Chapter 7
Bacterial Volatile-Mediated Plant Abiotic Stress Tolerance

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Abstract Plant growth-promoting rhizobacteria (PGPR) are beneficial soil microbes that can stimulate plant growth or increase plant tolerance to stresses. Some PGPR strains release volatile organic compounds (VOCs) that can directly and/or indirectly benefit the plants by increasing plant biomass, disease resistance, and abiotic stress tolerance. This chapter provides an overview of bacterial VOC-induced enhancement of plant tolerance to high salinity and drought stress, as well as of bacterial VOC-mediated improvement of sulfur and iron nutrition in plants.

Keywords Plant growth-promoting rhizobacteria (PGPR) · Volatile organic compounds (VOCs) · Abiotic stress · Salinity · Drought · Sulfur · Iron

7.1 Introduction

Plants in nature are closely associated with a large number of soil microbes, most of which being bacteria. Plant-associated soil microbes either live within the root tissues or in the rhizosphere, which is a thin layer of soil adhering to the roots (Bulgarelli et al. 2013, 2015). Plants release a variety of organic compounds into the

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soil through roots, via a process known as rhizodeposition (Nguyen 2009). The root exudates in the rhizosphere create a nutrient-rich environment for soil bacteria (Bulgarelli et al. 2013, 2015). On the other hand, while some rhizobacteria have no observable effects on plant growth or fitness, a plethora of other rhizobacteria can affect plants either negatively or positively by releasing certain bacteria-derived compounds (Vaishnav et al. 2017a, b). Among the rhizobacteria, plant growth-promoting rhizobacteria (PGPR) are beneficial bacteria that have been successfully used in agriculture to increase seedling emergence, plant weight, crop yield, and disease resistance (Beneduzi et al. 2012; Kashyap et al. 2017). These beneficial soil microbes promote plant growth and improve disease resistance through production of one or multiple bacterial factors including phytohormones such as auxin and cytokinin, the enzyme ACC (1-aminocyclopropane-1-carboxylate) deaminase that reduces plant ethylene levels, and siderophores that facilitate root uptake of metal nutrients (Glick 1999; Timmusk and Wagner 1999; Vaishnav et al. 2017a, b). In addition to these non-volatile compounds, some PGPR strains also release volatile organic compounds (VOCs) capable of affecting plant physiology under normal and stress conditions (Paré et al. 2011; Farag et al. 2013; Liu and Zhang 2015).

Since the first discovery of VOC-mediated bacteria regulation of plant growth (Ryu et al. 2003), bacteria VOC emission has been recognized as an important aspect of plant–microbe interactions, in addition to those interactions that are based on direct contact between the bacteria and the plant (Ryu et al. 2003; Wenke et al. 2010; Blom et al. 2011; Bitas et al. 2013; Farag et al. 2013). Bacteria can produce diverse volatile compounds (Schulz and Dickschat 2007), including both organic and inorganic (e.g., hydrogen cyanide or carbon dioxide) components. Although the identity and abundance of individual VOC components vary among different species, bacterial VOCs commonly can be categorized into the compounds including short-chain aliphatic aldehydes, esters, alcohols, organic acids, ethers, ketones, sulfur compounds, and hydrocarbons (Farag et al. 2006; Vaishnav et al. 2017a). Some VOCs have been shown to be toxic while some others can be beneficial to plants (Rudrappa et al. 2010; Blom et al. 2011; Ryu et al. 2003; Farag et al. 2006). An increasing interest concerning the biological function of bacterial volatiles has been documented and has clearly demonstrated that certain bacteria VOCs can increase plant biomass production and enhance plant resistance to biotic and abiotic environmental stresses (Ryu et al. 2003; Zhang et al. 2007, 2008a, 2009; Choi et al. 2014; Liu and Zhang 2015; Vaishnav et al. 2015; Sharifi and Ryu 2018). In this chapter, we focus on the important roles of bacterial VOCs on plant abiotic stress tolerance (Fig. 7.1).

7.2 Enhancement of Salt Tolerance

High salinity is one of the most adverse environmental factors that severely limits crop productivity, because excessive sodium (Na^+) in soil causes osmotic stress and ionic toxicity to plant cells (Zhu 2001; Rahnama et al. 2010; James et al. 2011;

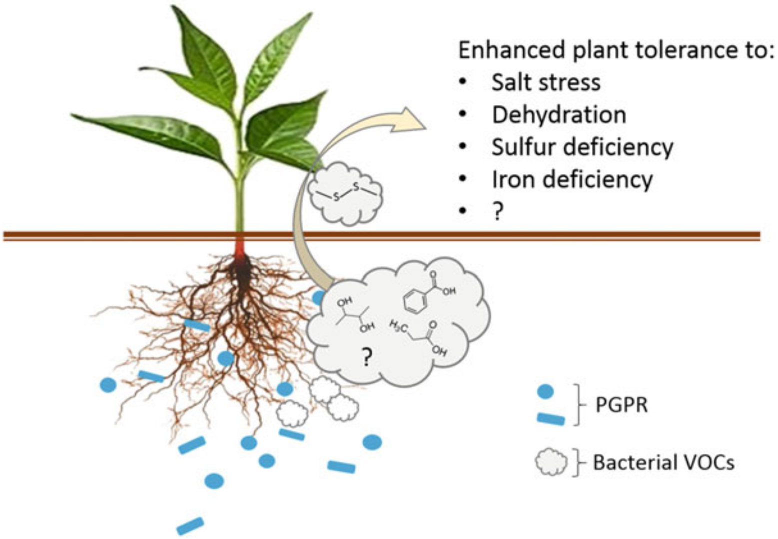

Fig. 7.1 A model of the enhanced plant stress tolerance that is triggered by bacterial volatiles. *PGPR* plant growth-promoting rhizobacteria, *VOCs* volatile organic compounds. Question marks indicate either unknown bioactive VOC components or yet-to-be-explored VOC effects. Also see Table 7.1 for detailed information

Shrivastava and Kumar 2015). Plants grown in saline conditions can minimize Na^+ toxicity by restricting its root uptake and the subsequent loading into xylem, as well as by promoting the shoot-to-root Na^+ recirculation and the Na^+ extrusion from root cells (Tester and Davenport 2003; Munns and Tester 2008; Zhang et al. 2008a; Kronzucker and Britto 2011; Zhang and Shi 2013). Plant tolerance to salt stress can be enhanced by some PGPR strains through bacterial VOC emissions (Zhang et al. 2008a; Vaishnav et al. 2015; Ledger et al. 2016; Bhattacharyya and Lee 2017).

Arabidopsis exposed to the VOCs released from *Bacillus amyloliquefaciens* GB03 acquired enhanced salt tolerance, as shown by the greater biomass production and the lower Na^+ accumulation compared to plants without VOC exposure (Zhang et al. 2008a; Choi et al. 2014). The enhanced plant salt tolerance probably involves HKT1-mediated Na^+ recirculation and SOS3-mediated Na^+ exudation. *Arabidopsis* HKT1 is a xylem parenchyma-expressed Na^+ transporter, which is responsible for Na^+ exclusion from leaves by removing Na^+ from the xylem sap (Sunarpi et al. 2005; Horie et al. 2009; Moller et al. 2009). In salt-stressed *Arabidopsis* plants, GB03 VOCs induced *HKT1* gene expression in shoots and concomitantly reduced shoot Na^+ accumulation; meanwhile, the *hkt1* null mutant accumulated high levels of Na^+ in shoots and was sensitive to salt stress regardless of the presence of GB03 VOCs (Zhang et al. 2008a). These results suggested that GB03 VOC-enhanced plant salt tolerance was mediated through HKT1-dependent shoot-to-root Na^+ recirculation. When stressed by salinity, wild type *Arabidopsis* exposed to GB03 VOCs showed reduced plant Na^+ levels by approximately 50% compared to plants without VOC treatment; by contrast, in the *Arabidopsis salt overly sensitive 3* (*sos3*) mutant, VOCs triggered only 15% reduction in plant Na^+ levels (Zhang et al. 2008a). SOS3 is required for post-transcriptional activation of the H^+/Na^+ antiporter SOS1, which controls root Na^+ exudation and long-distance Na^+ transport in plants (Shi et al. 2000). Therefore, in addition to HKT1, SOS3 also plays a critical role in mediating GB03 VOC-triggered plant tolerance to salt stress, possibly through its function in regulating root Na^+ exudation. GB03 VOCs contain acidic components and cause rhizosphere acidification (Farag et al. 2006; Zhang et al. 2009), which may result in a proton gradient that facilitates the SOS1-mediated export of Na^+ from roots. These observations with GB03 collectively suggest that plant salt tolerance can be enhanced by bacterial VOCs through integrated regulation of Na^+ homeostasis *in planta*.

Besides modulation of plant Na^+ homeostasis, bacteria VOCs may affect plant accumulation of osmoprotectants including secondary metabolites and stress-responsive proteins. *Pseudomonas simiae* strain AU produces VOCs that were shown to increase soybean tolerance to salt stress (Vaishnav et al. 2015). The volatiles were effective in lowering Na^+ levels and simultaneously increasing accumulation of the osmoprotectant proline in roots. VOCs from *P. simiae* AU also induced the production of several proteins, such as vegetative storage proteins, which are known to maintain plant growth under stress conditions (Vaishnav et al. 2015). *P. simiae* VOCs contain 4-nitroguaiacol and quinolone (Vaishnav et al. 2016). These two volatile compounds, in combination with sodium nitroprusside that is a nitric oxide donor, induced antioxidative enzymes and nitrate reductase gene expression, resulting in promoted germination rates of soybean seeds under salt stress (Vaishnav et al. 2016).

Bacterial regulation of plant hormone signaling pathways can also mediate VOC-enhanced plant tolerance to salt stress. VOCs from *Alcaligenes faecalis* strain JBCS1294 increased *Arabidopsis* tolerance to salt stress by inducing genes involved in auxin and gibberellin signaling pathways (Bhattacharyya et al. 2015). Consistently, JBCS1294 VOCs induced salt tolerance neither in wild type plants treated with auxin or gibberellin inhibitors nor in the *Arabidopsis* mutants *eir1* and *gai-1*, which are defective in the signaling pathways of auxin and gibberellin, respectively. In contrast, the phytohormones cytokinin, brassinosteroid, and ethylene played negative roles in mediating the beneficial effects caused by JBCS1294 VOCs, as shown by genetic disruption or chemical inhibition of the corresponding signaling pathways (Bhattacharyya et al. 2015). Bhattacharyya and Lee (2017) later examined individual components of JBCS1294 VOCs and found that plant salt tolerance could be induced by either butyric acid, propionic acid, or benzoic acid. Interestingly, compared to the individual VOC components, an optimized combination of the three volatile compounds displayed stronger capacity in enhancing plant stress tolerance to salinity, although the same VOC cocktail failed to induce growth promotion in plants without salt stress (Bhattacharyya and Lee 2017). Similar to natural VOCs from JBCS1294, the volatile cocktail failed to increase plant tolerance to salt stress in *eir1* and in wild type plants treated with auxin or gibberellin inhibitors. Intriguingly, *Arabidopsis* plants exposed to GB03 VOCs also displayed altered auxin homeostasis (Zhang et al. 2007), indicating a potential link between VOC-mediated modulation of plant salt tolerance and of auxin homeostasis. It is noteworthy that VOCs from some fungal species have also been reported to induce plant tolerance to salt stress in an auxin-dependent manner, as indicated by a failure of fungal VOC-induced increases in leaf surface area and lateral root density in the auxin signaling mutants *aux1-7, tir1-1,* and *axr1-3* (Li and Kang 2018).

Similar to the combination of butyric acid, propionic acid, and benzoic acid, another synthetic mixture of bacterial VOC components, including 2-undecanone, 7-hexanol, and 3-methylbutanol, was shown to mimic natural VOCs from *Paraburkholderia phytofirmans* PsJN in promoting *Arabidopsis* growth under both salt-stressed and non-stressed conditions (Ledger et al. 2016). In addition, it was shown that early exposure to *P. phytofirmans* PsJN VOCs was sufficient to stimulate long-term effects on plant growth promotion in the presence and absence of salinity (Ledger et al. 2016).

7.3 Protection from Dehydration

Under high salinity or drought conditions, plant cells suffer from osmotic stress that leads to water loss. Plants respond to dehydration by elevating cellular levels of osmoprotectants, such as choline and glycine betaine, in order to achieve a balanced water potential across the cell membrane and thereby prevention of water loss (Rhodes and Hanson 1993; Yancey 1994).

Arabidopsis treated with VOCs emitted by *B. amyloliquefaciens* GB03 showed increased tolerance to dehydration caused by mannitol supplemented to the growth medium; meanwhile, root inoculation of GB03 enhanced *Arabidopsis* tolerance to drought stress (Zhang et al. 2010). GB03 VOCs induced gene expression of *PEAMT*, which encodes an enzyme critical for choline and glycine betaine biosynthesis in *Arabidopsis*. GB03 VOCs increased the accumulation levels of choline and glycine betaine in osmotic-stressed plants, but failed to enhance plant dehydration tolerance in *PEAMT* defective mutant plants, consistent with a key role of PEAMT in mediating GB03 VOC-induced plant tolerance to dehydration (Zhang et al. 2010). Under osmotic stress conditions, GB03 VOC-treated plants and the untreated plants showed similarly elevated levels of abscisic acid (ABA), which is a stress-responsive phytohormone crucial for plant abiotic stress tolerance (Zhang et al. 2010). This pattern indicates that ABA mediates basal, but not VOC-triggered enhancement of stress tolerance in plants. In some other studies, PGPR-induced plant drought tolerance was not attributed to ABA either, because plants with PGPR treatments displayed lower ABA levels than the untreated plants (Cho et al. 2008; Kang et al. 2014). By contrast, salicylic acid (SA) seems to be critical for plant drought tolerance induced by *Pseudomonas chlororaphis* strain O6 and by 2,3-butanediol, which is a component of the VOCs emitted by *P. chlororaphis* O6 (Cho et al. 2008). This opinion was supported by the observations that drought-stressed plants with exposure to either O6 or 2,3-butandiol displayed higher SA levels compared to their control counterparts, and that the enhancement of plant drought tolerance was impaired in *Arabidopsis* mutant defective in SA signaling. At physiological level, the plant drought tolerance induced by O6 or 2,3-butanediol was correlated with increased stomatal closure (Cho et al. 2008). Consistently, later studies showed that 2,3-butanediol induced plant production of nitric oxide (NO), which is an important signaling molecule for stress-induced stomatal closure (Cho et al. 2013; Li et al. 2017). Similarly, 2,3-butanediol and acetoin released from *B. amyloliquefaciens* FZB42 activated SA and ABA signaling pathways and stimulated accumulation of hydrogen peroxide and NO, resulting in stomatal closure in Arabidopsis and *Nicotiana benthamiana* (Wu et al. 2018). Notably, Wu et al. (2018) also showed that adding these two bacterial VOCs directly to the soil was more effective in reducing stomatal apertures, compared to the volatilization treatment by setting the volatile compounds and the pot with plants next to each other within a glass container. Application of an inhibitor of nitrate reductase or an inhibitor of nitric oxide synthase decreased NO production as well as plant drought tolerance induced by 2,3-butanediol (Cho et al. 2013); this observation further supported an important role of NO in mediating 2,3-butanediol-induced plant drought tolerance. The compound 2,3-butanediol is also a component of VOCs from *B. amyloliquefaciens* GB03 (Farag et al. 2006), and thus it probably contributes to GB03 VOC-induced plant tolerance to dehydration, although it is unknown whether 2,3-butanediol induces *PEAMT* gene expression as the natural blend of GB03 VOCs does.

Some PGPR strains produce biofilms that are mainly composed of exopolysaccharides. Biofilm production can be induced by certain bacterial VOCs such as acetic acid (Chen et al. 2015); meanwhile, exopolysaccharides improve soil aggregation and maintain soil moisture in the rhizosphere and thus can help plants survive under water deficit conditions (Amellal et al. 1998; Niu et al. 2018). For instance, exopolysaccharide-producing PGPR strains, such as *Pseudomonas aeruginosa* Pa2 and *Pantoea agglomerans* NAS206, have been shown to increase drought resistance in plants (Naseem and Bano 2014). Therefore, VOC-induced plant dehydration tolerance may be achieved indirectly through stimulation of exopolysaccharide secretion, in addition to directly through affecting biological processes in plants.

7.4 Augmentation of Sulfur Acquisition

Sulfur is a macronutrient required for plants throughout the whole life cycle. As an essential element in many pivotal biomolecules, sulfur is important for plant development and for plant resistance to environmental stress (Aziz et al. 2016). Sulfur deficiency causes photosynthesis repression and disruption of primary metabolism (Burke et al. 1986; Gilbert et al. 1997; Liu and Zhang 2015). Plant acquisition of sulfur has been shown to be augmented by VOCs from *B. amyloliquefaciens* GB03 and *Bacillus* sp. B55 through different mechanisms.

Arabidopsis exposed to GB03 VOCs displayed transcriptional up-regulation of sulfur assimilation, as evidenced by VOC induction of the gene families encoding ATP sulfurlyase (ATPS), adenosine 5′-phosphosulfate reductase (APR), and adenosine 5′-phosphosulfate kinase (APK) (Aziz et al. 2016). Monitoring of sulfur uptake and translocation with radio-labeled sulfate ($^{35}SO_4{}^{2-}$) revealed that VOCs enhanced total sulfur uptake per plant within 30 min. Consistently, sulfur accumulation levels were increased by GB03 VOCs. The enhanced sulfur acquisition apparently resulted in augmented sulfur utilization. For instance, levels of the amino acid cysteine, which is a precursor of many organic sulfur metabolites, were increased by more than 90% in plants with 2 weeks of VOC exposure compared to the control plants. In addition, *Arabidopsis* genes responsible for the production of sulfur-rich aliphatic and indolic glucosinolates were also induced by GB03 VOCs, consistent with the elevated levels of glucosinolates that protected plants from the herbivore beet armyworm (Aziz et al. 2016).

Unlike GB03 VOCs that affect root uptake of $SO_4{}^{2-}$, VOCs from *Bacillus* sp. B55 augmented plant sulfur acquisition in the air (Meldau et al. 2013). With radio-labeled sulfur ^{35}S supplemented into the bacteria growth medium, B55-emitted VOCs was shown to transmit sulfur to *Nicotiana attenuata* plants. B55 VOCs contain at least two sulfur-containing compounds, dimethyl disulfide (DMDS) as a major component and *S*-methyl pentanethioate present at trace amounts. Plant growth retardation caused by sulfur starvation was rescued by either the natural VOC blends or synthetic DMDS, with the latter showing higher capacity than the former in rescuing the plant stress symptoms. Therefore, sulfur nutrition present in B55 VOCs was attributed mainly to DMDS (Meldau et al. 2013). Sulfur in $SO_4{}^{2-}$ is in an oxidative state that needs an energy-consuming reduction process for biological assimilation (Takahashi et al. 2011); by contrast, sulfur in DMDS is in a chemically reduced state. This difference seems to make DMDS superior to $SO_4{}^{2-}$ by providing energy-saving sulfur nutrition to plants. Consistently, sulfur assimilation as well as methionine biosynthesis and recycling in plants were transcriptionally repressed by DMDS, indicating a decreased demand for $SO_4{}^{2-}$ reduction (Meldau et al. 2013). DMDS is commonly detected in microbial VOCs; meanwhile, VOCs from microbes other than B55 can contain high levels of other sulfur-containing VOCs such as dimethyl sulfide and dimethyl trisulfide (Kanchiswamy et al. 2015). Thus, VOC-mediated sulfur assimilation might be a common event during plant–microbe interactions.

7.5 Improvement of Iron Homeostasis

Iron is a micronutrient that participates in electron transfer reactions via the transition between ferrous iron (Fe^{2+}) and ferric iron (Fe^{3+}). Although iron element is highly abundant in the earth’s crust, it is mostly present as insoluble oxyhydroxide polymers that are not readily taken up by plants (Guerinot and Yi 1994). Iron deficiency disrupts photosynthetic apparatus with easily observable leaf chlorosis symptoms

(Zhang et al. 2009). In order to increase iron mobility in the rhizosphere, graminaceous monocots secrete siderophores to chelate Fe^{3+} before its root uptake, while non-graminaceous monocots and dicots deploy a combined strategy including rhizosphere acidification, reduction of Fe^{3+} to Fe^{2+} by plasma membrane ferric reductase, and transporter-mediated Fe^{2+} import into roots (Curie and Briat 2003).

Bacteria VOCs do not contain any known siderophores; however, acidic compounds are common VOC components (Audrain et al. 2015) and can acidify the rhizosphere. For example, VOCs emitted from *B. amyloliquefaciens* GB03 have been shown to directly cause rhizosphere acidification (Zhang et al. 2009). GB03 VOCs also stimulated *Arabidopsis* root proton exudation, making further contribution to rhizosphere acidification (Zhang et al. 2009). Similarly, VOCs from *Sinorhizobium meliloti* caused rhizosphere acidification by induction of root proton exudation in *Medicago truncatula* (del Carmen Orozco-Mosqueda et al. 2013). Consistently, root ferric iron reductase activities were increased and iron uptake was enhanced in *Arabidopsis* exposed to GB03 VOCs and in *M. truncatula* exposed to *S. meliloti* VOCs. *Arabidopsis* treated with GB03 VOCs also displayed gene induction of FIT1, a transcription activator controlling gene expression of the root Fe^{3+} reductase FRO2 and the Fe^{2+} transporter IRT1. Concomitant with the up-regulation of *FIT1*, transcriptional activation of *FRO2* and *IRT1* was observed in wild type *Arabidopsis* exposed to GB03 VOCs, and was abolished in the *fit1* null mutant. Plant exposure to GB03 VOCs induced leaf cell expansion and photosynthesis augmentation (Zhang et al. 2007, 2008b). Given the importance of iron and sulfur to photosynthesis, it is possible that VOC-enhanced nutrient uptake is part of its coordinated regulation of plant biological processes. As a result of the fortified iron nutrition, increases in chlorophyll contents were observed in *Arabidopsis* exposed to GB03 VOCs and in *M. truncatula* exposed to *S. meliloti* VOCs. Consistent with VOC-mediated enhancement of iron uptake, direct inoculation of GB03 to cassava resulted in elevated iron accumulation (Freitas et al. 2015).

Plants that rely on siderophores for Fe^{3+} uptake also possess FRO genes. Strong induction of the leaf-specific *FRO1* gene was observed in *Sorghum bicolor* treated with VOCs emitted from *Arthrobacter agilis* UMCV2; concomitantly, the plants exhibited increases in chlorophyll content and biomass production (Castulo-Rubio et al. 2015). Dimethyl hexadecilamine (DMHDA), a component of *A. agilis* UMCV2 VOCs, was shown to mimic the natural VOC blends in triggering *FRO1* gene expression and plant growth promotion.

7.6 Future Perspectives

VOC emission is a common property of a wide variety of soil microorganisms. Although to date only a small number of PGPR strains have been reported to enhance plant tolerance to abiotic stresses, research on this topic has demonstrated the important role of VOCs (Table 7.1). The increasing interests in microbial VOCs should lead to identification of more VOCs that can enhance plant abiotic stress

Table 7.1 A list of bacterial volatile organic compounds that affect plant abiotic stress tolerance

PGPR effects on plants	PGPR species (strain)	Bacterial VOCs	In planta mediators	Plant species	References
Salt stress tolerance	*Bacillus amyloliquefaciens* (GB03)	Entire VOC blend	HKT1; SOS3	*Arabidopsis*	Zhang et al. (2008a)
Salt stress tolerance	*Pseudomonas simiae* (AU)	4-Nitroguaiacol; quinolone	Proline; antioxidative enzymes; nitrate reductase	Soybean	Vaishnav et al. (2015, 2016)
Salt stress tolerance	*Alcaligenes faecalis* (JBCS1294)	Butyric acid; propionic acid; benzoic acid	Auxin; gibberellin	*Arabidopsis*	Bhattacharyya et al. (2015) and Bhattacharyya and Lee (2017)
Salt stress tolerance	*Paraburkholderia phytofirmans* (PsJN)	2-Undecanone; 7-hexanol; 3-methylbutanol	Unknown	*Arabidopsis*	Ledger et al. (2016)
Osmotic stress tolerance	*Bacillus amyloliquefaciens* (GB03)	Entire VOC blend	PEAMT; glycine betaine; choline	*Arabidopsis*	Zhang et al. (2010)
Drought stress tolerance	*Pseudomonas chlororaphis* (O6)	2,3-Butanediol	Salicylic acid; nitric oxide	*Arabidopsis*	Cho et al. (2008, 2013)
Stomatal closure	*Bacillus amyloliquefaciens* (FZB42)	Acetoin; 2,3-butanediol	Salicylic acid; abscisic acid	*Arabidopsis*; *Nicotiana benthamiana*	Wu et al. (2018)
Improved sulfur acquisition	*Bacillus amyloliquefaciens* (GB03)	Entire VOC blend	ATP sulfurlyase; APRs; APKs	*Arabidopsis*	Aziz et al. 2016
Improved sulfur acquisition	*Bacillus* sp. (B55)	Dimethyl disulfide	Sulfur assimilation pathway	*Nicotiana attenuata*	Meldau et al. (2013)
Improved iron acquisition	*Bacillus amyloliquefaciens* (GB03)	Entire VOC blend; acidic components	FIT1; IRT1; FRO2; root proton exudation	*Arabidopsis*	Zhang et al. (2009)

(continued)

Table 7.1 (continued)

PGPR effects on plants	PGPR species (strain)	Bacterial VOCs	In planta mediators	Plant species	References
Improved iron acquisition	*Sinorhizobium meliloti*	Entire VOC blend	Root proton exudation	*Medicago truncatula*	del Carmen Orozco-Mosqueda et al. (2013)
Improved iron acquisition	*Arthrobacter agilis* (UMCV2)	Dimethyl hexadecilamine	FRO1	*Sorghum bicolor*	Castulo-Rubio et al. (2015)

tolerance. Meanwhile, potential complexities of VOC effects, such as dosage-dependent effectiveness, need to be taken into consideration (Liu and Zhang 2015). Importantly, key questions to be addressed include (1) what is the bioactive VOC component (or combination) that is responsible for the function of the natural VOC blends; (2) how are the bioactive VOCs perceived or utilized in the plants; and (3) how do the VOCs integrally modulate different biological processes in plants to achieve multiple beneficial effects. In addition to addressing interesting scientific questions, an equally important issue is to develop effective methods to apply natural or synthetic VOCs in agriculture for improved crop stress tolerance.

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