Characterization of Bacterial Volatiles and Their Impact on Plant Health Under Abiotic Stress

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Abstract

Bacterial released volatile compounds (VOCs) in air enable bacteria to interact with their surrounding environment. Soil bacterial volatiles are known to contribute to plant interactions, and several studies also identified their influence on plant stress tolerance. Plant growth-promoting rhizobacterial (PGPR)-mediated VOCs are reported to increase seedling emergence, plant weight, crop yield, and stress resistance. The present chapter describes the characterization of different bacterial VOCs and their roles in enhancement of plant abiotic stress tolerance, a new research area, with potential agriculture applications.

Keywords

Abiotic stress • Bacterium • Plant growth-ptomoting bacterium • Volatile organic compounds • C4-bacterial volatiles

2.1   Introduction

Plants live naturally with many microorganisms, and the nutrient-rich environment of the rhizosphere is especially conducive to interactions between microorganisms and plants. Plants release different products through the roots into the surrounding

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area that attract a tremendous diversity of microorganisms (Perry et al. 2007). Some of these microorganisms have no observable effects on plant; others enhance or inhibit plant growth. Plant growth-promoting rhizobacteria (PGPR) can stimulate plant growth or increase tolerance by producing nonvolatile substances, such as the hormones auxin and cytokinin, as well as 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which reduces plant ethylene levels, and siderophores, which facilitate root uptake of metal nutrients. In addition, certain PGPR promote plant growth by emitting volatile organic compounds (VOCs) (Vaishnav et al. 2017). Volatile compounds have low molecular weight (<300 Da) and high vapor pressure (0.01 kPa at 20 °C) in nature that can readily evaporate and diffuse through heterogeneous mixtures of solids, liquids, and gasses (Audrain et al. 2015). The spectrum of bacterial VOCs is influenced by heterogeneity of soil, which depends on bacterial/plant-secreted metabolites. Some VOCs are specific for a phylogenetic group and used for taxonomic purposes (Kai et al. 2016). The volatile compounds are generally produced as metabolic end products of anaerobic fermentation processes and extracellular degradation of complex organic molecules. The widely differing species of bacteria were capable of emitting a variety of volatile compounds, comprising of fatty acid derivatives, terpenoids, and 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 (Wenke et al. 2010). Many investigations concerning VOC pattern of soil microorganisms were performed under different treatment conditions. Bolm et al. performed a large screening of volatile-mediated effects on *Arabidopsis thaliana*. The VOC effect was found highly dependent on cultivation medium and the inoculum quantity. The production of beneficial VOC compound butanediol was found higher on the nutrient-rich media LB and MR-VP and less pronounced on MS and Angel. In another study, *P. simiae* strain AU changed VOC pattern in the presence of soybean seeds and sodium nitroprusside (SNP, a nitric oxide donor) treatment. Some compound expression was enhanced in the presence of soybean seedlings, and few compounds like 4-nitroguaiacol and quinolone are newly expressed in the presence of SNP. These compounds were showed significant enhancement of seed germination and higher fresh weight of soybean under 100 mm NaCl stress (Vaishnav et al. 2016). As a result of the increasing interests in VOCs in mediating plant-microorganism interactions, the present chapter focuses on the chemical nature of microbial VOCs, as well as the effects of microbial VOCs on tolerance level of plants under abiotic stresses.

2.2   Chemical Side of VOCs

Solid-phase microextraction (SPME) and dynamic headspace volatile analyses have revealed that PGPR strains have the requisite machinery to synthesize a wide range of volatiles, including short-chain aliphatic aldehydes, esters, alcohols, organic acids, ethers, ketones, sulfur compounds, and hydrocarbons.

2.3   Hydrocarbons

These products are derived from fatty acid biosynthetic pathways. Short-chain alkanes (decane to tetradecane) are found in bacteria, while longer hydrocarbons such as hexadecane are particularly abundant in cyanobacteria, which are also known for their ability to synthesize branched hydrocarbons (Audrain et al. 2015). In a volatiles profiling study, *Paenibacillus polymyxa* strain E681 was exclusively released long-chain C13 tridecane which augments ISR and protected *Arabidopsis* seedlings against the biotrophic pathogenic bacterium *Pseudomonas syringae* pv. maculicola ES4326 (Lee et al. 2012). The priming with pure tridecane compound at 10 mM increased 4.7-fold in transcription of pathogenesis-related gene (PR1) before pathogen challenge and 3.3-fold increase at 3 h after pathogen challenge. Some other hydrocarbons like isoprene, acetylene, cyclohexane, 1-undecane, and dodecane were also found in *P. polymyxa* E681-derived VOCs blend. An n-decanal volatile compound derived from different *Pseudomonas* sp. was found to completely inhibited *Sclerotinia sclerotiorum* suggesting its role in biological control (Fernando et al. 2005). Recently, Vaishnav et al. (2016) demonstrated the effect of pure tridecane compound on soybean seed germination under salt stress. Seed germination was found higher in the presence of tridecane as compared to control.

2.4   Ketones/Alcohols

PGPR strains *B. amyloliquefaciens* IN937 and *B. subtilis* GB03 were found to produce acetoin (3-hydroxy-2-butanone) compound that triggers growth promotion and resistance in *Arabidopsis* seedlings. The acetoin and its oxidized form 2, 3-butanediol are derived from anaerobic fermentation of pyruvate. In vitro production of 2, 3-butanediol is also favored in the presence of sucrose as a major nutrient in growth media (Ryu et al. 2004). 2R, 3R-butanediol derived from *P. chlororaphis* O6 was found as major determinant in inducing resistance to drought in *Arabidopsis* through an SA-dependent mechanism (Cho et al. 2008). In addition, short-chain-branched alcohols such as 3-methyl-1-butanol and 2-methyl-1-butanol were also found to accumulate in *B. amyloliquefaciens* IN937a producing VOCs. These compounds are formed by enzymatic conversion of branched chain amino acids, i.e., leucine and isoleucine via the Ehrlich pathway (Marilley and Casey 2004). Long-chain aliphatic alcohols (i.e., 1-octanol, 1-decanol, and 1-dodecanol) are commonly

associated with Enterobacteriaceae; they are produced through *β*- or *α*-oxidation of fatty acid derivatives, and thus, their concentration are markedly increased from cultures supplemented with fatty acids (Hamilton-Kemp et al. 2005). 1-Hexanol produced by *Pseudomonas* sp. (Fernando et al. 2005; Vaishnav et al. 2016) and *Bacillus* sp. (Chaurasia et al.) has been reported as a potential plant growth promoter and antifungal compound. During a large screening of VOCs, 1-hexanol was found most release compounds from 42 different bacterial strains and appeared to promote plant growth (Blom et al. 2011).

2.5   Acids

Short-chain fatty acids like acetic acid are derived from VOCs of an antagonist bacterium *Burkholderia tropica* which is found to inhibit the growth of four phytopathogenic fungi, *Colletotrichum gloeosporioides*, *Fusarium culmorum*, *Fusarium oxysporum*, and *Sclerotium rolfsii* (Tenorio-Salgado et al. 2013). A salt-tolerant PGPR bacterium *P. simiae* AU produced different types of acids in VOC blend, i.e., stearic acid, phthalic acid, acetic acid, oxalic acid, myristic acid, hexadecanoic acid, etc. The exposure of *P. simiae*-mediated VOCs is found to induce tolerance in soybean plants against salt stress (Vaishnav et al. 2016). These acids are major byproducts of anaerobic metabolism; indeed, they are formed during bacterial fermentation of carbohydrates.

2.6   Sulfur Compounds

Dimethyl disulfide (DMDS) and dimethyl trisulfide (DMTS) are produced by most of PGPR strains. Benzothiazole compound was derived from different *Pseudomonas* spp. and showed potential in the inhibition of sclerotial activity and enhanced salt tolerance in soybean plants (Fernando et al. 2005; Vaishnav et al. 2016).

2.7   Inorganic Compounds

Hydrogen cyanide is mostly produced by virulent bacterial strains (e.g., *Pseudomonas* or *Chromobacterium* species). It is a potent inhibitor of cytochrome *c* oxidase and of other metal-containing enzyme, hence responsible for plant-killing effects (Blom et al. 2011). Cyanide production by rhizosphere bacteria is considered as a plant growth-promoting trait which is used as biocontrol against phytopathogenic fungi (Voisard et al. 1989).

2.8   Test Systems

Two types of systems are mainly used for volatiles studies as follows: (a) a closed setup (Petri dish or box) and (b) a directed airflow in order to transport the volatiles to the plant.

2.9   Closed Systems

More than half of all volatile studies were operated by passive diffusion using partite Petri dishes. A plastic border separates the dish into two (I-shaped) or three (Y-shaped) compartments (Fig. 2.1a). Bacteria and plants/pathogens are inoculated in individual compartment which make them physically separate to each other. The exchange of VOCs is facilitated solely via headspace. To prevent the escape of VOCs, Petri dishes are sealed with parafilm. In order to extract the volatile compounds, experiment is performed in tripartite Petri dishes. In this, one partition contained bacterial culture, second inoculated with plant seeds/pathogen, and in third sterile-activated charcoal placed. Activated charcoal has a good adsorbent quality; therefore, it is mainly used to collect the VOCs in a closed setup. After incubation period, the activated charcoal is collected and washed with any organic solvent according to the aim of the study. In many studies, dichloromethane (DCM) was used to extract all trapped volatile compounds, which were posteriorly analyzed by gas chromatography-mass spectrometry (GC-MS). This way, Fernando et al. (2005) found that mycelial growth was completely inhibited in the presence of bacterial VOCs which streaked in a different compartment. Mycelial growth was unaffected by the presence of volatile-producing bacteria, when the third compartment of the
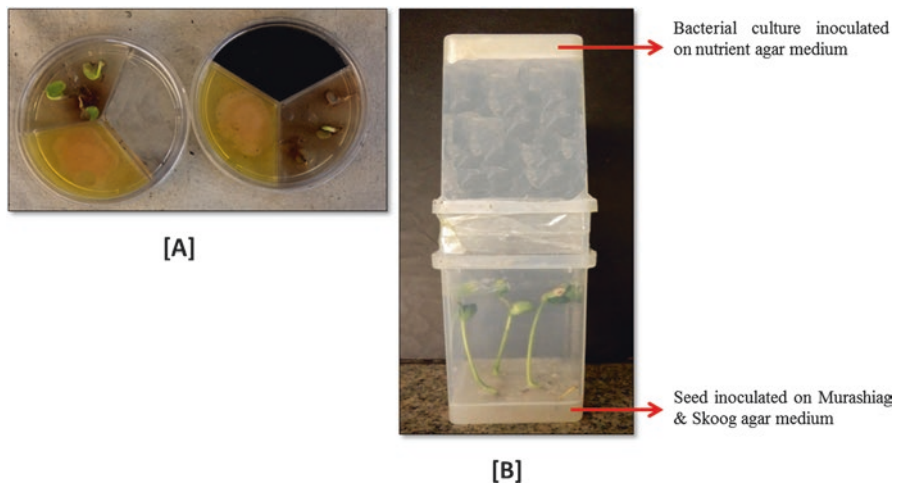

Fig. 2.1 Passive diffusion of VOCs in closed system (**a**) tripartite Petri plate with activated charcoal, bacterial culture and seed; (**b**) Magenta box

plates was amended with activated charcoal. Charcoal adsorbs volatiles as soon as they are produced, and hence no inhibitory effect was observed. Plant growth promotion was also observed with *partitie* Petri dish setup by Ryu et al. (2004), Blom et al. (2011), and Vaishnav et al. (2016). The limitation of this setup is narrow headspace; therefore, only young plant seedlings can be sampled. Most of the studies were performed with *A. thaliana* plants, because of its small size and its short life cycle. For other test plants and for attempts to use adult plants, bigger growth containers were designed (box systems) (Vaishnav et al. 2015) (Fig. 2.1b). In another approach, Park et al. (2015) inoculated *Pseudomonas fluorescens* SS101 in a plate which placed beneath the soil at the bottom of the pot. A filter is also placed above the plate to ensure that only VOCs could transfer between the plate and the soil. Tobacco seeds were sown onto the soil and after 4 weeks of sowing, the authors observed significant growth stimulation with an increase of fresh weight of tobacco.

2.10 Dynamic Air Stream Systems

In this system, a continue flow of purified air passed over bacterial culture plate and subsequently reached to targeted parts of plant (aerial/root) (Fig. 2.2). In this way, Kai and Piechulla (2009) performed experiment with *S. plymuthica*-derived VOCs by targeted aerial and roots of adult *A. thaliana* plants. For aerial part, they used a mini growth chamber in which VOCs enriched air directly reached from culture. For root, plants were kept in a perforated glass bowl and placed over a second glass bowl which attached with an air inlet. Air enriched with VOCs entered the lower compartment and reached to roots of the plants.

2.11 Characterization of Volatiles

The identification of volatiles is usually accomplished using gas chromatography coupled most often with mass spectrometry (GC-MS) in electron ionization mode (EI). The number of detectable volatiles in bacteria generally increases when
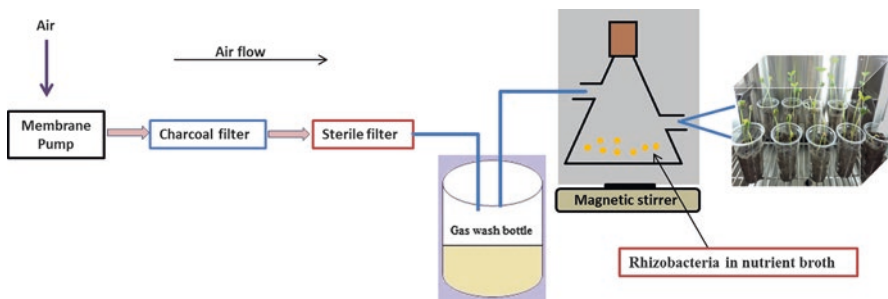

Fig. 2.2 Dynamic air stream system targeting the aerial plant parts

various techniques are applied. Hence, multiple approaches are used in combination with GC-MS., e.g., headspace airflow systems with GC-MS, trapping materials – static solid-phase microextraction (SPME) with GC-MS, and proton transfer reaction/mass spectrometry (PTR-MS). Headspace volatiles can be collected through air flow onto an absorbent filter and released by rinsing the filter with organic solvent. On the other hand, VOCs can be collected by SPME and directly released into a heated GC injector. SPME can extract volatiles from bacterial cultures in a relatively short amount of time and has been successfully used to collect them in several systems (Farag et al. 2013). In SPME, fiber plays role in absorbing of compounds based on their polarity and size. In the case of rhizobacterial volatiles, divinylbenzene/carboxen/PDMS fibers are mainly used. These fibers adsorb polar low molecular weight VOCs, which are the predominant VOCs released from rhizobacteria. Proton transfer reaction mass spectrometry (PTR-MS) technique allows online VOC measurements. This technique is also combined with GC or time of flight (TOF). After MS analysis, compounds are identified by comparison of their mass spectral fragmentation patterns with mass spectra libraries such as WILEY and NIST. Several times the identification cannot be possible on the basis of mass spectral libraries alone. In such condition, retention indices, derivatization, and comparison with reference compound are better alternate to elucidate the compound structure.

2.12 The Effects of Bacterial Volatile Emissions on Plant Abiotic Stress Tolerance

During the last few years, an increasing number of PGPR VOCs studies have demonstrated an effect on induced systemic tolerance (IST) against abiotic stresses. Under high salt concentration, excessive sodium (Na^+) creates both ionic and osmotic stresses in plants, leading to suppression of plant growth and reduction in crop yields. The entry of Na^+ ion is controlled by several transporters in which high-affinity K^+ transporter (HKT1) plays a major role. A soil bacterium *Bacillus subtilis* GB03-mediated VOCs has been reported to regulate HKT1 expression and conferred salt tolerance in *Arabidopsis thaliana*. The expression of HKT1 was tissue specific, GB03 concurrently down- and upregulates HKT1 expression in roots and shoots respectively, resulting lower Na+ accumulation in the plant as compared with controls (Zhang et al. 2008). Plants adjust their endogenous metabolism to cope with osmotic and ionic stress. Bacterial VOC-mediated salt tolerance was reported in soybean plants; *P. simiae* strain AU released such VOCs that not only decreased root Na^+ levels but also increased the accumulation of proline, which protect cells from osmotic stress. In addition, soybean plants showed higher level of vegetative storage protein (VSP), gamma-glutamyl hydrolase (GGH) and RuBisCo large-chain proteins that are known to help sustain plant growth under stress conditions (Vaishnav et al. 2015). *P. simiae* was found to emit 4-nitroguaiacol and quinolone compounds in the presence of nitric oxide donor sodium nitroprusside that were found to promote soybean seed germination under 100 mM NaCl. VOCs exposure

induced antioxidative enzymes and nitrate reductase gene expression in soybean plants that relieve the negative effects of salt stress (Vaishnav et al. 2016). *Paraburkholderia phytofirmans* PsJN emitted 2-undecanone, 7-hexanol, 3-methylbutanol, and dimethyl disulfide compounds that directly effect on bacterial colonization, increasing plant growth rate and tolerance to salinity (Ledger et al. 2016).

Plants have their own mechanism to protect against osmotic stress. During drought condition, plant accumulates osmolytes and increase antioxidant activity to nullify the effect of osmotic stress outside the cell and reactive oxygen species inside the cell, respectively. *Bacillus thuringiensis* AZP2 and *Paenibacillus polymyxa* B primed wheat seeds showed enhanced tolerance against drought stress. Primed seeds were exhibited higher survivorship, dry mass, water use efficiency, and antioxidant enzyme activity. Three volatile compounds benzaldehyde, b-pinene, and geranyl acetone were found to emit from wheat seedlings and effective to mitigate early phases of stress development (Timmusk et al. 2014). In addition to adaptive responses, an increase in the plant hormones abscisic acid (ABA) and salicylic acid (SA) causes stomatal closure to minimize water loss through transpiration. In an experiment, root colonization of *Arabidopsis* plants with *P. chlororaphis* O6 induced tolerance to drought that was correlated with reduced water loss with stomatal closure. Drought tolerance was found to mediate by 2R, 3R-butanediol volatile compound produced by *P. chlororaphis* O6. In the lack of 2R, 3R-butanediol production, no induction of drought tolerance was found. Further study demonstrated free SA, NO, and hydrogen peroxide in *P. chlororaphis* O6-colonized drought-stressed plants which suggested a primary role of these signaling molecules in induced drought tolerance (Cho et al. 2008, 2013). In a VOC assay setup, *Bacillus subtilis* GB03 exposure increased an enzyme expression of choline synthesis phosphoethanolamine *N*-methyltransferase (PEAMT) resulting enhanced pool of choline and glycine-betaine in *Arabidopsis* plant under osmotic stress. Certain bacterial VOCs are involved in biofilm formation, which contain exopolysaccharides as major constituents, and these polysaccharides maintain soil moisture content and increase drought tolerance in plants (Naseem and Bano 2014).

Iron is a limiting nutrient for plants due to its minimal solubility in soils. Iron solubility decreased in the presence of high salt concentration. As a result, iron deficiency can occur in the plants and affect their metabolism. In a study, *Bacillus subtilis* GB03-mediated VOCs activate the plant's iron acquisition machinery to increase assimilation of metal ions in *Arabidopsis*. GB03 VOCs upregulates gene expression of Fe-deficiency-induced transcription factor 1 (FIT1), which is necessary for two iron transporter induction FRO2 and IRT1. On the other hand, VOCs also enhanced the acidification media by enhancing root proton release, which increased iron mobility in plants (Zhang et al. 2009). Higher salt concentration also reduces sulfur (S) availability in the soil. Sulfur is an essential element in cysteine and methionine amino acids, and its deficiency represses the photosynthesis activity and productivity. Plant uptakes sulfur through soil or airborne compounds, including volatile compounds emitted by soil bacteria like dimethyl disulfide (DMDS). Emission of DMDS was found from a PGPR *Bacillus* sp. B55, which enhanced the

S content in *Nicotiana attenuata* plants grown in S-deficient soils or impaired S uptake/assimilation/metabolism (Meldasu et al. 2013).

2.13 Conclusion and Future Prospective

This chapter reports the potential role of bacterial VOCs as airborne signals in plant interaction with beneficial effects. In many reports, bacterial VOCs enable plants to adapt to various environmental stresses and ultimately enhance plant growth. Despite that, many aspects of VOC interaction with plants are still poorly characterized. The combined analysis of metabolic and gene expression profiles will likely be an increasingly powerful approach to identifying the mechanism of plant perception for bacterial VOCs. Moreover, systematic use of radiolabeled VOC compounds will reveal how plants assimilate VOC components as metabolites. The question of how bacteria respond to diverse environment to produce VOCs could be addressed by screening of compounds based on different parameters, as well as by monitoring transcriptomic, proteomic, and metabolomic changes in response to different environments.

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