Callaway 1991; Fang et al. 2013; Schmid et al. 2015). Various mechanisms that might explain how plants identify their neighbours have been proposed in the literature (Chen et al. 2012; Depuydt 2014). Because

the physiological integrity of plants seems to be necessary to discriminate self from non-self roots, it has been suggested that internal oscillations of hormone levels and/or electrical signals could be the primary mechanism used by plants to recognize roots as self (Falik et al. 2003; Gruntman and Novoplansky 2004). A role for root-emitted chemical signals in self/non-self recognition and kin recognition has also been suggested (Chen et al. 2012; Fang et al. 2013). Both laboratory and greenhouse experiments have shown that root exudates can carry information about the degree of genetic relatedness, allowing plants exposed to these compounds to distinguish kin and non-kin individuals. In *Arabidopsis thaliana* (L.) Heynh, the root system of plants exposed to the root exudates of unrelated seedlings was characterized by a greater number of lateral roots than the plants exposed to their own exudates or to the exudates of siblings (Biedrzycki et al. 2010). In a greenhouse experiment designed to mimic soil natural conditions (composition, microbial activity and exudate concentration), Semchenko et al. (2014) found that root exudates can also carry information about the species identity and population origin of neighbours. In their experiment, *Deschampsia caespitosa* (L.) plants showed an increase in specific root length and lateral root branching following the application of root exudates produced by unrelated conspecifics coming from the same population. Such alteration of root system architectural traits was suppressed in plants exposed to the chemicals released by sibling roots. Interestingly, root growth stimulation was not observed when *D. caespitosa* plants received chemicals secreted by the roots of a different plant species (*Lychnis flos-cuculi* L.), indicating that recipient plants can use information carried by root exudates to differentiate kin from non-kin neighbours and recognise individuals living in the same population (Semchenko et al. 2014).

Taken together, these results show that root exudates play significant roles in plant-plant interactions and can affect receiver plants both aboveground (herbivore resistance, stomatal aperture, flowering timing) and belowground (allelopathy, kin recognition).

Plant roots release VOCs involved in belowground biotic interactions

The release of VOCs by plant roots has been suggested for both monocotyledonous and dicotyledonous plant

species submitted to biotic (insect herbivore, phytopathogenic fungi and bacteria) and/or abiotic stresses (mechanical damage and water/drought stress) (Table 1). Depending on the plant species studied, volatile blends released belowground by plant roots can be characterized by compounds belonging to various chemical families, particularly terpenoids (Rasmann et al. 2005; Lin et al. 2007; Ali et al. 2010), fatty acid derivatives (Gfeller et al. 2013) or sulphur-containing compounds (Ferry et al. 2007; Crespo et al. 2012; Danner et al. 2015). Important ecological roles have been associated with root-emitted VOCs (Fig. 1). Briefly, they have been shown to mediate interactions between plants and phytophagous pests such as insect herbivores (Sutherland and Hillier 1974; Guerin and Ryan 1984; Palma et al. 2012; Weissteiner et al. 2012; Robert et al. 2012a) and plant parasitic nematodes (Ali et al. 2011; Farnier et al. 2012). Volatile cues released by roots damaged by insect herbivores are also implicated in belowground plant indirect defences because they attract organisms of the third trophic level, such as insect predators (Neveu et al. 2002; Ferry et al. 2007) and entomopathogenic nematodes (van Tol et al. 2001; Boff et al. 2002; Rasmann et al. 2005; Ali et al. 2011). In addition to the review articles published so far and focusing on belowground VOCs (Wenke et al. 2010; Rasmann et al. 2012; Peñuelas et al. 2014), Table 1 presents a chronological literature review of the studies on root VOC production and VOC-mediated interactions between plant roots and soil organisms. This review gives the plant model(s) used in experiments, the (a)biotic stresses experienced by plants, the questions raised, the type of biological sample and the analytical techniques used to trap and analyse VOCs produced by plant roots. It shows that more than half the studies published so far focus on root VOC production by three major plant models: *Z. mays*, *Citrus* spp. and *Brassica* spp.

When submitted to *Diabrotica virgifera virgifera* LeConte feeding, maize roots systemically produce a specific VOC blend dominated by (*E*)-β-caryophyllene (Rasmann et al. 2005; Hiltpold et al. 2011), a sesquiterpene produced from farnesyl diphosphate via the maize terpene synthase 23 (TPS23) (Köllner et al. 2008) and possessing remarkable diffusion properties in sand and soil (Hiltpold and Turlings 2008). When released by insect-damaged maize roots, (*E*)-β-caryophyllene was identified as the main belowground chemical attractant for entomopathogenic nematodes (*Heterorhabditis megidis* Poinar, Jackson & Klein and *Heterorhabditis*

bacteriophora Poinar) in laboratory and field experiments (Rasmann et al. 2005; Rasmann and Turlings 2007, 2008; Hiltpold et al. 2010a). The discovery that a root-emitted signal produced by plants infested by *D. virgifera virgifera* larvae is able to recruit organisms of the third trophic level as an indirect plant defence mechanism led to the development of new crop protection strategies using entomopathogenic nematodes as biological control agents to reduce *D. virgifera virgifera* emergence and root damage in the field (Hiltpold et al. 2010c; Hiltpold and Turlings 2012). Several attempts to improve the searching efficiency of entomopathogenic nematodes were made, notably by selecting an entomopathogenic nematode strain for enhanced responsiveness to (*E*)-β-caryophyllene (Hiltpold et al. 2010a, b) or by genetically engineering a maize variety that had lost the ability to produce (*E*)-β-caryophyllene in order to restore the release of the sesquiterpene signal (Degenhardt et al. 2009). Although both pest management strategies led to a decrease in *D. virgifera virgifera* adult emergence in the field (Degenhardt et al. 2009; Hiltpold et al. 2010a), there were physiological and ecological costs involved in the use of the selected entomopathogenic nematode strain (small decrease in infectiousness) (Hiltpold et al. 2010a), and the genetically engineered maize plants (decrease in seed germination, plant growth and yield, and increased attractiveness to adults and larvae of an aboveground plant pest) (Robert et al. 2013a). When searching for a suitable host, *D. virgifera virgifera* larvae also use (*E*)-β-caryophyllene as a volatile attractant in a plant background odour to locate plants with increased susceptibility infested by conspecifics and aggregate in a density-dependent manner (Robert et al. 2012a, b).

As for root herbivory, maize leaf infestation by an insect herbivore also induces changes in VOC emissions by plant roots (Rasmann and Turlings 2007; Robert et al. 2012a). Root VOC analyses showed that the (*E*)-β-caryophyllene production of plants infested simultaneously by a leaf (*Spodoptera littoralis* Boisduval) and a root (*D. virgifera virgifera*) herbivore is significantly lower than that of plants infested by *D. virgifera virgifera* larvae only. This decrease in (*E*)-β-caryophyllene production by maize roots correlated with a reduction in the attraction of double infested plants for *H. megidis* (Rasmann and Turlings 2007). In addition, when performing behavioural assays, Robert et al. (2012a) showed that *D. virgifera virgifera* larvae were significantly more attracted by the roots of healthy

Table 1 Chronological literature review of studies investigating biotic interactions mediated by root volatiles

References	Plant species	Biotic and abiotic stresses	Experiments	Root VOC analysis		VOC extraction/ concentration	VOC separation/ identification
				Sample			
(Plhak and Urbankova 1969)	Hordeum distichum Triticum vulgare Secale cereale Avena sativa	×	Impact of volatile substances emitted by H. distichum roots on growth, dry matter production, respiration and SH-groups content of S. cereale	×		×	×
(Sutherland and Hillier 1974)	Lolium perenne Medicago sativa Lotus pedunculatus Trifolium pratense Trifolium repens Rumex sp.	×	Attraction of Costelytra zealandica larvae to roots of several pasture plants	×		×	×
(Guerin and Ryan 1984)	Daucus carota	Psila rosae	Resistance measurement of some carrot cultivars to Psila rosae larvae in field experiments	Bare or diced roots		Atmospheric steam distillation DS (Porapak Q)	GC
(Witcosky et al. 1987)	Pseudotsuga menziesii	Ceratocystis wageneri Mechanical damage	Trapping of Hylastes nigrinus and Steremnius carinatus using traps baited with a C. wageneri-infected root section, a healthy root section or pure chemical compounds (α-pinene and ethanol)	×		×	×
(Boff et al. 2001)	Fragaria × ananassa	Galleria mellonella Otiorhynchus sulcatus	Attraction of Heterorhabditis megidis to strawberry roots	×		×	×
(van Tol et al. 2001)	Thuja occidentalis L.	O. sulcatus	Attraction of H. megidis to T. occidentalis roots	T. occidentalis roots		Tenax TA	TD-CT-GC-MS
(Boff et al. 2002)	Fragaria × ananassa T. occidentalis	O. sulcatus Mechanical damage	Attraction of H. megidis to strawberry and T. occidentalis roots	×		×	×
(Neveu et al. 2002)	Brassica campestris	Delia radicum Mechanical damage Water stress	Attraction of Trybliographa rapae females to B. campestris leaves or roots of D. radicum-infested plants	×		×	×
(Steeghs et al. 2004)	Arabidopsis thaliana	Pseudomonas syringae pv tomato DC3000 Escherichia coli (OP50) Alternaria brassicola Diuraphis noxia Mechanical damage	Analysis of VOCs emitted by A. thaliana roots submitted to bacteria or fungi infection, aphid infestation or mechanical wounding	Hairy root cultures		×	GC-MS GC-FID PTR-MS
(Köllner et al. 2004)	Zea mays	Spodoptera littoralis	Spatial (organ distribution) and temporal (development) analysis of the sesquiterpene content/ emission of maize inbred line B73 plants	Crushed roots		Solvent extraction	GC-MS
(Rasmann et al. 2005)	Z. mays	Diabrotica virgifera virgifera	Attraction of H. megidis to maize roots attacked by WCR larvae, nematode attraction evaluation in the field (larvae infection rate and adult emergence) and	Crushed roots		SPME (PDMS)	TD-GC-MS

Table 1 (continued)

References	Plant species	Biotic and abiotic stresses	Experiments	Root VOC analysis — Sample	VOC extraction/concentration	VOC separation/identification
			identification of the chemical attractant ([E]-β-caryophyllene)			
(Weissteiner and Schütz 2006)	D. carota spp. sativus Quercus sp.	Melolontha hippocastani Mechanical damage	Attraction of M. hippocastani to D. carota or Quercus roots	Bare roots	DS (charcoal)	LD-GC-MS
Ferry et al. 2007)	Brassica napus	D. radicum	Attraction of two staphylinids (Aleochara bilineata and Aleochara bipustulata) and carabid beetles (Bembidion spp.) to VOCs emitted by roots of B. napus infested by D. radicum larvae or traps releasing dimethyl disulphide in the field	Bare roots	SPME (PDMS)	TD-GC-MS
(Lin et al. 2007)	Pinus pinea	Drought stress	Analysis of the root content in monoterpenes and sesquiterpenes of well-watered and drought-stressed Pinus roots	Crushed roots	Solvent extraction and concentration on Tenax TA/Carbotrap adsorbents	TD-CT-GC-MS
			Analysis of monoterpenes emitted by well-watered and drought-stressed Pinus roots	Roots surrounded by soil Shaken roots Washed roots	DS (Tenax TA/Carbotrap)	TD-CT-GC-MS
(Rasmann and Turlings 2007)	Z. mays	S. littoralis D. virgifera virgifera	Attraction of Cotesia marginiventris and H. megidis to maize plants infested with a foliar herbivore, a root herbivore, or both	Crushed roots	SPME (PDMS)	TD-GC-MS
(Tapia et al. 2007)	T. pratense	×	Olfactory response of male and female Hylastinus obscurus to red clover root extracts or pure volatile compounds	Bare roots	Supercritical CO₂	GC-MS
(Hiltpold and Turlings 2008)	×	×	Study of the diffusion properties of various maize VOCs in sand and standard soil at selected moisture levels	Synthetic VOC blends	SPME (PDMS or Corboxen™-PDMS)	TD-GC-MS
(Köllner et al. 2008)	Z. mays	S. littoralis D. virgifera virgifera	Cloning of an (E)-β-caryophyllene synthase gene (tps23) and biochemical characterization of TPS23 + transcript accumulation of tps23 in maize leaves and roots infested by S. littoralis and/or D. virgifera virgifera, respectively	×	×	×
(Rasmann and Turlings 2008)	Z. mays Gossypium herbaceum Vigna unguiculata	D. virgifera virgifera Diabrotica balteata Agriotes ustulatus Ditylenchus dipsaci	Comparison of plant, herbivore and entomopathogenic nematode species (H. megidis, Heterorhabditis bacteriophora and Steinernema feltiae) with regard to their specificity in belowground tritrophic interactions	Crushed roots	SPME (PDMS)	TD-GC-MS
(Degenhardt et al. 2009)	Z. mays	D. virgifera virgifera	Evaluation in a field experiment of D. virgifera virgifera emergence and H. megidis attraction to roots	Crushed roots	SPME (PDMS)	TD-GC-MS

Table 1 (continued)

References	Plant species	Biotic and abiotic stresses	Experiments	Root VOC analysis		
				Sample	VOC extraction/ concentration	VOC separation/ identification
			of genetically engineered maize plants expressing an (E)-β-caryophyllene synthase gene from Origanum vulgare			
(Ens et al. 2009)	Chrysanthemoides monilifera spp. rotundata, Acacia longifolia var. sophorae	×	Chemical characterization of a hydrophobic extract from bitou bush roots and evaluation of its growth inhibition potential on Isolepis nodosa	Chopped roots	Solvent extraction	GC-MS
(Ali et al. 2010)	Citrus paradisi × Poncirus trifoliata	Diaprepes abbreviatus; Mechanical damage	Attraction of Steinernema diaprepesi to Citrus roots attacked by D. abbreviatus larvae or mechanically damaged roots and identification of the potent chemical attractants (pregeijerene)	Transplanted roots	DS (Super-Q)	LD-GC-MS
(Hiltpold et al. 2010c)	Z. mays	D. virgifera virgifera	Evaluation of the field efficacy of three entomopathogenic nematodes (H. megidis, H. bacteriophora, S. feltiae) on the reduction of D. virgifera virgifera emergence and root damage of an (E)-β-caryophyllene emitting and a non-emitting maize variety	×	×	×
(Hiltpold et al. 2010a, b)	Z. mays	D. virgifera virgifera	Selection of a new H. bacteriophora strain with an enhanced responsiveness to root-emitted (E)-β-caryophyllene and evaluation of its control efficiency in a field experiment	×	×	×
(Jassbi et al. 2010)	Artemisia tridentata	×	Analysis of VOCs emitted by A. tridentata roots and evaluation of the phytotoxic potential of the main identified VOCs on Nicotiana attenuata (germination and seedling growth)	Bare roots, Potted roots, Potted roots	DS (Super-Q), SPME (DVB/CAR/PDMS), HSME (hexadecane)	LD-GC-MS, TD-GC-MS, GC-MS
(Ali et al. 2011)	P. trifoliata, C. paradisi × P. trifoliata, Citrus aurantium	D. abbreviatus	Attraction of entomopathogenic nematodes (S. diaprepesi, Steinernema carpocapsae, Steinernema riobrave and Heterorhabditis indica) and a plant parasitic nematode (Tylenchulus semipenetrans) to D. abbreviatus-infested Citrus roots and analysis of constitutive and induced shoot and root volatiles	Transplanted roots	DS (Super-Q)	LD-GC-MS
(Erb et al. 2011)	Z. mays	Jasmonic acid, S. littoralis	Measurement of correlations (synergies and trade-offs)	Crushed roots	SPME (PDMS)	TD-GC-MS

Table 1 (continued)

References	Plant species	Biotic and abiotic stresses	Experiments	Root VOC analysis		
				Sample	VOC extraction/concentration	VOC separation/identification
		D. virgifera virgifera Colletotrichum graminicola Setosphaeria turcica	between insect and pathogen resistance and VOC production/emission by leaves and roots of 21 maize genotypes			
(Hiltpold et al. 2011)	Z. mays	D. virgifera virgifera	Analysis of the local and systemic (E)-β-caryophyllene production and tps23 gene expression in maize roots damaged by D. virgifera virgifera and attraction of H. megidis to systemically induced or locally damaged root tissues	Crushed roots / Transplanted roots	SPME (PDMS) / DS (Super-Q)	TD-GC-MS / LD-GC-MS
(Lawo et al. 2011)	Vitis berlandieri × Vitis riparia	Daktulosphaira vitifoliae	Analysis of VOC production by D. vitifoliae-infested or uninfested Vitis roots	Crushed roots	SPME (DVB/CAR/PDMS)	TD-GC-MS
(Laznik et al. 2011)	Z. mays	Mechanical damage	Analysis of VOCs produced by mechanically-damaged roots of some European and American maize genotypes	Crushed roots	SPME (PDMS)	TD-GC-MS
(Rasmann et al. 2011)	Asclepias syriaca	Tetraopes tetraophthalmus	Evaluation of the efficacy and the genetic correlations between direct and indirect defences, as well as constitutive and inducible defences of milkweed using a tritrophic system involving T. tetraophthalmus and H. bacteriophora	Bare roots / Crushed roots	DS (charcoal) / SPME (PDMS)	LD-GC-MS / TD-GC-MS
(Ali et al. 2012)	C. paradisi × P. trifoliata	D. abbreviatus	Analysis of VOCs found in the root zone of Citrus trees in the field or emitted by Citrus roots infested by D. abbreviatus larvae and study of entomopathogenic nematode attraction in the field using VOCs emitted by infested roots or isolated pregeijerene	Transplanted roots / Root zone of Citrus trees in the field	DS (Super-Q)	LD-GC-MS
(Crespo et al. 2012)	Brassica nigra	Mechanical damage D. radicum	Identification of VOCs emitted by D. radicum-infested Brassica roots by GC-MS and VOC temporal dynamics recording using PTR-MS, particularly in relation to the larval developmental stage	Potted roots / Potted roots	DS (Tenax TA and Carbopack B) / ×	GC-MS / PTR-MS
(Danner et al. 2012)	Brassica rapa subsp. rapa Brassica juncea	D. radicum	Monitoring of VOCs emanating from Brassica roots infested by D. radicum larvae	Potted roots	×	PTR-MS
(Farnier et al. 2012)	Solanum tuberosum	×	Attraction of white potato cyst nematodes (Globodera pallida) to potato root volatiles	×	×	×
(Palma et al. 2012)	T. pratense	×	Analysis of VOCs produced by differently aged red clover roots	Bare roots	SPME (DVB/PDMS)	TD-GC-MS

Table 1 (continued)

References	Plant species	Biotic and abiotic stresses	Experiments	Root VOC analysis	VOC extraction/ concentration	VOC separation/ identification
				Sample		
			and their attractiveness to *H. obscurus*			
(Robert et al. 2012a)	*Z. mays*	*S. littoralis* *D. virgifera virgifera*	Host preference of WCR larvae between maize plants with roots infested by conspecifics or leaves infested by *S. littoralis* larvae and identification of the attractants (ethylene and [E]-β-caryophyllene)	Crushed roots (VOCs) Bare roots (ethylene)	SPME (PDMS) Headspace sampling with a gas-tight syringe	TD-GC-MS GC-FID
(Robert et al. 2012b)	*Z. mays*	Jasmonic acid *D. virgifera virgifera*	Impact of the larval density on performance and attraction of WCR larvae feeding on maize roots, identification of the chemical attractants ([E]-β-caryophyllene) responsible for the aggregation of WCR larvae, and study of the WCR larvae-induced systemic susceptibility in maize roots	Crushed roots	SPME (PDMS)	TD-GC-MS
(Turlings et al. 2012)	×	×	Attraction of *H. megidis* to different sources of synthetic VOCs released into a sandy soil alone or with carbon dioxide	×	×	×
(van Dam et al. 2012)	*Brassica carinata* *Brassica oleracea* *B. juncea* *B. napus* *B. nigra* *B. rapa*	Mechanical damage *D. radicum*	Real-time analysis of VOCs emitted by *D. radicum*-infested or mechanically damaged roots of several *Brassica* species	Potted roots	×	PTR-MS
(Weissteiner et al. 2012)	*Quercus petraea* × *Quercus robur*	*Melolontha hippocastani* Mechanical damage	Analysis of VOCs emitted by undamaged, mechanically damaged, or infested oak roots and study of the electrophysiological and behavioural responses of *M. hippocastani* to root-emitted VOCs + description of the *M. hippocastani*'s olfactory apparatus	Potted roots Bare roots	SPME (CAR/PDMS) DS (Tenax) SPME (CAR/PDMS) DS (Tenax) DS (charcoal)	TD-GC-MS TD-CT-GC-MS TD-GC-MS TD-CT-GC-MS LD-GC-MS
(Ali et al. 2013)	×	×	Attraction of free-living bacterivorous nematodes (*Acrobeloides*) and nematophagous fungi to sources of pregeijerene located in the soil of a citrus orchard and a blueberry planting	×	×	×
(Fiers et al. 2013)	*Hordeum vulgare*	*Cochliobolus sativus* *Fusarium culmorum*	Identification of VOCs released by uninfected barley roots and roots infected by *C. sativus* and/or *F.*	Bare roots	SPME (DVB/CAR/PDMS)	TD-GC-MS

Table 1 (continued)

References	Plant species	Biotic and abiotic stresses	Experiments	Root VOC analysis		
				Sample	VOC extraction/ concentration	VOC separation/ identification
			culmorum and study of the effects of VOCs released by pathogenic fungi or (un)infected barley roots on barley and fungal growth, respectively			
(Gfeller et al. 2013)	*H. vulgare*	×	Characterization of VOCs emitted by barley roots and their attractiveness to wireworms (*Agriotes sordidus*)	Bare roots	SPME (DVB/CAR/PDMS)	TD-GC-MS
(Robert et al. 2013b)	*Z. mays*	*D. virgifera virgifera*	Effect of the presence/absence of an endosymbiont (*Wolbachia*) on WCR larval performance and on the induction of direct and indirect plant defences	Crushed roots	SPME (PDMS)	TD-GC-MS
(Robert et al. 2013a)	*Z. mays*	*D. virgifera virgifera* *Diabrotica undecimpunctata howardii* *Spodoptera frugiperda*	Evaluation of the costs and benefits of constitutive VOC emission by maize plants genetically engineered to overexpress an (*E*)-β-caryophyllene synthase gene	×	×	×
(Demarta et al. 2014)	*Z. mays*	×	Influence of root system architecture (RSA) and (*E*)-β-caryophyllene perception on the foraging behaviour of *H. megidis* using stainless steel model root systems or two maize genotypes exhibiting contrasted RSAs	×	×	×
(Rostás et al. 2015)	*Festuca pratensis × Lolium perenne*	*Neotyphodium uncinatum*	Analysis of VOCs emitted by the roots of *F. pratensis × L. perenne* plants whose aerial parts are infected or not by the endophytic fungus *N. uncinatum* and study of the host-locating behaviour of *C. zealandica* larvae	Bare roots	DS (SuperQ) ×	LD-GC-MS PTR-MS
(Sohrabi et al. 2015)	*A. thaliana*	Jasmonic acid *Pythium irregulare*	Study of the (*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT) synthesis in *Arabidopsis* roots via the cytochrome P450 monooxygenase (CYP705A1)-catalysed and jasmonate-dependent breakdown of arabidiol, and the role of this volatile homoterpene in resistance against *P. irregulare*	Bare roots	SPME (PDMS)	TD-GC-MS
(Danner et al. 2015)	*B. rapa*	*P. brassicae* *D. radicum*	Temporal analysis of volatile sulphur compounds emitted by shoots and roots of *B. rapa* plants singly or simultaneously infested by aboveground and belowground insect herbivores	Potted roots	× DS (Tenax TA)	PTR-MS TD-CT-GC-MS
(Eilers et al. 2015)	*Taraxacum sect. ruderalia*	×		Roots potted in a mesocosm	PDMS	TD-CT-GC-MS

Table 1 (continued)

References	Plant species	Biotic and abiotic stresses	Experiments	Root VOC analysis		
				Sample	VOC extraction/ concentration	VOC separation/ identification
			Analysis of VOCs emitted by undamaged dandelion roots using a passive and inexpensive sampling system, and comparison of the recovery of synthetic VOCs from different substrates			
(Abraham et al. 2015)	Malus × domestica rootstock M9	Melolontha melolontha	Analysis of VOCs emitted by shoots and roots of apple rootstocks infested by M. melolontha larvae	Roots potted in a semi-vertical rhizobox	DS (charcoal)	LD-GC-MS

HSME headspace solvent microextraction; SPME solid phase microextraction; DVB divinylbenzene; CAR carboxen; PDMS polydimethylsiloxane; DS dynamic sampling; LD liquid desorption; TD thermal desorption; CT cold trap; GC gas chromatography; MS mass spectrometry; FID flame ionisation detector; PTR-MS, proton transfer reaction-mass spectrometry; WCR Western corn rootworm

plants than those of plants infested by *S. littoralis*. Although solid phase microextraction and gas chromatography–mass spectrometry (SPME-GC-MS) analyses did not show any differences between VOCs produced by the roots of healthy and infested plants, complementary analyses focusing on ethylene emission showed that roots of *S. littoralis*-infested plants released significantly less ethylene than those of healthy plants. These results led to the hypothesis that, in addition to (*E*)-β-caryophyllene, *D. virgifera virgifera* larvae are also able to use ethylene emission as a general cue to detect healthy plants in the host selection process (Robert et al. 2012a).

Tritrophic interactions between plant roots, a phytophagous insect and soil nematodes were also studied using the rootstock *Citrus paradisi* Macf. × *Poncirus trifoliata* L. Raf. ('Swingle citrumelo'), the larvae of the root weevil (*Diaprepes abbreviatus* [L.]), and entomopathogenic (*Steinernema diaprepesi* Nguyen & Duncan, *Steinernema carpocapsae*, *Steinernema riobrave* and *Heterorhabditis indica*) and plant parasitic (*Tylenchulus semipenetrans*) nematodes (Ali et al. 2010, 2011). Using in situ dynamic sampling systems to trap and concentrate VOCs emitted by roots before GC-MS analyses, the C_{12} terpene pregeijerene (1,5-dimethylcyclodeca-1,5,7-triene) was identified as the main VOC released by the roots of the Swingle citrumelo rootstock infested by *D. abbreviatus* larvae (Ali et al. 2010, 2011), as well as the main VOC found in the root zone of *Citrus* trees in an unmanaged orchard (Ali et al. 2012). Depending on the plant species studied, pregeijerene can be produced by roots constitutively, as in the Swingle citrumelo's parent line *P. trifoliata*, or only in response to insect feeding. The volatile blend emitted by *D. abbreviatus*-infested roots was shown to attract entomopathogenic nematodes both in olfactometer assays (Ali et al. 2010, 2011) and in field experiments (Ali et al. 2012). Among all the VOCs emitted by insect-damaged *Citrus* roots, it has been demonstrated that isolated pregeijerene was enough to attract naturally occurring entomopathogenic nematodes, as well as free-living bacterivorous nematodes (*Acrobeloides*), and to increase the mortality rate of insect larvae in the field (Ali et al. 2012, 2013). Given that VOCs emitted by *Citrus* roots infested by *D. abbreviatus* appeared to attract plant parasitic nematodes, the use of a root-emitted cue to attract entomopathogenic nematodes as an indirect plant defence strategy could have ecological costs for the plant emitter (Ali et al. 2011). As suggested

by Ali et al. (2011), these costs could be reduced in plant lines susceptible to plant parasitic nematodes by using volatile cues that would be released only after herbivore attack. As observed in SPME-GC-MS analyses of maize roots (Robert et al. 2012a), aboveground herbivory on the Swingle citrumelo rootstock by *D. abbreviatus* did not seem to induce the production of root VOCs that differed from that produced by healthy plants (Ali et al. 2011).

VOCs emitted by *Brassica* roots infested by cabbage root fly larvae (*Delia radicum* L.) were also shown to be attractive for insects of the third trophic level, such as females of the parasitoid species *Trybliographa rapae* Westwood, rove beetles (*Aleochara bilineata* and *Aleochara bipustulata*), and carabid beetles in the genus *Bembidion* (Neveu et al. 2002; Ferry et al. 2007). GC-MS and proton transfer reaction-mass spectrometry (PTR-MS) analyses have shown that insect-damaged *Brassica* roots release mainly highly volatile sulphur compounds (methanethiol, dimethyl sulphide, dimethyl disulphide and dimethyl trisulphide) and glucosinolate breakdown products (thiocyanates and isothiocyanates) in the soil, with a VOC emission pattern depending on the plant species studied (van Dam et al. 2012; Danner et al. 2012; Crespo et al. 2012; Danner et al. 2015). To date, PTR-MS analyses of root-emitted VOCs have been performed only on potted *Brassica* spp. root systems (Crespo et al. 2012) and on hairy root cultures of *A. thaliana* submitted to bacteria or fungi infection, aphid infestation or mechanical wounding (Steeghs et al. 2004).

Aboveground, VOCs emitted by damaged plant parts can prime or induce direct/indirect defence mechanisms in yet undamaged parts of the same plant (Das et al. 2013). Both VOCs emitted at the site of attack and chemical signals (e.g., plant hormones) travelling inside the vascular tissues of the attacked plant mediate interactions between damaged and undamaged plant parts (Erb et al. 2008; Das et al. 2013). Given that the roots of plants attacked by insect herbivores also synthesise and release VOCs in the soil (Table 1), their roles in mediating interactions between the roots and shoots of the same plant are worth investigating (Fig. 2). Whether or not root-emitted VOCs diffusing from the rhizosphere into the phyllosphere can mediate root-shoot interactions is still poorly documented, but this within-plant signalling mechanism has been hypothesized as a possible way for plants to coordinate aboveground and belowground defences (Erb et al. 2008).

Studying VOC-mediated root-root interactions: challenges and opportunities

Given that (1) VOCs play important ecological roles in plant-plant interactions aboveground, (2) plants can detect chemical signals emitted in the rhizosphere of their neighbours (roots and associated microorganisms), and (3) roots are able to synthesise and release VOCs in the soil (Table 1), questions arise relating to the ecological roles played by belowground VOCs in root-root interactions (Schenkel et al. 2015). With regard to allelopathic interactions, plant VOCs are able to generate oxidative stress (Zunino and Zygadlo 2004; Singh et al. 2006). In addition, they can affect germination, root and shoot growth (Bradow and Connick 1990; Fischer et al. 1994; Kong et al. 2002; Singh et al. 2002; Barney et al. 2005), mitosis and cell size (Romagni et al. 2000; Nishida et al. 2005), chlorophyll content and fluorescence (Romagni et al. 2000; Kong et al. 2002; Singh et al. 2002), mitochondrial respiration (Abrahim et al. 2000, 2003; Singh et al. 2005), DNA synthesis (Nishida et al. 2005), and gene expression in exposed plants (Horiuchi et al. 2007). Compared with VOC-mediated plant-plant interaction studies performed aboveground, the amount of published research on the roles played by root VOCs in plant-plant interactions is much lower. For example, using an in vitro experimental set-up, it has been documented that some volatile terpenoids emitted by the bitou bush (*Chrysanthemoides monilifera* spp. *rotundata* [DC.] T. Norl.) (Ens et al. 2009) and sagebrush roots (Jassbi et al. 2010) in the soil can be phytotoxic to *Isolepis nodosa* (Rott.) R. Br. and *Nicotiana attenuata* Torr., respectively. In addition, sesquiterpenoids released by roots (e.g., sesquiterpene lactones) can also act as germination stimulants for parasitic plants (*Striga* and *Orobranche* spp.) (Bouwmeester et al. 2003; Rasmann et al. 2012). With regard to volatile phytohormones, ethylene was reported to be constitutively emitted by maize root systems (Robert et al. 2012a). Although ethylene can act as a non-specific volatile signal aboveground (Pierik et al. 2003), a role of this VOC in mediating root-root interactions is still unknown. In the next section, we will discuss the environmental fate of VOCs emitted by plant roots and, given the belowground location of root systems, we will look at some of the technical challenges in the design of experimental devices for (1) analysing the VOCs released by plant roots and (2) studying the ecological roles played by root-emitted VOCs in plant-plant interactions.

Environmental fate of root-emitted VOCs

The distance at which volatile cues can act as interplant signals is an important issue when studying their ecological roles, particularly when moving from controlled laboratory assays to field experiments. Aboveground, VOC-mediated plant-plant interactions are reported to occur over distances that vary depending on the plant species and environmental parameters (such as atmospheric ozone concentration) (Blande et al. 2010). In field experiments involving sagebrush and tobacco, plant-plant signalling was demonstrated to occur over distances ranging from 10 cm (sagebrush to tobacco) to 60 cm (sagebrush to sagebrush) (Karban et al. 2003, 2006). Similarly, the secretion of extra floral nectar by lima bean leaves was reported to occur in receiver plants located up to 50 cm away from the emitter (Heil and Adame-Álvarez 2010). Given that a volatile compound must be perceived at a physiologically active concentration by a neighbouring plant before it can be considered as a signal mediating plant-plant interactions (Firn and Jones 1995; Preston et al. 2001), the environmental fate of root-emitted VOCs in the soil is of crucial importance and will be linked to their chemical stability, their production rate by plant roots, and their interactions with the solid, liquid and gaseous components of the soil ecosystem (Perry et al. 2007; Zeng 2014). For instance, they can be diluted in the gaseous phase of the soil matrix, solubilized into the soil solution (particularly polar oxygenated VOCs) (Fischer et al. 1994; Hiltpold and Turlings 2008; Peñuelas et al. 2014), used as a carbon source by soil microorganisms (Misra et al. 1996; Cleveland and Yavitt 1998; Kleinheinz et al. 1999; Owen et al. 2007; Ramirez et al. 2009), adsorbed into soil particle surfaces (Inderjit and Dakshini 1995; Ruiz et al. 1998) or subjected to physico-chemical degradation (Perry et al. 2007). Taken together, these phenomena lead to a decrease in VOC concentration with increasing distance from the source. The distance that a volatile signal can travel will depend on its physico-chemical properties (particularly polarity) and its ability to interact with the soil environment (Fischer et al. 1994; Ruiz et al. 1998). For example, it has been shown that volatile sesquiterpenes ([*E*]-β-caryophyllene, [*E*]-β-farnesene) have better diffusion capacities in sand and soil than green leaf volatiles ([*E*]-hex-2-enal and [*Z*]-hex-3-en-1-ol) and that both soil moisture level and soil composition affect the distance travelled by volatile signals (Hiltpold and Turlings 2008). In addition,

oxygenated monoterpenes have greater water solubilities than monoterpene hydrocarbons with a similar skeleton and are thus more likely to be solubilized into the soil solution (Fischer et al. 1994). More research efforts are needed to determine the distances over which VOCs emitted by undisturbed root systems can travel in the soil environment (either solubilized into the soil solution or diffusing in the soil gaseous phase).

Technical challenges and perspectives

Due to their belowground location, studying root-root interactions mediated by VOCs is challenging and requires innovative tools in order to (1) identify the volatile signals released into the plant rhizosphere (Rasmann et al. 2012; Campos-Herrera et al. 2013; Hiltpold et al. 2013), (2) follow the temporal variations in VOC emission (composition of the VOC blends and individual VOC concentrations) (Danner et al. 2012) and (3) conduct bioassays on the roles played by root-emitted VOCs in plant-plant interactions.

As in the case of VOCs that are synthesised and released by aboveground plant tissues (Tholl et al. 2006), VOCs produced by belowground plant organs have been analysed mainly using GC-MS and PTR-MS (Table 1). A major drawback with GC-MS is that VOCs need to be sampled and concentrated before being injected into the injection port of a gas chromatograph. Belowground VOCs can be collected using static sampling methods such as SPME or solvent microextraction (HSME). These methods concentrate VOCs located in the headspace of a sample either in a small volume of solvent (for HSME) or on a fused silica fibre coated with ab/adsorbent materials (for SPME) (Tholl et al. 2006; Jassbi et al. 2010). Depending on the physico-chemical properties of the solvent used in HSME or on the characteristics of both the liquid phase (polarity and film thickness) and porous particles (specific surface area, pore sizes and distribution) used to coat the SPME fibres, the selectivity of the sampling method can be adjusted for VOCs of known polarity and volatility (Shirey 1999; Tholl et al. 2006). Both SPME and HSME have been successfully applied to crushed root tissues (Rasmann et al. 2005; Hiltpold et al. 2011; Laznik et al. 2011; Erb et al. 2011; Lawo et al. 2011; Robert et al. 2012a), isolated root parts (Palma et al. 2012; Weissteiner et al. 2012; Fiers et al. 2013; Gfeller et al. 2013) and unexcavated root systems (Jassbi et al. 2010; Weissteiner et al. 2012). In addition to these techniques,

passive sampling approaches involving the use of polydimethylsiloxane (PDMS) sorbents were successfully used to collect non-polar compounds (thiophenes) that are constitutively released by *Tagetes* roots (Mohney et al. 2009), and VOCs that are emitted by *Taraxacum* sect. *ruderalia* roots growing in a mesocosm (Eilers et al. 2015). Compared with dynamic sampling devices, these static sampling methods are easier to set up and allow the rapid identification of VOCs produced by root tissues that were extracted or not from the soil. In situ soil VOC collection on packed adsorbents using dynamic sampling methods have also been used with root systems that were initially transplanted in an autoclaved sandy soil (Ali et al. 2010, 2011; Hiltpold et al. 2011) or with roots growing in a semi-vertical rhizotron (Abraham et al. 2015). In comparison with static sampling methods, the use of a purified airflow to trap VOCs located in the soil porosity allows the emission rate of VOCs emitted by plant roots to be measured in situ (Rasmann et al. 2012; Hiltpold et al. 2013), but it has the disadvantage of modifying the composition of the soil atmosphere if ambient air is used for the sampling of VOCs. Several packed carbon-based adsorbents or organic polymers are commercially available for the concentration of VOCs using a dynamic sampling device. As these materials do not have the same selectivity for VOCs, it is often necessary to combine different matrices (e.g., in multi-bed tubes) in order to trap VOCs of different polarity and volatility (Tholl et al. 2006). Whatever the sampling method used for VOC trapping, the extraction of roots from the soil prior to VOC collection can induce the release of VOCs by roots that had been mechanically damaged during the excavation process. As these molecules would not have been emitted by undisturbed root systems, experimental devices enabling VOCs to be sampled without extracting the roots from the soil are therefore needed for a better characterisation of root-emitted VOCs (Inderjit and Dakshini 1995; Jassbi et al. 2010; Abraham et al. 2015).

Once they have separated by GC, VOCs can then be detected by MS and tentatively identified by comparing their mass spectra with those stored in mass spectral databases. These identifications can then be confirmed by comparing calculated retention indices and MS data with those of authentic standards injected under the same chromatographic conditions. The significant volatile background associated with the soil ecosystem, however, complicates the identification and quantification of VOCs emitted at low concentrations in the soil

Fig. 3 Diagram of experimental devices designed to study plant-plant interactions mediated by root VOCs. (**a**) Active/dynamic exposure system. A pump (1) pushes clean air into a glass bottle (4a) filled with soil and containing the growing roots of a plant species A (5, emitter plants). The incoming air is filtered on a cartridge filled with activated charcoal (3). The air containing VOCs emitted by the roots of the plant species A is sent to the bottom of a PTFE container (8) filled with soil and containing the growing roots of a plant species A (intraspecific interaction) or B (interspecific interaction) (9, recipient plant). A PTFE/glass airflow meter (7) and a flow divider (2) are used to measure and control the airflow rate of the system, respectively. All connections are made via PTFE/glass tubing (6). (**b**) Passive/static exposure systems. VOCs emitted by the roots of a plant species A (4a) or by slow-release dispensers (4b) in a glass bottle move passively to the bottom of a PTFE container (8) filled with soil and containing the growing roots of a plant species A (intraspecific interaction) or B (interspecific interaction) (9, recipient plant). The emitter compartments are sealed with a non-porous synthetic rubber paste in order to prevent air leakage. (Drawing: Ir Carolina Levicek)
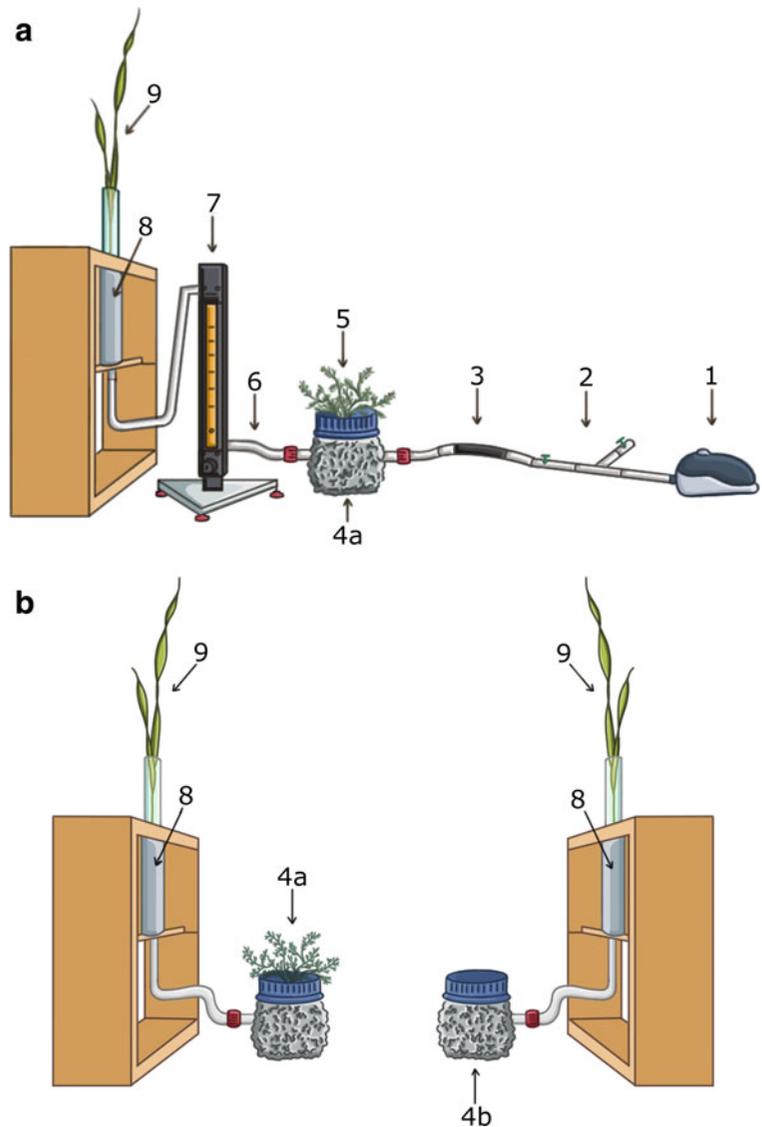
atmosphere because both VOCs released by the roots and the soil environment (including microbial VOCs) are trapped during the sampling of VOCs and injected into the chromatographic column. In order to facilitate the quantification of VOCs emitted by unexcavated root systems, the use of a mass spectrometer synchronously in SCAN (VOC identification) and Selected Ion(s) Monitoring (SIM, VOC quantification) modes can help to overcome this problem. In SIM mode, only the *m/z* ratios possessing a high specificity for the target root-emitted VOCs and a low specificity for the volatile background (the 'noise' of a chromatogram) will be filtered by the mass spectrometer. The full mass spectra

obtained in SCAN mode will be used to identify the target VOCs following the procedure described earlier.

PTR-MS has been shown to be an efficient tool for the real-time analysis of root-emitted VOCs in situ (van Dam et al. 2012; Danner et al. 2012; Crespo et al. 2012; Danner et al. 2015). The identity of the molecules entering the ionization chamber, however, cannot be determined using the mass spectral data acquired with this technique because only the mass of a small number of product ions (particularly cluster ions) can be obtained (Campos-Herrera et al. 2013). Combining GC-MS and PTR-MS analyses offers a promising tool for the study of VOCs emitted by roots in their rhizosphere by

exploiting the advantages of both analytical techniques. Whereas GC-MS enables biogenic VOCs to be rapidly identified by comparing their recorded mass spectra with those contained in mass spectral databases, PTR-MS enables the temporal dynamics of root-emitted VOCs to be monitored with a high time resolution, particularly for highly volatile and low molecular weight molecules that are not easily trapped using packed adsorbents prior to GC-MS analyses (Danner et al. 2012; Crespo et al. 2012).

Aboveground, the roles played by volatile cues in interplant signalling have been investigated using various types of experimental devices, including sealed (Farmer and Ryan 1990; Arimura et al. 2000a; Engelberth et al. 2004) or open-flow chambers (Shulaev et al. 1997; Ninkovic 2003; Ton et al. 2006) containing detached leaves/branches or intact plants, and most of these experimental set-ups have been criticized for their lack of ecological relevance (Baldwin et al. 2006; Paschold et al. 2006). In addition to these assays performed under laboratory conditions, field experiments (Karban et al. 2000; Dolch and Tscharntke 2000; Heil and Silva Bueno 2007) and bioassays using transgenic plants unable to release ('mute emitters') or perceive ('deaf receivers') the key volatile signals (Baldwin et al. 2006; Paschold et al. 2006; Inderjit et al. 2009) have demonstrated that VOCs can act as interplant signals in nature. Belowground, original experimental devices have been designed to study the roles played by root-emitted VOCs in biotic interactions. For example, sand-filled olfactometers have been successfully used to test the attractiveness of root volatiles for entomopathogenic nematodes (Rasmann et al. 2005; Ali et al. 2010). With regard to the roles played by root VOCs in plant-plant interactions, only in vitro experiments have been performed to test the involvement of these compounds in interplant signalling (Ens et al. 2009; Jassbi et al. 2010). Because the experimental conditions do not reflect those found in a natural population (VOC concentrations, absence of soil, exposure of shoots to VOCs emitted by roots, etc.), this type of experiment has been criticized because it does not fully demonstrate the role of isolated chemicals in plant-plant interactions in nature (Inderjit and Dakshini 1995; Inderjit and Weston 2000; Inderjit and Callaway 2003; Inderjit and Nilsen 2003). Given these criticisms, several aspects of the experimental set-up need to be carefully addressed in order to test the implication of root-emitted VOCs in interplant signalling: (1) the ecological relevance of the biological model (do the emitter and receiver plants grow next to each other in a natural population?); (2) the developmental stages of the emitter and receiver plants used in the bioassays (how old are the emitter plants when they start synthesising and releasing VOCs? How old are the receiver plants when they start to be exposed to VOCs emitted by their neighbour in a natural population?); (3) the actual emission rates of VOCs released in the soil by unexcavated root systems; (4) the environmental factors modulating the emission of VOCs, (5) the environmental fate of VOCs in the rhizosphere; and (6) the possibility of differentiating the effects of volatile cues from that of resource competition. Because of their high vapour pressure at ambient temperatures, all the volatile compounds (VOCs and small inorganic volatiles such as O_2 and CO_2) located in a compartment containing one or more emitter plants can move to a second compartment containing one or more recipient plants. They can travel from one compartment to another either passively (Park et al. 2015) or actively using a purified airflow at a controlled flow rate (Ninkovic 2003; Ton et al. 2006). With regard to belowground biotic interactions, such systems have been used to expose the roots of *A. thaliana* plantlets to the volatiles released by a Gram-negative rhizobacteria (*Serratia odorifera*) cultivated in a liquid medium (Kai and Piechulla 2009) or to demonstrate the volatile-mediated growth promotion of tobacco plantlets (*Nicotiana tabacum*) by *Pseudomonas fluorescens* strain SS101 (Park et al. 2015). With these types of experimental devices, it is also possible to test the effects of particular VOCs on recipient plants using slow-release formulations of the pure chemical standards placed in the emitter compartment (Heuskin et al. 2011). When focusing on root-root interactions, the source of VOCs should be unexcavated root systems growing in a soil and, depending on the issues being investigated by the experimenter, roots can be submitted to biotic and/or abiotic stresses or left undamaged. Morphological (biomass production and allocation, root system architecture), physiological and/or molecular parameters can then be measured on plants that have been exposed to volatiles. Given that the roles played by root VOCs in interplant signalling have been far less studied than aboveground VOC-mediated plant-plant interactions, we would argue that the experimental devices described above can be modified in order to target root VOCs and investigate their ecological roles in interplant signalling (Fig. 3).

Conclusions

Plant roots are able to synthesise and release a large number of organic compounds in the rhizosphere as solutes or volatile compounds that can diffuse at various distances from the source, depending on their physico-chemical properties and environmental parameters (soil type, water content, microbial population, etc.). It is now well documented that root VOCs can act as signals mediating belowground biotic interactions between plants and organisms of the second and third trophic levels but, surprisingly, much less is known about their potential roles in between- and within-plant signalling (root-root and root-shoot). In this review, our aim was to show that root-root interactions mediated by volatile cues deserve more research attention and that the analytical tools and methods developed to explore volatile-mediated plant-plant interactions aboveground can be adapted to investigate the roles played by VOCs in root-root signalling. Given the growth in our knowledge about soil chemical ecology (van Dam 2014), particularly in relation with volatile-mediated biotic interactions, we conclude that future research in this area should include well-designed and ecologically relevant experiments aimed at investigating the roles played by root-emitted VOCs in between- and within-plant signalling.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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