Bacterial Volatiles for Plant Growth

18

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Abstract

The rhizosphere is defined as the zone of soil surrounding the plant roots. Plant roots secrete a variety of plant exudates rich in nutrients resulting in accumulation of more bacteria in the rhizosphere region, generally 10–100 times higher than in the bulk soil. The bacteria colonizing this rhizosphere region are called as rhizobacteria, and those which help in promoting the growth of plants are called as plant growth-promoting rhizobacteria (PGPR). Currently, many biological approaches have gained importance for improving the crop production. One of the approaches includes using microbes as bioinoculants to promote growth and development of plants. Many rhizobacteria are presently being used as bioinoculants. They possess different mechanisms to enhance the plant growth such as nitrogen fixation, phosphate solubilization, production of siderophores, production of 1-aminocyclopropane-1-carboxylate deaminase (ACC), phytohormone production exhibiting antifungal activity, quorum sensing (QS) signal interference, induction of systemic resistance, interference with pathogen toxin production, and production of volatile organic compounds (VOCs). The production of VOCs by microorganisms can be considered as a novel characteristic property of PGPR in promoting the plant growth. The chemicals produced by microorganisms like bacteria and fungi as a part of their metabolism are called as microbial volatile organic compounds (MVOCs). These can modulate the physiology of plants and microorganisms and thus can provide an alternative method to use of chemicals in protecting plants from pathogens and increasing crop yield. MVOCs can be considered as ecofriendly and cost-effective strategy for sustainable agriculture.

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Rhizosphere • Plant growth promoting Rhiobacteria (PGPR) • Bioinoculants • Volatile organic compounds

18.1 Introduction

The soil has the most dynamic biological component with diverse types of living organisms – microorganisms as well as larger soil fauna such as nematodes, earthworms, ants, insects, rodents, etc. A wide range of microorganisms inhabit soil, but the most important ones are bacteria, actinomycetes, fungi, algae, protozoa, and viruses. These microbes vary in numbers and types owing to the vast differences in the physical and chemical characteristics of soils and also differences in agricultural practices. Microorganisms in soil are important in affecting soil structure and maintaining soil fertility. Microbes play an important role in cycling of nutrient elements (C, N, P, S, Fe) and are sources of industrial products such as enzymes, antibiotics, organic acids, vitamins, etc.

The bacteria are the most dominant of all the soil microorganisms, and they range from 10^5 to 10^8 per gram of soil. They vary in both numbers and types depending upon the physical, chemical, and biological conditions of the soil. Bacteria are the vital components of soils involved in various activities in the soil improving the soil fertility and enhancing the crop production (Ahmad et al. 2008; Chandler et al. 2008; Ahemad and Khan 2009). They promote plant growth by solubilizing or providing nutrients, producing plant growth hormones, controlling or inhibiting plant pathogens, sequestering toxic heavy metals from soils, etc. (Braud et al. 2009; Hayat et al. 2010; Rajkumar et al. 2010; Ahemad and Malik 2011; Ahemad 2012).

18.1.1 Rhizosphere and Rhizobacteria

The narrow zone of soil directly surrounding the root system (plant roots and root hairs) is referred to as rhizosphere. There are three separate but interacting components in the rhizosphere region: the rhizosphere (soil), the rhizoplane, and the root itself (Fig. 18.1). Many microorganisms are especially abundant in this rhizosphere. The zone of soil surrounding the roots is called rhizosphere and is influenced by substrates released by roots which affect microbial activity. The root surface including the strongly adhering soil particles is called rhizoplane also harbors microbes. The root itself is also a component of the system and many microorganisms (like endophytes) colonize the root tissues (Barea et al. 2005).

Plant roots majorly play a role by providing the mechanical support and facilitating water and nutrient uptake. Apart from this, plant roots also synthesize and secrete a variety of compounds which act as chemical attractants for diverse kinds of soil microbes (Walker et al. 2003). The bacteria lodging around the plant roots are called as rhizobacteria (Kloepper et al. 1991; Dakora and Phillips 2002). The

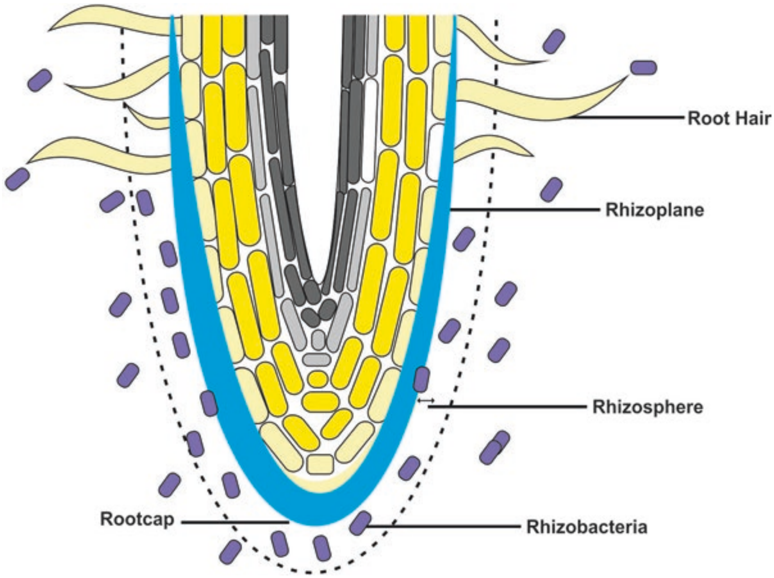

Fig. 18.1 Longitudinal cross section of a root with the surrounding rhizosphere and rhizobacteria

chemicals which are secreted by roots of different plant species into the soils are called as root exudates. These include a wide range of chemical compounds such as amino acids, organic acids, sugars, vitamins, enzymes, inorganic ions, and gaseous molecules (Table 18.1). These exudates regulate the structure of soil microbial community in the immediate vicinity of root surface by modifying the chemical and physical properties of the soil.

18.1.2 Plant Growth-Promoting Rhizobacteria

The bacteria colonizing the rhizosphere region around plant roots are called as rhizobacteria. Rhizobacteria are more versatile and efficient in transforming, mobilizing, and solubilizing the nutrients when compared to bacteria from bulk soils. Therefore, the rhizobacteria are considered as important in recycling of soil nutrients and thus improving the soil fertility (Hayat et al. 2010; Glick 2012). All these attributes of rhizobacteria help in promoting growth of plants, and thus these bacteria are termed as plant growth-promoting bacteria (PGPR). PGPR should have the following inherent characteristics: (1) they must colonize the root surface or the rhizosphere region; (2) they must be able to survive, multiply, and compete with other microorganisms and establish themselves; and (3) they must express the plant growth promotion activities and result in plant growth (Ahmed and Kibret 2014).

Table 18.1 Various compounds in root exudates of different plant species

S. No.	Type of root exudate compounds	Examples
1	Amino acids	α-Alanine, β-alanine, c-aminobutyric acid, a-aminoadipic acid, arginine, asparagines, aspartate, cysteine, cystine, glutamate, glycine, histidine homoserine, isoleucine, leucine, lysine, methionine, ornithine, phenylalanine, proline, serine, threonine tryptophan, and valine
2	Organic acids	Acetic acid, aconitic acid, aldonic acid, butyric acid, citric acid, formic acid, fumaric acid, glutaric acid, glycolic acid, lactic acid, malic acid, malonic acid, oxalic acid, pyruvic acid, succinic acid, tetronic acid, and valeric acid
3	Sugars	Hexoses and pentoses such as glucose, fructose, galactose, ribose, xylose, rhamnose, arabinose, oligosaccharides, raffinose, and maltose
4	Vitamins	Biotin, niacin, pantothenic acid, riboflavin, and thiamine
5	Purines	Adenine and guanine
6	Enzymes	Amylase, invertase, protease, and phosphatase
7	Inorganic ions and gaseous molecules	H^+, OH^-, HCO^{-3}, CO_2, and H_2

Source: Dakora and Phillips (2002)

PGPR can be divided on the basis of their location into two types:

1. Extracellular (ePGPR) – those which exist in the rhizosphere or on the rhizoplane or in the spaces between root cortical cells. Examples include *Bacillus*, *Azotobacter*, *Azospirillum*, *Pseudomonas*, *Agrobacterium*, *Arthrobacter*, *Burkholderia*, *Caulobacter*, *Chromobacterium*, *Erwinia*, *Flavobacterium*, *Micrococcus*, *Serratia*, etc.
2. Intracellular (iPGPR) – those which exist inside root cells, generally in specialized nodular structures. Most of rhizobacteria belonging to this group are Gram-negative rods, and examples include genera such as *Allorhizobium*, *Azorhizobium*, *Bradyrhizobium*, *Mesorhizobium*, and *Rhizobium* (Figueiredo et al. 2011; Bhattacharya and Jha 2012).

PGPR can also be classified based on their functional activities as (1) biofertilizers increasing the availability of nutrients to plants, (2) phytostimulators causing plant growth promotion through phytohormone production, (3) rhizoremediators degrading organic pollutants, and (4) biopesticides controlling diseases, mainly by the production of antibiotics and antifungal metabolites (Somers et al. 2004; Antoun and Prevost 2005).

18.1.3 Mechanism of Plant Growth Promotion by PGPR

Plant growth promotion mediated by PGPR occurs through the production of various substances and mechanisms resulting in the alteration of the whole microbial community in rhizosphere region. Large quantities of growth-promoting substances

Table 18.2 Growth-promoting substances released by PGPR

S. No.	Plant growth-promoting substances	PGPR
1.	IAA	*Pseudomonas putida*, *Pseudomonas aeruginosa*, *Klebsiella* sp., *Rhizobium* sp., *Enterobacter* sp., *Bacillus* sp., *Bradyrhizobium* sp., *Mesorhizobium* sp., *Paenibacillus polymyxa*, *Acinetobacter* spp., *Azospirillum* sp., *Rahnella aquatilis*, *Serratia marcescens*, *Stenotrophomonas maltophilia*, *Burkholderia*, *Azotobacter* sp., *Brevibacillus* spp., *Xanthomonas* sp., *Sphingomonas* sp., *Mycobacterium* sp., *Rhodococcus* sp., and *Cellulomonas* sp.
2.	Gibberellin and kinetin	*Azotobacter chroococcum*
3.	HCN and ammonia	*Pseudomonas* sp., *Rhizobium* sp., *Bradyrhizobium* sp., *Enterobacter* sp., *Bacillus* sp., *Klebsiella* sp., *Mesorhizobium* sp., and *Serratia marcescens*
4.	Cytokinins	*Rhizobium leguminosarum*
5.	ACC deaminase	*Kluyvera ascorbata*, *Rahnella aquatilis*, *Stenotrophomonas maltophilia*, *Acinetobacter* sp., *Pseudomonas* sp., and *Burkholderia*
6.	Siderophores	*Brevibacterium* sp., *Bacillus* sp., *Azotobacter* sp., *Bradyrhizobium*, *Rhizobium*, *Mesorhizobium*, *Kluyvera ascorbata*, *Variovorax paradoxus*, *Rhodococcus* sp., *Pseudomonas* sp., *Burkholderia*, *Enterobacter* sp., *Serratia marcescens*, *Paenibacillus polymyxa*, *Proteus vulgaris*, *Ralstonia metallidurans*, *Acinetobacter* spp., and *Klebsiella* sp.
7.	Exopolysaccharides	*Pseudomonas* sp., *Rhizobium* sp., *Bradyrhizobium* sp., *Mesorhizobium* sp., *Enterobacter* sp., *Bacillus* sp., and *Klebsiella* sp.

Adapted from Ahemad and Kibret (2014)

are produced by these rhizosphere microorganisms that influence the overall morphology and growth of the plants (Table 18.2). The beneficial effects of these rhizobacteria on plant growth can be direct or indirect. PGPR promote plant growth directly by either facilitating or increasing the availability of nutrients such as nitrogen, phosphorus, and other essential minerals or modulating plant hormone levels, stimulating of root growth, or degrading organic pollutants and plant stress control. Rhizobacteria can also promote plant growth indirectly by mechanisms of biological control by reducing the disease incidence by inhibiting various plant pathogens and development in the form of biocontrol agents which include antibiosis, induction of systemic resistance, and competition for nutrients and niches (Kloepper and Schroth 1981; Glick 2012).

A wide range of plant growth-promoting traits have been studied in various microbes (Fig. 18.2). They include phytohormone production (Joo et al. 2005; Tank and Saraf 2010; Ahemad and Khan 2012c); production of siderophores (Tian et al. 2009; Jahanian et al. 2012); production of compounds such as 1-aminocyclopropane-1-carboxylate (ACC), hydrogen cyanate (HCN), and ammonia; nitrogenase

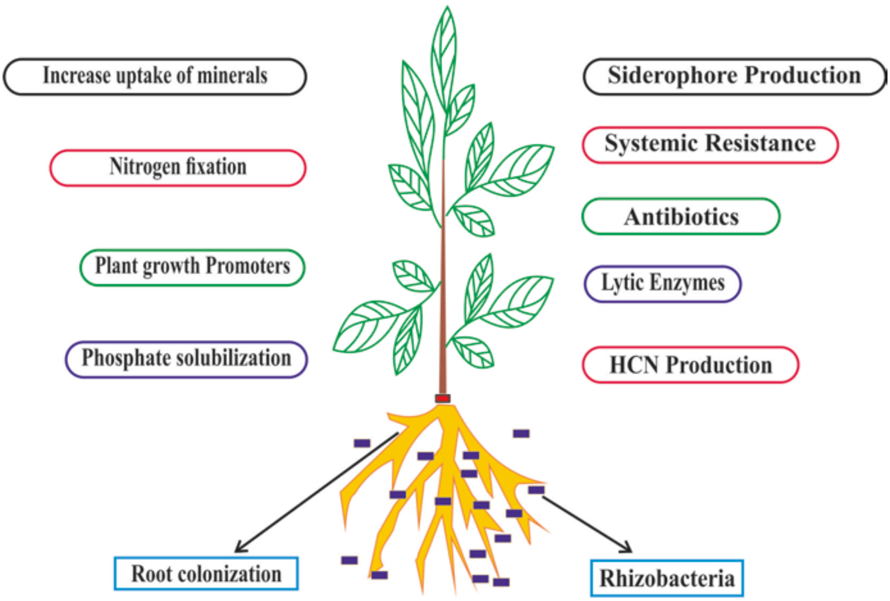

Fig. 18.2 Mechanisms of plant growth promotion by rhizobacteria

activity (Glick 2005); phosphate solubilization (Ahemad and Khan 2012c); detoxification of heavy metals (Khan 2005; Wani and Khan 2010; Ma et al. 2011a); pesticide degradation or tolerance (Ahemad and Khan 2012a, b); salinity tolerance (Mayak et al. 2004; Tank and Saraf 2010); and biological control of phytopathogens and insects (Murphy et al. 2000; Hynes et al. 2008; Russo et al. 2008). These traits of microorganisms are responsible for the plant growth promotion and increased yield through the action of multiple mechanisms (Bashan and Holguin 1997). Thus PGPR offers an attractive way to replace the use of chemical fertilizers, pesticides, and other supplements, increasing their potentiality in agriculture.

18.2 Novel Attributes of PGPR in Plant Growth Promotion

Agricultural crop yield and food security are alarmingly scaring due to rapidly evolving plant pathogens and climate changes all over the world. The increased use of chemical fertilizers and pesticides provides immediate solutions for the plant disease control and increase crop yield. But their excessive use negatively effects human health and environment. Therefore biological approaches have become important for enhancing/ increasing the crop production especially among agronomists and environmentalists. Diverse rhizobacteria possessing different mechanisms are now being used as bioinoculants all over the world to promote growth and development in plants. Bioinoculants are easy to deliver and cause an increase in biomass production and crop yield. Although hazardous synthetic fertilizers and pesticides are replaced by biofertilizers, biopesticides, and biocontrol agents derived from living microbes, alternatives are searched for, owing to their high costs, their reduced efficiency, and inconsistent field performance (Glare et al. 2012). Research is being carried out to explore new attributes of microbes in promoting plant growth and crop protection. Emission of volatile organic compounds (VOCs) is one of the most widespread mechanisms by which microorganisms modulate growth and development of plants. Microbial volatile organic compounds (MVOCs) can become an alternative to chemicals in providing disease resistance against plant pathogens and can be exploited as a cost-effective strategy for enhancing plant growth and productivity.

18.2.1 Volatile Organic Compounds (VOCs)

Volatiles organic compounds (VOCs) are low-molecular-weight compounds with high vapor pressure. They exist in the gaseous state at room temperature and are characterized by low to medium water solubility. All these properties of VOCs allow them to easily evaporate into air. VOCs can be produced through industrial processes, usually formed as by-products during the manufacture of paints, petroleum fuels, pharmaceuticals, refrigerants, household cleaners, and other products. VOCs can also be produced by microorganisms as a part of their metabolism called as microbial volatile organic compounds (MVOCs).

18.2.2 Microbial Volatile Organic Compounds (MVOCs)

Microbial volatile organic compounds (MVOCs) are a type of volatile compounds produced by microorganisms during their metabolism. Microbial volatile organic compounds (MVOCs) are produced by different groups of microbes especially bacteria and fungi. Very few, around 1,000 MVOCs released by 400 bacteria and fungi, have been described so far in the literature (Effmert et al. 2012; Lemfack et al. 2014). A high proportion of unknown compounds are yet unexplored as revealed by GC-MS analyses, suggesting a great potential for the discovery of new compounds.

MVOCs are a complex mixture of low-molecular-weight lipophilic compounds and include low-molecular-weight alcohols, aldehydes, ketones, amines, terpenes, aromatic and chlorinated hydrocarbons, and sulfur-based carbon compounds. Furfural, butanoic acid, propanoic acid, 5-hydroxy-methyl-furfural, β-caryophyllene, geosmin, 2-methyl-isoborneol, 1-octen-3-ol, α-pinene, camphene, camphor, methanol, and acetaldehyde are among the most frequently emitted compounds. MVOCs are derived from different biosynthetic pathways during microbial metabolism – primary and secondary metabolism. In primary metabolism, MVOCs are produced as by-products, while the organism breaks down food in the environment to extract nutrients needed for the maintenance of cell structures. Examples include ethanol, 1-octen-3-ol, 2-octen-1-ol, and benzyl cyanide produced by some fungi such as

Aspergillus niger, *Aspergillus flavus*, and *Penicillium roqueforti* and *Botrytis cinerea*. In secondary metabolism, the production of MVOCs is driven by the competition for resources in a nutrient-poor environment. Examples include 2-methyl-isoborneol, geosmin (1-10-dimethyl-*trans*-9-decalol), and terpenes produced by fungi such as *Chaetomium* sp., *Penicillium aurantiogriseum* and *Penicillium vulpinum*, and *Aspergillus*. Few bacteria such as *Streptomyces griseus* and *Streptomyces odorifer* produce MVOCs such as geosmin, 3-methyl-butanol, and 2-methyl-isoborneol. These emitted volatile compounds vary quantitatively and qualitatively depending on the age and genetic profiles of the producing species as well as also on external variables such as substrate, temperature, moisture level, and pH of microbial growth (Sunesson et al. 1995; Claeson et al. 2002; Matysik et al. 2008).

A number of microorganisms interact with different ecological components via the volatiles they release. MVOCs are produced both below- and aboveground and interfere with the rhizosphere and the atmosphere in different ways (Tirranen and Gitelson 2006; Wenke et al. 2010; Kanchiswamy et al. 2015). VOCs play an important role in signaling between species that are present in a common ecological niche as they can diffuse through the atmosphere and the soil. Different organisms respond variedly to different MVOCs produced, and thus complex interactions can result at trophic levels. Moreover, species-specific MVOCs can also serve as marker compounds for the selective detection of microorganisms in the environment (Fiedler et al. 2001).

Microbial volatile organic compounds can travel through the atmosphere, porous soils, and liquids and serve as chemical windows through which the information about the molecular basis of microbial activities is released. They function as semiochemicals and help in mediating both short- and long-distance interactions at intercellular and organisms level (Liang et al. 2008; Korpi et al. 2009). Thus MVOCs are considered as ideal info-chemicals and are responsible for inter- and intraorganismic communication and interactions between plants, antagonists, and symbionts both below- and aboveground (Beattie and Torrey 1986; Maffei 2010; Maffei et al. 2011; Morath et al. 2012; Kanchiswamy et al. 2015).

18.3 Bacterial VOCs

Bacteria produce a wide variety of volatile compounds depending on the specific metabolism or metabolic pathway(s) active in the bacteria. Bacterial VOCs comprise of hydrocarbons, alcohols, ketones, alkanes, alkenes, esters, sulfur compounds, and terpenoids (Fig. 18.3). They occur over a range of concentrations and can act over long distances (Wheatley 2002; Schulz and Dickschat 2007; Kai et al. 2009). These volatiles emitted by bacteria trigger many physiological changes in a broad range of organisms and influence interactions among various populations and communities. Bacterial volatiles play an important role in bacterial–plant, bacterial–bacterial, and bacterial–fungal interactions and affect either positively or negatively.

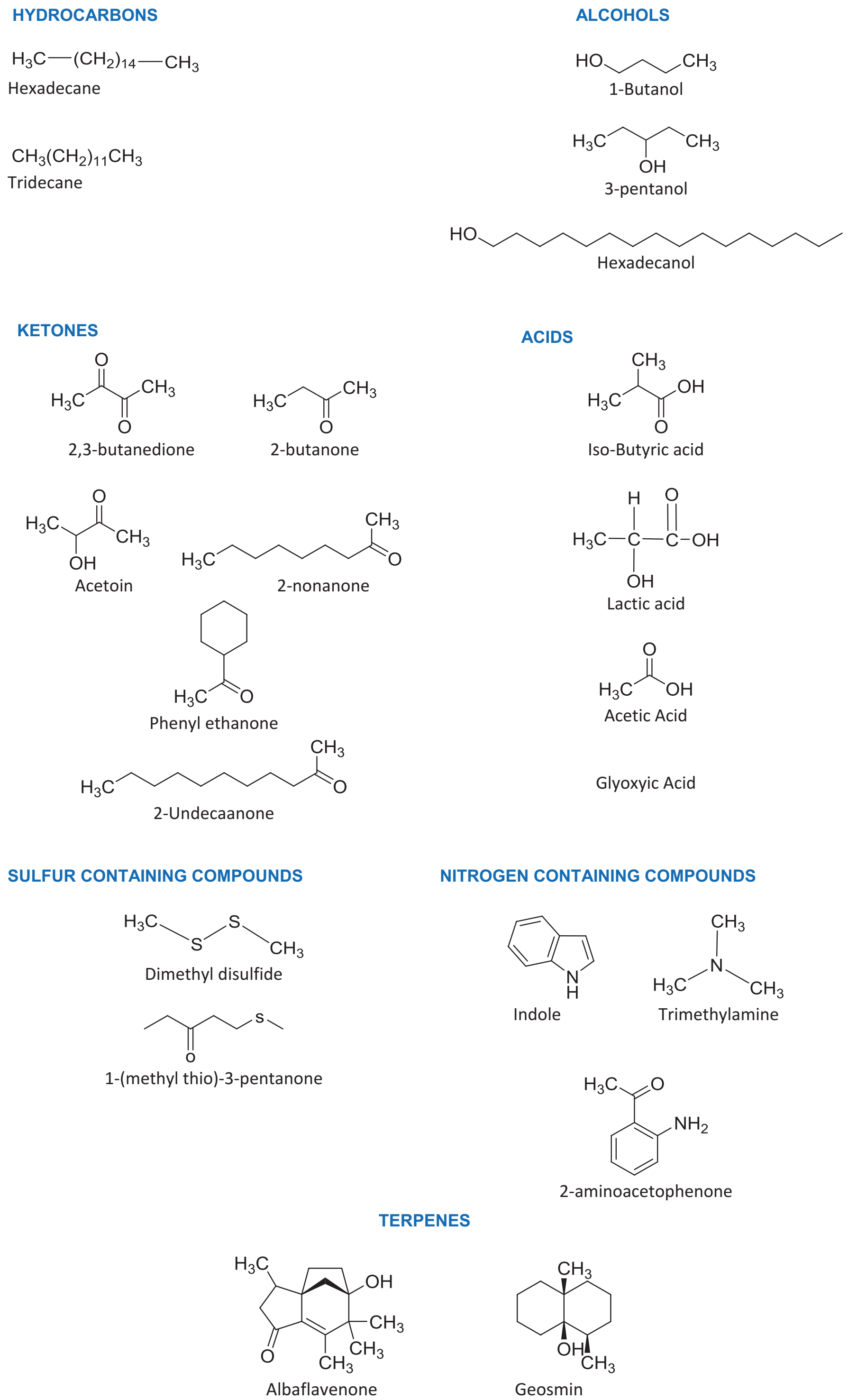

Fig. 18.3 Bacterial volatile organic compounds (VOCs)

They cause plant growth promotion, induce systemic resistance in plants, are effective against a wide range of plant-pathogenic bacteria and fungi, and act as biocontrol agents (Chen et al. 2008; Kai et al. 2008; Wan et al. 2008; Lee et al. 2010; Leroy et al. 2011; Davis et al. 2013; D'Alessandro et al. 2014; Kanchiswamy et al. 2015). These progressive studies on MVOCs made by various scientists demonstrate critical roles in multitrophic interactions affecting agriculture and entire ecosystem.

18.4 MVOCs in Bacterial–Plant Interactions

Many bacteria colonize around the host plant and establish themselves in the rhizosphere region. Extensive communication occurs between soil microorganisms and plants during the different stages of plant development by signal molecules produced from the two partners. Bacteria play an important role by producing plant growth-regulating substance such as auxins and/or cytokinins (Ortiz-Castro et al. 2009). Apart from these, the MVOCs produced are known to involve in various inter- and intraspecific interactions, above- and belowground, resulting in genetic, phenotypic, and morphologic alteration of both the interacting organisms (Effmert et al. 2012; Penuelas et al. 2014; Piechulla and Degenhardt 2014).

VOC-mediated interactions between bacteria and plants are widespread. Bacterial volatile organic compounds (VOCs) are highly complex in nature and act as signaling molecules causing an interaction between bacteria and plants in the ecosystem. They are found to have varied effects causing positive or negative impact on plant growth. These VOCs released by bacteria can promote plant growth. Many studies have shown bacteria to produce volatiles that cause plant growth promotion such as *Bacillus* sp. (Ryu et al. 2003, 2004, 2005; Farag et al. 2006; Zhang et al. 2007; Yang et al. 2009) and *Pseudomonas chlororaphis* (Han et al. 2006). Deleterious effects of bacterial volatiles on plants such as chlorosis, inhibition of plant growth, and plant death have also been observed (Vespermann et al. 2007; Blom et al. 2011b). The negative effects observed on plant growth include both inorganic and organic compounds. Inorganic volatiles include hydrogen cyanide (HCN) and NH3, and organic volatile compounds include dimethyl disulfide and 3-phenylpropionic acid (Rudrappa et al. 2008; Chung et al. 2010; Kai et al. 2010; Blom et al. 2011b; Weise et al. 2013).

18.4.1 MVOC Role in Plant Growth Promotion

Rhizosphere bacteria are the bacteria which preferentially live in the soil closely associated with the plant roots. A characteristic property of these rhizobacteria is production of plant growth-modulating volatiles. These MVOCs usually have molecular mass below 300 daltons with relatively low boiling points. They are lipophilic in nature. Rhizosphere bacteria emit different VOCs that can modulate plant growth promotion. VOCs produced by rhizobacteria show antimicrobial property against plant-pathogenic microorganisms and help in plant growth promotion. A number of research works have been published reporting the effect of volatiles on plant growth promotion. Meldau et al. (2013) found that *Bacillus* B55 strain isolated from *Nicotiana attenuata* (coyote tobacco) roots released VOCs which has strong plant growth promotion effects on wild-type *N. attenuata*. A study by Blom et al. (2011a) showed that many soil and rhizosphere strains produced volatiles which had significant effects on plant growth of *Arabidopsis thaliana*. Studies by Kai et al. (2010) have shown that *Bacillus subtilis* (GB03) and *Bacillus amyloliquefaciens* (IN937a) emitted two volatiles, namely, 2,3-butanediol and acetoin, which had a positive effect on the growth of *Arabidopsis thaliana*.

18.4.2 MVOC Role in Inducing Phenotypic Plant Responses

N-Acyl homoserine lactones (AHLs) belong to a class of amino compound-containing lipids produced by many plant-associated bacteria, especially PGPR. They mediate communication between bacterial cells and produce MVOCs inside the plant and play a role in morphogenetic processes of plants. AHLs alter gene expression in roots and shoots and modulate defense and cell growth responses in plants. Studies by Ortiz-Castro et al. (2008) and Von Rad et al. (2008) have shown that AHL compounds such as *N*-hexanoyl-homoserine lactone and *N*-3-oxo-hexanoyl-homoserine lactone, *N*-octanoyl-homoserine lactone, etc., showed an effect on root architecture and altered primary root growth, lateral root formation, and root hair development of *Arabidopsis*. Volatiles released from different microbial species are also found to have an effect on leaf starch metabolism and promoted starch accumulation in leaves of both mono-and dicotyledonous plants (Ezquer et al. 2010).

18.4.3 MVOC Role in Induced Systemic Response

MVOCs also act as initiators of defense responses in plants mediated through induced systemic response (ISR) (Ryu et al. 2003, 2004; Cortes-Barco et al. 2010a, b; D’Alessandro et al. 2014). Application of 2,3-BD to the soil protected against fungal pathogens *Microdochium nivale*, *R. solani*, or *Sclerotinia homoeocarpa* and had shown to reduce the diseased leaf area of *Agrostis stolonifera* by 20–40 %. Application of 3-pentanol and 2-butanone on cucumber seedlings triggered plant systemic defense responses against *P. syringae* pv. *lachrymans*. These compounds play a role in an indirect defense strategy that protects plants from herbivores by inducing gene expression of plant green leaf volatile signaling pathway to attract natural enemies of pests (Scala et al. 2013). Studies by Song and Ryu (2013) also showed that these compounds result in a significant increase in the number of ladybird beetles, *Coccinella septempunctata*, a natural enemy of aphids.

18.5 MVOCs in Bacterial–Bacterial Interactions

MVOCs play key roles in interspecific interactions among bacteria. VOCs of bacteria can influence the metabolism in certain bacterial species and stimulate their growth. For example, the growth of *Pseudomonas fluorescens* is stimulated by volatiles produced by *Collimonas pratensis* and *Serratia plymuthica*. A number of unique volatile compounds emitted by *C. pratensis* and *S. plymuthica* include benzonitrile, methyl thiocyanate, *S*-methyl thioacetate, and DMDS. Specific MVOCs are also by these bacteria such as 2-methyl propanal, ethenyl acetate, 3-methyl-2-pentanone, methyl 2-methylbutanoate, 3-hexanone, myrcene, terpinene, methyl salicylate, etc., produced by *C. pratensis* and chlorobenzene, dimethylsulfone, ethyl butanoate, 2-pentadecanone 1H-pyrrole, 2-octanone, and 5-dodecanone produced by *S. plymuthica* (Garbeva et al. 2014a).

MVOCs are also known to inhibit the growth of certain bacteria. Examples include 1-undecene as produced by some *P. fluorescens* and DMDS as produced by *S. plymuthica* strains which inhibited the growth of *Agrobacterium tumefaciens* and *A. vitis* strains in vitro. It has also been demonstrated that the growth of *Burkholderia cepacia* complex (Bcc) strains is inhibited through the synthesis of VOCs by bacteria. The main VOCs emitted by the *P. chlororaphis* strain 449 such as 1-undecene, 2-nonanone, 2-heptanone, and 2-undecanone DMDS were effective against *A. tumefaciens* strain C58 and the cyanobacterium *Synechococcus* sp. (Papaleo et al. 2012, 2013; Orlandini et al. 2014; Popova et al. 2014).

The AHLs produced by certain bacteria have the ability to disrupt quorum sensing networks in Gram-negative bacteria which usually regulates characteristics such as bioluminescence, biofilm formation, and production of virulence factors, antibiotics, and pigments. This phenomenon is termed as quorum quenching (QQ) and can be considered as a new approach in controlling plant pathogens (Rasmussen and Givskov 2006; Chernin et al. 2011).

18.6 MVOCs in Bacterial–Fungal Interactions

MVOCs have both positive and antagonistic interactions between bacteria and fungi in the rhizosphere (Effmert et al. 2012). Many bacterial volatiles have suppressive effects on soil fungi that might be harmful to agricultural crops. Rhizobacterial isolates like *Serratia* sp. (*S. plymuthica*, *S. odorifera*), *Pseudomonas* sp. (*P. fluorescens*, *P. trivialis*), and *Stenotrophomonas* sp. (*S. maltophilia* and *S. rhizophila*) synthesize and emit complex blends of MVOCs that inhibit growth of fungi – phytopathogens and nonpathogens (Vespermann et al. 2007; Zou et al. 2007; Kai et al. 2010; Verginer et al. 2010; Garbeva et al. 2014a, b). *Staphylococcus pasteuri* strain inhibited the mycelia growth of fungi *T. borchii* due to the production of MVOCs such as γ-patchoulene (antifungal), 3-methyl butanal, and 1-octen 3-ol. Typical metabolites of the *Staphylococcus* sp. were 2-undecanone, 3-methylbutanoate, 2-nonanone, ethanethioic acid, 2-methylbutan-1-ol, 4-methyl-2-heptanone, and dimethyl trisulfide (Barbieri et al. 2005).

Studies have shown the negative effects of VOCs produced by bacteria on growth of *R. solani*, a soilborne plant pathogen. Kai et al. (2007) reported that MVOCs such as β-phenylethanol and 2-(benzyloxy)benzonitrile emitted by *Stenotrophomonas* sp., *Serratia* sp., *Pseudomonas* sp., and *Bacillus subtilis* showed strong negative influence on the mycelial growth of *R. solani*. Weise et al. (2012) have reported that *Xanthomonas campestris* pv. *vesicatoria 85–10* emit more than more than 50 volatile compounds (mostly ketones and methylketones) to cause either promotion or inhibition effects on the fungus *R. solani*. Elshafie et al. (2012) reported that *Burkholderia gladioli* pv. *agaricola* strain produced MVOCs, the most effective being limonene compound, which inhibited the growth of fungi *F. oxysporum and R. solani.*

Zhang et al.'s (2013) studies showed that *Bacillus atrophaeus CAB-1* produced many volatile compounds, the most abundant being the O-anisaldehyde, hexadecane, and 2,3-dimethoxybenzamide, and were found to inhibit the growth of the fungal pathogen *Botrytis cinerea.* Also MVOCs such as DMDS, dimethyl trisulfide, 2-undecanone, S-methyl methanethiosulfonate 4-octanone, and 1-phenylpropan-1-one emitted by *Burkholderia ambifaria* caused a significant growth inhibition of two phytopathogenic fungi, *R. solani* and *Alternaria alternata* (Groenhagen et al. 2013). *B. tropica* strain MTo431 emitted a range of VOCs such as α-pinene, DMDS, ocimene, limonene, and fenchone which are known to have antagonistic effect on fungi and significantly inhibited the mycelial growth of four plant-pathogenic fungi – *Colletotrichum gloeosporioides*, *Fusarium culmorum*, *F. oxysporum*, and *Sclerotum rolffsi* (Tenorio-Salgado et al. 2013).

18.7 Conclusion

Volatile organic compounds emitted by microorganisms (MVOCs) are involved in various kinds of interactions between plants and microbes – antagonistic effects, mutualistic effects, and regulation of cellular and developmental processes at intra- and interspecies level as well as modification of their surrounding environments. MVOCs can modulate the physiology of plants and microorganisms especially impacting plant health. Bacterial VOCs are chemically heterogeneous molecules and produced in low concentrations. They are fully biodegradable and have no hazardous effects as in case of use of chemical pesticides or fertilizers. Thus MVOCs can be exploited as an ecofriendly and cost-effective approach for sustainable agriculture. The vast diversity of microbial communities in nature and their importance in modulating ecology, health, and growth of plants necessitate the need to systematically explore and characterize the biological functions and ecological roles of plethora of microbial VOCs. This will not only help in discovering novel mechanisms for controlling diverse biological processes critical to plant health but also provide practical solutions to various agricultural and environmental problems.

- Microbes produce a wide range of MVOCs and exert an immense effect on plant growth and development. Till now, only a few VOCs emitted by microbes (bacteria and fungi) have been identified and characterized. There is a need to explore new microbial volatile compounds and characterize their biological functions and ecological roles and study the underlying mechanisms so that they can be employed for controlling plant health thus reducing agricultural and environmental problems.

- Most of the studies conducted on MVOCs are in vitro studies (laboratory). In situ studies have to be performed, i.e., field trials are to be done to demonstrate their effects on growth and development of plants. Moreover physiological and molecular studies should be conducted for a better understanding of the role of MVOCs at field level. New understanding of the importance of MVOCs for crop plants both at the lab and open field conditions will provide further scientific evidence to adopt them for sustainable crop protection. All these studies can be used to develop production strategies and assess the cost effectiveness of naturally produced MVOCs for crop welfare and sustainable agriculture.
- MVOCs may modulate growth or defense of plants in a species-dependent manner. The effect of these volatile compounds varies depending on crop species, soil types, and environmental conditions. Thus there is difference in results obtained between lab scale studies and field trials. This implies the necessity to evaluate single MVOCs as well as blends of different MVOCs in modulating growth and defense of different crop species both at lab and field conditions.
- MVOCs should be characterized for their bioactive molecules, their proper bioactive dosage, and their role on plant growth. The requirement of energy and resources for the synthesis of MVOCs should also be considered. MVOCs may have side effects, many of them exert inhibitory effects, and some of them are also toxic. Hence the dose-response effect on specific crops is assessed before their use and then can be suggested for crop protection and productivity.
- Another challenging aspect is the manner of application of MVOCs since most of them have rapid evaporation rates, thus making them difficult to use in open field conditions. An appropriate method of MVOCs delivery in the field is still lacking, and therefore future studies are needed to understand and devise a better, cost-effective, durable, and efficient delivery of MVOCs.

The future research works on MVOCs should focus on expanding the knowledge on the MVOC biodiversity, exploring the physiological and ecological roles of single as well as blends of MVOC mixtures, establishing plant response analyses to MVOCs, and devising a more efficient delivery system to crop fields. Thus the potential MVOCs will provide a plethora of applications for protection, growth, and development of plants paving a way for sustainable agriculture.

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