Bacterial Volatiles in Promotion of Plant Under Biotic Stress

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Abstract

Confined to a narrow region but rich in nutrients, rhizosphere is always favorable to interactions between microorganisms and plants. While many soil microorganisms have no obvious effects on plants, some have negative as well as positive effects on plant growth. Plant growth-promoting rhizobacteria (PGPR) are beneficial microbes which have been fruitfully applied in agriculture to enhance seedling emergence, plant weight, crop yield, and disease resistance. Among these, some PGPR strains mediate plant growth promotion in direct and/or indirect manner by releasing volatile organic compounds (VOCs). Bacteria emitted a wide array of volatiles ranging from inorganic such as hydrogen cyanide (HCN) and nitric oxide (NO) to organic such as hydrocarbon, ketone, acids, terpenes, etc. Bacterial VOCs promote plant growth by eliciting different signaling pathway and show correlation with plant growth hormones also. In particular, 2,3-butanediol and acetoin were reported for the heightened level of plant growth promotion and triggering induced resistance against fungal pathogens. This chapter focuses on recent research study and role of bacterial volatiles in plant growth promotion and protection against pathogens.

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16.1   Introduction

For the good health, healthy food is the main concern which is directly related to the present agroecosystem. Agricultural products are the primary dietary source of proteins, carbohydrates, fat, vitamins, and other nutrients. With the increasing population, the need of dietary sources is increasing day by day drastically that ultimately leads to use of different chemicals in the form of phytohormones and pesticides to promote plants growth and amelioration of pathogens, respectively, to get quick result. Presently, the primary concern for the cultivator is to cultivate disease-free plant and to gain high yield in any adverse condition. Plants act in response to attack by pathogens or herbivores by inducing resistance phenomena through extensive changes in the gene expression, resulting in expression of various traits de novo or at much higher intensities, which diminish or put off further tissue damage (Karban and Baldwin 1997). Such plant responses expressed systemically because pathogens and herbivores can spread from the preliminary site of attack to other organs. This systemic response gets regulated by long-distance signaling of three plant hormones, namely, jasmonic acid (JA), ethylene, and salicylic acid (SA). SA and JA are transported either themselves or in the form of derivatives within the plant to elicit systemic responses against pathogen (Jain et al. 2017; Wasternack 2007; Heil and Ton 2008). Belowground, around the roots, rhizosphere is a narrow region where root-secreted exudates in the form of secondary metabolites affect the growth of indigenous microflora. This area can also be considered as a battlefield where beneficial bacteria and deleterious microorganisms compete for the resources. Among the diverse microbial population of the rhizosphere, the beneficial root-associated bacteria, also referred to as plant growth-promoting rhizobacteria (PGPR), have been used to control plant diseases and enhance plant growth and yield. Such a disease controlling strategy is referred to as biological control in contrast to chemical control. Several mechanisms have been explained till now to elucidate PGPR-mediated plant growth stimulation. These mechanisms are broadly categorized as direct and indirect where phosphate solubilization and production of different plant hormones, i.e., indole acetic acid (IAA), gibberellic acid (GA), and cytokinin, directly enhance the plant growth, while biocontrol of plant pathogens and deleterious rhizosphere microorganisms indirectly promotes growth by avoiding growth-limiting conditions (Glick 1995; Idriss et al. 2002; Kloepper 1992). This indirect mechanism of suppression of harmful microorganisms is known as induced systemic resistance (ISR) (Kloepper 1992; Dobbelaere et al. 2003).

Research studies have revealed that signaling molecules involved in the long-distance signaling through the vascular system can also be volatile compounds that move in the headspace outside the plant (Heil and Ton 2008). Volatile organic compounds (VOCs) released from bacteria act as signaling molecules for other bacteria, animals, insects, plants, and microorganisms (Farag et al. 2013). Zoller and Clark first of all reported microbial VOCs. These signaling molecules have been reported to have considerable role in plant growth, ameliorating abiotic stress in plants and as inhibitor of fungal pathogens (Baily and Weisskopf 2012; Davis et al. 2013). Plant-plant communication has been reported in several taxonomically unrelated

plants due to freely moving nature of VOCs in the air (Tscharntke et al. 2001; Engelberth et al. 2004; Heil and Kost 2006; Paschold et al. 2006; Heil and Bueno 2007; Ton et al. 2007; Godard et al. 2008). These studies show the role of VOCs in herbivore resistance via plant-plant communication phenomenon, and similar volatile compounds from beneficial bacteria can also mediate the beneficial effects (Ryu et al. 2003, 2004b). Volatile derivatives of two major signaling molecules SA and JA play a major role in plant defense. Methyl salicylate (MeSA), volatile derivative of SA, has been projected as the most probable systemic signal in the plant (Park et al. 2007). In tobacco, active resistance-inducing compounds were formed by SA after being converted back from MeSA that shows resistance induction in tobacco plants by higher exposure of MeSA (Kumar and Klessig 2003; Forouhar et al. 2005; Shulaev et al. 1997).

In context to the plant defense, PGPB-produced VOCs elicited plant growth promotion, and induced systemic resistance provides a new insight in plant growth-promoting bacteria (PGPB)–plant interaction (Chung et al. 2016; Weisskopf et al. 2016). Bacteria produce a wide range of VOCs that have been reported to play a crucial role in plant defense. Some of the most common VOCs included dodecane, 2-undecanone, 2-tridecanone, 2-tridecanol, tetramethylpyrazine 2, 3-butanediol, 3-hydroxy-2-butanone (acetoin), etc. Volatile compounds, 2, 3-butanediol and 3-hydroxy-2-butanone, were reported to be the most important one and found to be consistently released by the bacterial strain *B. subtilis* GB03 and *B. amyloliquefaciens* IN937a. *A. thaliana* plants primed with these strains have shown that significant resistance upon challenge inoculation of *Erwinia carotovora* subsp. *carotovora* SCC1 concluded the role of VOCs in elicitation of ISR. Furthermore, genetically modified *Bacillus* strain, lacking VOC-producing ability, was also used to justify the priming activity of such VOCs to induce resistance against diseases (Ryu et al. 2003). Besides *Bacillus*, several strains of *P. fluorescens* were also reported for the production of VOCs and shown more effectiveness in controlling root and seedling diseases (Landa et al. 2002).

16.2 Bacterial VOCs: Diversified in Nature

Bacterial VOCs are diversified in nature as bacteria that produce a wide variety of volatiles ranging from inorganic to organic compound with different subcategories. In addition to the role in communication, several bacterial volatiles have been reported for the antifungal activity, and most probably ketones have been proposed to be responsible for this effect. Bacterial volatiles were found effective against a wide range of fungi such as VOCs from *Streptomyces* that inhibit growth of entomopathogenic fungi while from *Staphylococcus pasteuri* inhibit mycorrhizal fungi. Furthermore, VOCs were also reported for the plant growth-promoting activity and protection against bacterial phytopathogens (Schulz and Dickschat 2007). Bacteria produce a wide array of inorganic and organic volatile compounds.

16.2.1 Inorganic Compounds

Different types of inorganic VOCs such as nitric oxide (NO), hydrogen sulfide (H_2S), ammonia, or hydrogen cyanide (HCN) have been reported to release from bacteria. Biosynthesis of HCN is catalyzed by HCN synthase, encoded by *hcnABC* gene that converts glycine into HCN and CO_2. Few bacterial species including *Pseudomonas*, *Chromobacterium*, and *Rhizobium* have been reported for the production of HCN, and it is produced under low-oxygen concentration at the end of the exponential phase. Another volatile ammonia production is catalyzed by aspartate ammonia lyase via conversion of aspartate to fumarate resulting in release of ammonia (Bernier et al. 2011). In addition to these, NO is produced mostly from L-arginine by nitric oxide synthases, while most H_2S-producing bacteria generate this gas through degradation of cysteine (Mattila and Thomas 2014).

16.2.2 Organic Compounds

Organic VOCs released from bacteria include different types of chemical classes such as fatty acid derivatives, acids, sulfur, and nitrogen-containing compounds and terpenes.

16.2.2.1 Fatty Acid Derivatives

These types of volatiles are most likely formed by alteration of products of the fatty acid biosynthetic pathway, for example, hydrocarbons, aliphatic alcohols, ketones, and other components. Short-chain hydrocarbons such as decane to tetradecane are rarely found in microbes, while longer hydrocarbons such as hexadecane reported particularly in abundant manner in cyanobacteria (Ladygina et al. 2006). Hydrocarbons and acids occur fewer often than ketones and alcohols. Acetoin (3-hydroxy-2-butanone), one of the most notable VOCs, belongs to ketone class and is derived from pyruvate fermentation under anaerobic conditions (Ryu et al. 2003), while another important compound 2,3-butanediol falls under short-chain alcohols and is produced by *Proteobacteria* and *Firmicutes* under low-oxygen conditions (Farag et al. 2013; Whiteson et al. 2014). Comparative to ketones and alcohols, organic acids are found less abundant in bacterial volatiles which include several short-chain fatty acids such as acetic, propionic, or butyric acids (Schulz and Dickschat 2007).

16.2.2.2 Sulfur Compounds

Being one of the important components of proteins and primary metabolism in plants and animal, sulfur is the most important macronutrient after nitrogen, phosphorus, and potassium, and its deficiency affects plant and animal health. Due to sulfur deficiency, chlorophyll content and synthesis of ribulose-1,5-bisphosphate carboxylase/oxygenase are reduced that restricts CO_2 assimilation and leads to suppression of the photosynthetic machinery (Burke et al. 1986; Gilbert et al. 1997; Aziz et al. 2016). The biogenesis of S-containing compounds, such as methanethiol,

dimethyl disulfide (DMDS), dimethyl sulfide, or dimethyl trisulfide and 1-(methyl thio)-3-pentanone, is often mediated by bacteria. Meldau et al. (2013) reported the role of VOC DMDS emitted by B55 in plant growth promotion by priming the *N. attenuata 35S-etr1*plant which is impaired in SO_4^{-2} uptake, with B55, and found significant promotion in seedling growth.

16.2.2.3   Terpenes

Terpenes are derived via mevalonate pathway or deoxyxylulose phosphate pathway from the terpene building units dimethylallyl pyrophosphate and isopentenyl pyrophosphate. Only monoterpenes (C_{10}), sesquiterpenes (C_{15}), and their derivatives or degradation products have been reported from bacterial volatile blends. Some of the notable terpene volatiles from bacteria are earthy odorant geosmin and antibiotic albaflavenone out of which the former is reported in several bacterial species, while the latter one is exclusively found in *Streptomyces* (Schulz and Dickschat 2007).

16.2.2.4   Nitrogen-Containing Compounds

Bacteria released several nitrogen-containing VOCs such as trimethylamine (TMA), 2-amino-acetophenone (2-AA), indole, etc. Among these, indole is reported to be produced by most of the PGPB and play an important role in plant growth. In *Escherichia coli*, tryptophanase enzyme catalyzed the biosynthesis of indole as it converts substrate tryptophan into indole, pyruvate, and ammonia (Lee and Lee 2010). Another VOC, 2-AA, can be used for the diagnosis of *P. aeruginosa* infections as it is aromatic in nature and responsible for the grape-like aroma of *P. aeruginosa* (Que et al. 2013; Schulz and Dickschat 2007).

16.3   Bacterial VOCs: Plant Growth Booster

Arabidopsis thaliana, the model of the plant world, has been used for the most of VOC-related studies using I-plate methods (divided plates), where compartments are separated by a plastic border. This facilitates exchange of volatile compounds without any physical diffusion of nonvolatile metabolites. Apart from that, research studies have also been done on some other plants. Initially Ryu et al. (2003) revealed that volatiles released from specific bacterial strains of PGPR have positive role on the growth of *Arabidopsis thaliana* seedlings. PGPR consist of a broad range of beneficial root-colonizing bacteria which can promote plant growth by means of enhancing different plant growth-promoting traits such as seed emergence, plant weight, and crop yields (Kloepper 1992; Ciancio et al. 2016). PGPR have been widely used for seed or seedling treatment to increase the growth of several crops and to restrain the growth of plant pathogens and harmful rhizosphere microorganisms (Glick 1995). Apart from enhancing plant growth, certain PGPR provide protection against pathogen also by means of triggering ISR in plant through VOCs. Several in vitro condition experiments have shown role of VOCs emitted by different genera of PGPR strains in the promotion of plant growth and elicitation of ISR against phytopathogens (Ryu et al. 2003, 2004a, b, c; Li et al. 2016). Two VOCs

2,3-butanediol and its precursor 3-hydroxy-2-butanone (acetoin) released from the strains GB03 and IN937a have been reported for the plant growth promotion through I-plate method. Furthermore, *A. thaliana* plants were reported with dose-dependent stimulation in growth upon exogenous application of commercial acetoin and 2,3-butanediol, which suggest the effects of the volatile blend produced by the two *Bacillus* sp. Later on, the role of these compounds as plant growth-promoting volatile determinants was confirmed by applying 2,3-butanediol mutant strains of *B. subtilis*, that results in no effect on plants' growth (Ryu et al. 2003, 2004a). VOCs released by bacteria also play an important role in signaling of plant growth hormones by regulating expression of some pathway genes. Correlation between some hormones and VOCs has been described here.

16.3.1 Ethylene

Ethylene is a gaseous plant growth hormone in nature and plays an important role in the VOC-mediated bacteria–plant interaction, and loss of the positive regulator of the ethylene pathway EIN2 led to different growth behaviors in response to bacterial strain IN937a and GB03 VOCs (Stepanova and Alonso 2009). VOCs from GB03 were found to be unable to trigger biomass increase in mutant *ein2 (ethylene insensitive2)* (Guzm'n and Ecker 1990; Ryu et al. 2003), while in another study VOCs of IN937a failed to show significant change in the growth promotion effect in the ethylene-insensitive mutants *etr1* (*ethylene response1*) (Bleecker et al. 1988), *ein2*, and *eir1* (*ethylene-insensitive root1*) (Luschnig et al. 1998). It implies that the plant amends its response by means of a strain-specific signal transduction pathway. Further in transcriptomic study, a subset of ethylene biosynthesis (*ACO2*, *ACS4*, *ACS12*, and *SAM-2*) and ethylene response (*CHIB*, *ERF1*, and *GST1*) genes have been shown to respond to bacterial volatiles (Kwon et al. 2010). Different expression of four enzymes, namely, aspartate aminotransferase, aspartate semi-aldehyde dehydrogenase precursor, methionine adenosyltransferase (MAT3), and S-adenosylmethionine synthetase 2 (SAM-2), has been reported upon exposure to bacterial volatiles. Conclusively, it shows significant role of ethylene pathway in the growth-promoting effect of bacterial volatiles.

16.3.2 Cytokinins

Plant growth hormone cytokinins play a major role in cell division processes and control the leaf size, root and shoot meristem maintenance, and root architecture (Argueso et al. 2010). Earlier, Arkhipova et al. (2005) have described the relationship between microbial production of cytokinins and plant development. It is also reported that *B. megaterium* failed to promote plant growth in plants devoid of the histidine kinase cytokinin receptors and cytokinin receptor-deficient (CRE1)/ AHK4, AHK2, and AHK3. Ryu et al. (2003) have also proven cytokinin role in mediation of PGPR signals as *Arabidopsis* mutant's *cre1* and *ein2* were found

insensitive to GB03 volatiles. Though no recognition of cytokinin-related genes was reported in the succeeding microarray or proteomics studies (Kwon et al. 2010). Taken together, it shows that cytokinins are crucial for the root development and physiology; hence the importance of cytokinin pathway with respect to change in plant growth mediated by bacterial volatiles appears to be worthy for deep investigation.

16.3.3 Abscisic Acid

The abscisic acid (ABA) originally known to be involved in abscission and bud dormancy also plays an important role in plant responses to environmental stresses and pathogens. Its signaling pathway overlaps widely with sugar sensing *in planta* (Rolland et al. 2006). Sugars, being a product of photosynthesis, play an important role in plant growth and development. In this context, increased level of sugar concentration via increase in photosynthetic activity and chlorophyll content was reported in the *Arabidopsis* seedlings treated with GB03 volatiles that conclude role of VOCs in photosynthesis (Zhang et al. 2008). In another study, although increased photosystem efficiency was observed in *Arabidopsis* lines *gin1* and *gin2*, impaired in hexokinase-dependent sugar sensing but found with no response to GB03 VOCs (Moore et al. 2003). These studies suggested that VOCs promote photosynthesis by means of triggering the repression of the hexokinase-dependent glucose signaling pathway. Further, Zhang et al. (2009) have also confirmed the VOCs' role in plant growth by showing reduced concentration of ABA contents in aerial parts of the plants exposed to bacterial VOCs in comparison to control plants. It was also observed that GB03 volatiles increase photosynthetic capacity in the plants via acidification of the rhizosphere and consequent increase in iron uptake.

16.3.4 Auxin

Auxin is one of the main plant growth hormones found in different natural forms. It conducts a complex signaling pathway that involves the spatial and temporal coordination of auxin synthesis, transport, and perception. Plant growth-promoting rhizobacteria have been reported to synthesize IAA to trigger plant growth promotion (Kim et al. 2011; Kochar et al. 2011). Zhang et al. (2007) have shown in a transcriptome study that genes associated with auxin synthesis and response showed differential regulation upon exposure of *Arabidopsis* to volatiles of GB03. Müller et al. (1998) have reported upregulation of enzymes, namely, tryptophan synthase, an anthranilate synthase, and three nitrilases (two of these expressed specifically in the aerial tissues of the plant), involved in the tryptophan-dependent IAA biosynthesis pathway. Zhang et al. (2007) further supported this finding by using auxin transport inhibitor naphthylphthalamic acid (NPA) that results in abolishment of this response.

Differential expression of expansin genes associated with cell wall remodeling and cell expansion was also reported in the *Arabidopsis* leaves exposed to bacterial

VOCs (Zhang et al. 2007). Similar upregulation has been reported for *Lactuca sativa EXPA5* and *Nicotiana tabacum EXP2* and *EXP6* (Wang et al. 2009; Minerdi et al. 2011). Conclusively, these studies suggested the role of IAA biosynthesis, its transportation and local tissue concentration in the enhancement of aerial part of the plants, and hence its superlative role for the auxin machinery in the VOC-mediated plant growth promotion.

16.4   Bacterial VOCs: Invisible Weapons Against Pathogens

Bacterial VOCs work as bacterial determinants that play an important role in plant protection against invading pathogens. Volatiles 2,3-butanediol and phenazines are known to possess antimicrobial activity and often been considered harmful to a wide variety of biological systems. Priming the defense pathways by external elicitors allows the potentiated induction of defense response while not forthwith activating the defense signal cascades, which might be accompanied by the outflow of energy for defense mobilization (Paré et al. 2005). PGPR priming is not directly associated with direct changes in gene expression in leaves, but it is assumed that elicitation ends in a rise within the quantity or activity of cellular elements that play vital roles in defense signaling (Lee et al. 2012). Transcriptional expression of the marker genes *PR1*, *ChiB*, and *VSP2* involved in salicylic acid, jasmonic acid, and ethylene signaling, respectively, was observed in the plants exposed to long-chain VOC tridecane, released from *P. polymyxa* against the biotrophic pathogen *P. syringae* pv. *tomato*. In another study, Han et al. (2006) reported that volatile 2,3-butanediol and acetoin from *B. subtilis* elicited a stronger ISR against *P. carotovorum* subsp. *carotovorum*, whereas direct application of 2,3-butanediol failed to trigger ISR against *P. syringae* pv. *tabaci*. In another study, Sharifi and Ryu (2016) found increased resistance in *Arabidopsis* plants against the necrotrophic fungus *B. cinerea* via ISR elicitation through bacterial VOCs exposure and suggested major role of volatiles in biocontrol against fungal phytopathogens. Recently, Tahir et al. (2017) have reported induced protection in tobacco against bacterial wilt-causing pathogen *Ralstonia solanacearum* upon priming with *Bacillus* whose volatiles adversely affect the physiology and ultrastructure of the pathogens. This study suggests that different defensive cascades are elicited in response to different pathogens.

Furthermore, transcriptomic and proteomic analysis of *A. thaliana* exposed to bacterial volatiles revealed that three major plant defense signaling pathways, including salicylic acid, jasmonic acid, and ethylene, mediate these effects (Kwon et al. 2010; Zhang et al. 2010). This study has shown that upon treatment with GB03, significant upregulation of VOCs was observed in the transcript of five ET biosynthesis-related genes, namely, *MAT3*, *SAM-2*, *ACS4*, *ACS12*, and *ACO2*, while strong induction was also found in the ET marker genes *ERF1*, *GST2*, and *CHIB*. Another proteome study has shown the independency of ISR elicited by *B. subtilis* FB17 to JA pathway but dependency on SA and ET signaling pathways against *P. syringae* pv. tomato DC3000.

Ethylene-insensitive plants treated with 2,3-butanediol did not elicit ISR, suggesting that ethylene is a major player in this interaction (Farag 2014). Different signaling pathways are responsible for the VOC-mediated induction of ISR. Mutants and transgenic plant lines of plants exposed to volatiles have been used to reveal the pathway (Han et al. 2006; Ramos et al. 2000; Ryu et al. 2003). Comparative study of the signal transduction pathways potentiated by individual VOCs in the presence or absence of exogenous priming agents offers more insight into the roles of elicitors and priming agents in eliciting plant defense responses and in increasing long-term protection of plants (Lee et al. 2012). Different VOCs produced by bacteria may help plants to change defense signaling pathways resulting in protection them against various types of pathogens, i.e., necrotrophs and biotrophs. Ryu et al. (2004a) reported independency of ISR triggered by GB03 emissions to the salicylic acid, NPR1, and jasmonic acid signaling pathways although this response seems to be mediated via ethylene. On the other hand, independency of ISR triggered by strain IN937a to all the signaling pathways tested shows the possibility that additional VOCs utilize alternative pathways *in planta.* In fact, the ethylene (ET)-dependent plant defense signaling pathway is more effective against a necrotrophic pathogen such as *P. carotovorum* subsp. *carotovorum* than against *P. syringae*, which requires an SA-dependent resistance response (Pieterse et al. 2009). Failure to elicit ISR by C4-alcohol biosynthetic pathway mutants stain of *Bacillus subtilis* confirms the role of acetoin and 2,3-butanediol as ISR volatile determinants. Significant upregulation in the transcript profile of *PDF1.2* gene was also observed upon priming with *B. subtilis* strain GB03 and strain FB17 (Ryu et al. 2004a). However, how plants modulate and recognize PGPR VOC-elicited defense straight away after pathogen infection remains to be fully elucidated.

16.5   Conclusion

With the diverse and rapidly evolving pathogens and global climate changes, adverse effects have been increasing in food security by reduction in the world crop yield. Although day-by-day increased application of pesticides and chemical fertilizers provides instant solutions for the plant disease and crop yield problems, respectively, it ultimately leads to affect human and environment health in negative manner. A wide array of research study on bacterial VOC–plant interactions has led to an ever more conceptual understanding of the nature of bacterial VOCs and their potential role in enhancing plant protection and productivity in a sustainable manner. Significant modulation of plant metabolomics, physiology, and transcriptional status upon exposing to bacterial VOCs shows the plants' ability to recognize and react to bacterial VOCs. These studies evidently revealed the necessity for implementation of bacterial VOCs in open-field conditions and stress their multiple roles to extend pathogen resistance, protection against herbivores, and in general as biocontrol agents. Bacterial VOC–plant interaction studies opened up a new era of bacterial VOC application for a sustainable development of agriculture with respect

to crop protection and production strategies as a possible replacement for hazardous pesticides and chemical fertilizers. Although bacterial VOCs are equivalent to biopesticides or biofertilizers, effective use of bacterial VOCs still, however, remains a big challenge.

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