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REVIEW

Belowground volatiles facilitate interactions between plant roots and soil organisms

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Abstract Many interactions between organisms are based on the emission and perception of volatiles. The principle of using volatile metabolites as communication signals for chemo-attractant or repellent for species-specific interactions or mediators for cell-to-cell recognition does not stop at an apparently unsuitable or inappropriate environment. These infochemicals do not only diffuse through the atmosphere to process their actions aboveground, but belowground volatile interactions are similarly complex. This review summarizes various eucaryotes (e.g., plant (roots), invertebrates, fungi) and procaryotes (e.g., rhizobacteria) which are involved in these volatile-mediated interactions. The soil volatiles cannot be neglected anymore, but have to be considered in the future as valuable infochemicals to understand the entire integrity of the ecosystems.

Keywords Volatiles · VOCs · Belowground · Soil · Rhizosphere · Rhizobacteria · Plant roots · Soil fungi

Abbreviation

VOC	Volatile organic compound

Introduction

The ability to synthesize, emit and/or perceive volatiles is established not only in the eukaryotic world but also in prokaryots. The odors enable information exchange between organisms because of the special properties of these molecules. The majority of volatile organic compounds (VOCs) tend to be lipophilic, they have a small molecular mass (less than 300 Da) and a high vapor pressure (0.01 kPa or higher at 20°C). These features together support evaporation. They are produced in the aqueous cellular phase and are released when the solution equilibrium is exceeded. In principle volatiles can be emitted via diffusion or alternatively via passive or active transport mechanisms (Effmert et al. 2006). Most of the volatile compounds belong to the following three chemical groups: terpenoids, phenylpropanoids, and fatty acid derivatives. Individual scent compounds or bouquets of odors are essential and suitable for inter- and intra-species recognition, attraction, and defense in the respective ecological niche, because they can be detected in small amounts by the organisms and diffuse over long distances in the atmosphere. Especially due to this latter property, until recently most of the research on volatiles centered around organisms or parts of plants, which live aboveground or possess aerial parts (Laothawornkitkul et al. 2009). But scents are not only found in the atmosphere, they also appear in the soil and permeate through the air-filled pores. The efficiency of volatile penetration in the soil however, depends on the type of mineral, the texture and particle architecture (Aochi and Farmer 2005), and in fact, different VOC exchange rates indicate that soils have the potential to act as VOC sinks rather than VOC sources (Asensio et al. 2007). Recently, the importance of belowground volatile trafficking attracted more notice since soil-dwelling organisms and underground

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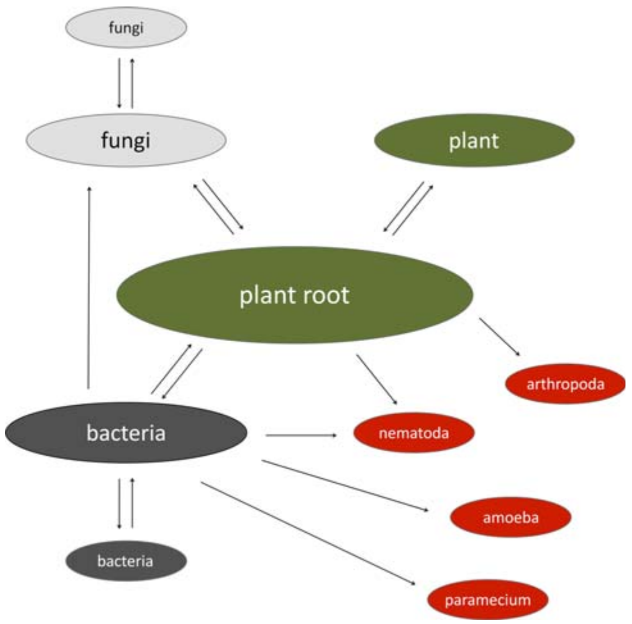

Fig. 1 Multiple volatile mediated interactions in the soil. The scheme presents the status quo of known belowground intra- and interspecies interactions. *Arrows* may indicate positive and/or negative effects. For further details see text and Table 1 in the supplement

growing parts of plants were shown to synthesize, excrete, and perceive volatiles (Fig. 1). These soil organisms and their populations can use these volatile compounds as infochemicals, probably to a much greater extent than previously assumed. Some aspects of this "newly discovered zone" for volatiles and their potential for diverse interactions are described here.

Plant root volatiles

It has been realized that the confrontation plants experience with other organisms particularly in the underground is an extremely important feature of plant survival. The soil zone surrounding the roots of plants (rhizosphere) provides a very attractive environment for a vast number of organisms, since plants can release up to 20% of the photosynthetically fixed carbon by roots (Barber and Martin 1976). Root exudates are chemically diverse, beginning with compounds such as amino acids and amides, sugars, organic acids, phenols, as well as a wide variety of secondary metabolites, polysaccharides, and proteins of high molecular mass (Roshchina and Roshchina 1993). But also volatile compounds could be detected in the rhizosphere of several plant species. Volatile metabolites emitted in the underground enable plants to influence directly or indirectly the community of soil-dwelling organisms (summarized in Table 1 of the supplement), and plants attempt to defend themselves against herbivores and plant pathogenic fungi and bacteria, support beneficial symbioses, and combat competitive plant species (Nardi et al. 2000) (Fig. 1).

Root volatile mediated interactions between plants

The release of allelochemicals (organic compounds) into the rhizosphere that mediates the interaction between plant species, can be performed by (1) volatilization, (2) leaching from leaves, (3) degradation of plant residues, and (4) root exudation (Bertin et al. 2003 and references therein). Muller and Muller (1964) showed for the first time an inhibitory effect of volatiles, especially monoterpenes on the seed germination and growth of several plant species. However, they were not aware that belowground plant parts could be the source of the volatile allelochemicals. In the meantime, several studies demonstrated the emission of terpenoids by plant roots, particularly obvious in forest soils (Hayward et al. 2001; Rohloff 2002; Lin et al. 2007). An indirect allelopathic effect of several monoterpenoids via inhibition of nitrification in forest soils was also described (Paavolainen et al. 1998).

Furthermore, a blend of unidentified root volatiles of *Echinacea angustifolia* showed allelopathic effects on different plant species like *Lactuca sativa*, Switchgrass (*Panicum virgatum*) and Prairie Dropseed (*Sporobolus heterolepis*) (Viles and Reese 1996).

Root volatiles for communication with microbes

The microbial community in the rhizosphere, usually limited by carbon availability but carbon-containing root volatiles, especially monoterpenes (e.g., geraniol) contribute significantly to the belowground carbon cycle (Zak et al. 1994; Owen et al. 2007). Furthermore, *Pseudomonas fluorescens* and *Alcaligenes xylosoxidans* were able to use α-pinene as sole carbon and energy source (Kleinheinz et al. 1999). The indirect allelopathic effect of several monoterpenoids by inhibiting the nitrification in forest soils may be due to a direct effect on the cell physiology of nitrifiers or immobilization of ammonium by microbial activity (Paavolainen et al. 1998). Another ecological important effect of plant emitted monoterpenes was the potential of enhancing the biodegradation of xenobiotic contaminants in soils (McLoughlin et al. 2009).

The root emission of carbon dioxide as primary plant metabolite is a general feature of all plant species (Johnson and Gregory 2006). Bécard and Piché (1989) were the first, who could demonstrate that carbon dioxide is a crucial root volatile, which stimulates hyphal growth of vesicular–arbuscular mycorrhizal fungus. They showed a synergistic interaction between volatile and exudated root factors on *Gigaspora margarita*, an obligate biotrophic symbiont. Elevated carbon dioxide promoted hyphal length of arbuscular mycorrhizal fungi, and depresses the growth of non-mycorrhizal fungi at low nitrogen availability. One example for the attraction of bacteria via carbon dioxide was *P. fluorescens* (Scher et al. 1985). Other simple compounds like acetaldehyde, acetone, acetic acid, ethanol and methanol were emitted by *Arabidopsis thaliana* roots (Steeghs et al. 2004). Acetaldehyde is known for its antifungal effect against *Alternaria alternata*, *Botrytis cinerea*, and *Colletotrichum acutatum* (Almenar et al. 2007).

Root volatiles are important for defense against microbial populations. Effective against the fungal root pathogen, *Fomes annosus* was the monoterpene β-phellandrene (Cobb et al. 1968), which was emitted by the roots of the alexanders, *Smyrnium olusatrum* (Bertoli et al. 2004) and by the rhizomes of *Rhodiola rosea* (Rohloff 2002). The blend of the rhizome of *R. rosea* comprised 86 compounds, several of them being biologically active (Smith 1965; Cobb et al. 1968; Cheng et al. 2008; Park et al. 2009; Oyedemi et al. 2009). The monoterpene 1,8-cineol, released for example by *A. thaliana* roots in response to compatible bacterial and fungal pathogens (Steeghs et al. 2004), had antimicrobial potential against several microbes (Kalemba et al. 2002; Vilela et al. 2009).

Symbiotic microbes were also negatively affected, e.g., by terpenoids. Roots of *Pinus sylvestris* infected by the mycorrhizal fungus *Boletus variegates* lead to an increased production and/or accumulation of volatiles compared to control roots (Krupa and Fries 1971). These volatiles, primarily terpenes and the sesquiterpene longifolene inhibited the vegetative growth of *B. variegates* and *Rhizopogon roseolus* (Melin and Krupa 1971).

Effects of root volatiles on arthropods

Host choice of soil-dwelling arthropods via root volatiles is a common phenomenon. Several disulfides and trisulfides were identified as volatile components of onions, *Allium cepa* (Carson and Wong 1961), which possessed strong attractive effects on the underground living larvae of *Delia antiqua* (Matsumoto 1970). Volatiles of the fresh perennial ryegrass roots attracted larvae of *Costelytra zealandica* (Sutherland 1972), and roots of *Medicago sativa* and *Trifolium pratense* allured larvae of *Sitona hispidulus* (Wolfson 1987). Also adult insects can locate host plants for oviposition in the underground via volatile compounds, e.g., *Hylobius abietis* was positively or negatively affected, depending on the concentrations of the conifer root volatiles (Nordlander et al. 1986, Selander et al. 1976).

A direct correlation between the composition of volatiles and the choice of the host plants carrot roots (*Daucus carota* ssp. *sativus*) or oak roots (*Quercus* sp.) was shown for the larvae of the forest cockchafer *Melolontha hippocastani* (Weissteiner and Schütz 2006). These larvae had a selective preference for carrots, which mainly emitted monoterpenes, while oak roots primarily released fatty acid derivatives. Females of *Neoseiulus cucumeris*, predatory mites of rust mites (*Aceria tulipae*) responded to belowground volatiles of tulip bulbs infested by *A. tulipae* but not to volatiles of untreated or wounded bulbs (Aratchige et al. 2004). These induced unknown root volatile cues were used for indirect plant defense, such as attracting natural enemies of the herbivores. Neveu et al. (2002) documented this phenomenon also for the larvae of *Delia radicum* feeding on roots of turnips, which induced root volatiles that allured the endoparasitoid wasp *Trybliographae rapae*. Production and release of volatile host root attractants by *Pseudotsuga menziesii* due to the infection with the root colonizing fungus *Ceratocystis wageneri* lead to an increased attraction of *Hylastes nigrinus* and *Steremnius carinatus* (Witcosky et al. 1987). Furthermore, Tapia et al. (2007) showed that responses of the clover root borer *Hylastinus obscures* to root volatiles depended on the age of the host plant *T. pratense*. Qualitative and quantitative differences of the VOC profiles either attracted *H. obsucurus* or acted as deterrent. Also cultivar-specific differences of volatile blends of underground plant parts resulted in different resistance to herbivorous arthropods (Guerin and Ryan 1984). Intact roots of resistant carrot cultivars emitted generally less chemo-attractive volatiles, but emanated trans-2-nonenal as a strong repellent that immobilized and killed the larvae of *Psila rosae*.

Soil insects, larvae as well as adults were able to detect very small differences in the concentration of the CO_2 and moved towards the carbon dioxide sources (Johnson and Gregory 2006). Conversely, a repellent effect of high concentrations of carbon dioxide may cause disorientation or even anesthesia of the arthropods. The role of carbon dioxide as a common cue changing the movement of the insects by functioning as a ‘search trigger’ was accentuated, but the orientation of insects within carbon dioxide gradients could be “masked” by gustatory and olfactory stimuli exudated by roots (Reinecke et al. 2008).

Root volatiles for communication with nematodes

The underlying mechanism of plant-parasitic nematode orientation towards their hosts is an important aspect for agriculture. Carbon dioxide is one of the root volatiles identified as attractant for these plant parasites, e.g., *Meloidogyne incognita* (Pline and Dusenbery 1987), *Ditylenchus dipsaci* (Klinger 1963), and *Caenorhabditis elegans* (Dusenbery 1987). Plants may use some known nematicidal cues like benzaldehyde, thymol, limonene, neral, geranial, and carvacrol for defending themselves against the attacker in the underground (Bauske et al. 1994; Oka et al. 2000;

Rohloff 2002; Kokalis-Burelle et al. 2002; Bertoli et al. 2004; Weissteiner and Schütz 2006).

In contrast, some nematodes were used by plants for the indirect defense of plant herbivores in the underground (van Tol et al. 2001). When the evergreen conifer *Thuja occidentalis* or the strawberry roots were attacked by the weevil *Otiorhynchus sulcatus*, it emitted unidentified volatile attractants of the parasitic nematode *Heterorhabditis megidis* (Boff et al. 2001). *H. megidis* also was attracted by (E)-β-caryophyllene, which was released upon feeding damage of corn roots and thus protected corn against *Diabrotica virgifera virgifera*, an extremely devastating pest that is spreading worldwide (Rasman et al. 2005). Such belowground tritrophic interactions depend specifically on the volatile emission and perception profiles of the plant species, plant herbivores and nematodes (Rasman and Turlings 2008).

Soil fungal volatiles

Wild boars have always made use of the scents of truffles (*Tuber* spp.) to locate these fungi growing in the underground. Truffles can emit up to 200 volatile metabolites. Typical components have a chain length of eight carbon atoms, for example, trans-2-octenal, 1-octen-3-ol, and octanol, which are the main components of the typical mushroom odor (Chitarra et al. 2004; Buzzini et al. 2005). Interestingly, the various types of truffles differ in their scent spectra, e.g., due to altered proportions of sulfurous substances; *Tuber borchii* and *T. melanosporum* were distinct to *T. indicum* or *T. magnatum* (Menotta et al. 2004; Splivallo et al. 2007; Gioacchini et al. 2008). New investigations revealed that truffles live in symbiosis with various yeasts, which also contributed to the scent bouquet (Buzzini et al. 2005).

Fungi or fungal parts growing underground (e.g., mycelia) are just as capable of emitting volatile metabolites as are fruiting bodies growing aboveground (Splivallo et al. 2009a) (Fig. 1). The fungal volatiles may be of importance for self-recognition and/or defense processes. The VOCs were also used in interspecies recognition, for example, when hyphae of different fungi (*Hypholoma fasciculare* and *Resinicium bicolor*) came into contact (Hynes et al. 2007). Approaching fungi released a different set of volatiles, which caused growth retardation of both fungi so that they can "avoid" each other. Fungistasis (soil disease suppressiveness) may also result from the presence of fungal volatiles, which e.g., blocked the germination process or affected the protein synthesis (Strobel et al. 2001; Wheatley 2002; Humphris et al. 2002; Chuankun et al. 2004). 1-octen-3-ol emitted by fungal spores were shown to be a volatile germination self-inhibitor (Chitarra et al. 2004). Furthermore, VOCs emitted from the antagonistic *Fusarium oxysporum* wildtype negatively influence the mycelial growth of different pathogenic *F. oxysporum formae speciales* by repressing (virulence) gene expression (Minerdi et al. 2009).

Volatile metabolites involved in the interaction of plant roots (e.g., trees) and establishment of infection by mycorrhizing fungi was also documented, e.g., between *Pinus sylvestris* and *Boletus variegatus* (Krupa and Fries 1971), and *T. borchii* and its host plant *Tilia americana* (Menotta et al. 2004). Particularly ethylene emission of truffle mycelia regulated root morphogenesis by reducing primary root length, increasing secondary root formation and hairiness of the host plant *Cistus incanus* (Splivallo et al. 2009b). However, there were not only positive effects on plants. The emission of truffle VOCs could cause zones of scarce herbaceous growth ("burnt areas"), and mixtures of VOCs (e.g., high concentrations of ethylene) from different truffles have been shown to inhibit growth of *A. thaliana* in the laboratory (Splivallo et al. 2007, 2009b).

Rhizobacterial volatiles

A rich source of volatile compounds that likewise had not been explored extensively is the bacterial realm (Stotzky and Schenck, 1976). 350 bacterial volatiles were summarized by Schulz and Dickschat (2007). The widely differing species of bacteria were capable of emitting a variety of volatile compounds, comprising fatty acid derivatives, terpenoids, aromatic, nitrogenous, and sulfurous compounds. Interestingly, many of the substances found in the bacterial scent spectra have not been identified yet and their biological roles are also unknown. By referring to a few known examples and by comparison with known functions of scents from other groups of organisms, it is assumed that the bacterial scents serve as signal compounds for interspecies and intraspecies communication or from cell to cell, for the disposal of excess carbon compounds, or as substances that stimulate or inhibit growth (Fig. 1).

The most well-known scent emitted by bacteria living in the soil is geosmin, emanating the typical earthy odor (Gerber and Lechevalier 1965). It was also recognized as "off-flavor" of contaminated food, wine, and water (Darriet et al. 2000). Geosmin is mainly produced by *Streptomyces* species (Gerber 1968; Medsker et al. 1968; Dickschat et al. 2005b), but also by cyanobacteria (*Anabena* spp., *Oscillatoria* spp.; Izaguirre et al. 1982), myxobacteria (Yamamoto et al. 1994; Dickschat et al. 2004, 2005a), liverworts (Spörle et al. 1991), and soil-dwelling, aquatic or airborne fungi (Mattheis and Roberts 1992; Breheret et al. 1999).

Rhizobacteria, which live in the soil in close association with the roots of plants, have also been identified as producers of volatile compounds, whereby primarily bacteria of the genera *Bacillus*, *Serratia,* and *Pseudomonas* were investigated (Ryu et al. 2003; Fernando et al. 2005; Chaurasia et al. 2005; Kai et al. 2007; Zou et al. 2007). Beside CO_2 emission, *Serratia odorifera* emitted a complex volatile spectrum (Kai et al. 2007; Kai and Piechulla 2009). Two *Bacillus* species emitted 2,3-butanediol and acetoin, which promoted the growth of *A. thaliana*, by regulating the auxin homeostasis and cell expansion (Zhang et al. 2007), and augmenting photosynthetic capacity by increasing photosynthetic efficiency and chlorophyll content (Zhang et al. 2008). In addition, a racemic mixture of 2,3-butanediol could also induce resistance of *A. thaliana* against pathogens (Ryu et al. 2004; Farag et al. 2006). This finding was supported, since during co-cultivation of basil plants and *Bacillus subtilis*, volatile oils, comprising α-terpineol and eugenol, accumulated in the plants possibly to defend microbial infestation (Banchio et al. 2009). Furthermore, the volatiles of antagonistic rhizobacteria such as *Serratia*, *Pseudomonas*, and *Stenotrophomonas* caused a dramatic inhibition of Arabidopsis root and leaf growth (Vespermann et al. 2007; Kai et al. 2009).

Negative and positive growth effects of bacterial volatiles were documented on phytopathogenic and non-pathogenic fungi (e.g., *Rhizoctonia solani, Verticillium dahliae*, *Sclerotinia sclerotiorum*, *Aspergillus niger*, *Neurospora crassa*, *Paecilomyces carneus*, *Phoma betae*) (Fiddaman and Rossall 1993; Kai et al. 2007; Vespermann et al. 2007; Fernando et al. 2005; Chuankun et al. 2004; Zou et al. 2007). Most of the bacteria investigated till date exerted negative effects on mycelial growth, sporulation, and spore germination of the fungi. Bacterial volatiles with a positive effect on sclerotial and fruiting body development as well as mycelial growth had been reported in association with pseudomonads and further unidentified bacteria (Hayes et al. 1969, Mackie and Wheatley 1999). The mycorrhiza-helper-bacterium (MHB) *Pseudomonas monteilii* was also capable of supporting the hyphal growth of *Pisolithus albus* (genus of the “pea stone” fungi), resulting in promotion of mycorrhizal development and, in turn, of plant growth (Duponnois and Kisa 2006). The observed effects and their strength depended on the growth conditions of the bacteria, e.g., the addition of L-glucose led to significantly less synthesis of antifungal volatiles by *B. subtilis*, compared to D-glucose (Fiddaman and Rossall 1994).

Beside fungi, unicellular and multicellular animals are also members of the rhizosphere community. In respect to rhizobacterial volatiles, the latter were investigated little so far. We showed that the nematode *C. elegans* was attracted by blends of bacterial volatiles from *S. odorifera* and *P. fluorescens* (Kai et al. 2009). Both bacteria excreted dimethyl sulfides, which were previously considered as a plant chemo-attractant (Borg–Karlson et al. 1994). For some compounds, such as trimethylamine, benzaldehyde, cyclohexanol, decanol, and dimethyl disulfide negative biological effects had been observed (Chuankun et al. 2004; Fernando et al. 2005; Kai et al. 2009).

In a comprehensive study involving 200 bacterial isolates (mostly *Bacillus* spp.) from the rhizosphere of tobacco plants, 149 and 165 of the bacterial isolates influenced the nematodes *Panagrellus redivivus* and *Bursaphelenchus xylophilus* negatively, respectively (Gu et al. 2007). Rhizobacterial volatiles also inhibited protozoan growth. Co-cultivation of *Serratia*, *Bacillus* and *Xanthomonas* with *Acanthamoeba castellanii* and *Paramecium caudatum* was lethal to these protozoans (Kai et al. 2009).

Volatile compounds can also serve as signals in cell-to-cell communication. Indole is a typical odor component of the intestinal and soil bacterium *E. coli*, served as regulator of various genes and was an inhibitor of biofilm formation administrated by *E. coli*, *P. fluorescens*, and *P. aeruginosa*. Similarly, *S. plymuthica* exerted varies VOC dependent effects on the growth of *R. solani* and *V. dahlia*e, by regulating VOC emission via the quorum sensing signal *N*-acyl homoserinlactones (AHLs) (Müller et al. 2009).

Conclusions

The interactions between organisms in the soil that are based on the emission and perception of volatiles are just as diverse as that already shown for aboveground organisms. To round out the picture of communication within ecosystems certainly the ability of organisms growing in the underground and using volatiles as infochemicals cannot be neglected anymore, but have to be considered in the future to understand its entire integrity. Most of the research so far was performed with complex blend mixtures, comprising known as well as structurally unknown compounds, of which often the bioactive compounds remain to be identified and laboratory experimental set ups need to be improved to simulate the natural habitat. Beside this, however, it is conceivable that these bioactive substances constitute a new source of “volatile antibiotics” that can be employed in agriculture against animal and plant pathogens.

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