Chapter 14
Effects of Microbial Signaling in Plant Growth and Development

Sahana Basu, Preeti Priyadarshini, Ram Prasad, and Gautam Kumar

Abstract Agricultural sustainability is predominantly regulated by the functional equilibrium between soil processes and productivity of plants. Growth and productivity of plants frequently depend on their intimate association with the microbial organisms present in the rhizosphere. The present chapter summarizes an updated knowledge on the role of microbial signaling in regulating plant growth and also recommends future research prospects in this area. Plant roots release various organic compounds in its surrounding soil, known as root exudates leading to the induction of the beneficial rhizospheric microbes. Microorganisms also modify the plants' behavior by producing inter-organismal signaling molecules. Plant growth-promoting rhizobacteria (PGPR) play an important role in the signaling, metabolism, and hormonal homeostasis in plants. They also produce antibiotic compounds that inhibit the growth of poisonous rhizospheric microbes, thereby promoting plant growth. The PGPR also increase the availability and uptake of nutrients and provide resistance to abiotic and biotic stresses leading to agricultural sustainability. Free-living beneficial fungi in the soil microbiome efficiently spread over the rhizosphere and eliminate pathogenic fungal strains by competitive inhibition. They also contribute in the antibiotic production and elicitation of defense responses in plants. Signaling process is executed by other classes of molecules, including N-acyl-l-homoserine lactones (AHLs) and microbial volatile organic compounds (MVOCs). The AHLs and MVOCs play a crucial role in the bacterial downstream signaling, by which the bacterial genes may express. These molecules are also recognized by the plants further contributing in the improvement of plant development and defense mechanisms by upregulating different genes.

S. Basu
Department of Biotechnology, Assam University, Silchar, Assam, India

P. Priyadarshini · G. Kumar (✉)
Department of Life Science, Central University of South Bihar, Gaya, Bihar, India
e-mail: gautam@cub.ac.in

R. Prasad
Department of Botany, Mahatma Gandhi Central University, Motihari, Bihar, India

14.1 Introduction

Plants play a pivotal role in maintaining the ecosystem. They have been established to have many evolutionary benefits, which actually help them in acclimatizing with the stressful environments. Additionally, several studies have revealed the plants to possess a complicated nutritional organization (Marschner 1995). Plant-microbe interactions comprise of rhizomicrobiome (microbes associated with root), phyllomicrobiome (microbes associated with aboveground tissues), and endosphere (microbial colonization of internal tissues) (Basu and Kumar 2020a). However, rhizomicrobiome has been extensively studied than the other components.

Root system in plants is the most important morphologically and physiologically plastic structure forming a vigorous assembly after entering inside the soil. In addition to providing anchorage, root has other major contributions directly or indirectly associated with the plant growth and development (Kumar et al. 2022a). Root system also directly perceives various environmental stresses (Kumar et al. 2022b; Mishra et al. 2021). Therefore, development of plants eventually depends upon the environment (Kumar et al. 2021). Root in the soil continuously interacts with the microbial community, supporting in the plant development and immunity. Roots also secrete various chemical components, which play a significant role in regulating the phytomicrobiome.

Soil ecosystem plays a crucial role in the assimilation of the organic compounds in soil, deterioration of living particles, eradication of pathogenic components, and detoxification (Behera and Prasad 2020). In the soil ecosystem, the microorganisms survive with the support of soil carbon, which actually comes from the plants' rhizosphere. It is the zone of soil surrounding the plant root, which harbors a variety of microbes (Shrivastava et al. 2014). Numerous studies have shown the occurrence of root-microbes and intra-inter-microbial interaction through the soil ecosystem, facilitating the soil fertility, plant growth, root and shoot formation, and development of leaf primordia and flowers (Basu et al. 2020a). However, interactions between the rhizosphere and microbes are still not completely understood.

Higher plants interact with their associated microbes in diverse ways affecting each other (Berendsen et al. 2012). Microorganisms modify the plants' behavior by producing inter-organismal signaling molecules, and plant-synthesized signaling compounds regulate the microbial populations. Thus, plants and microbes alter each other's behavior for their individual benefit leading to symbiotic association. The signaling in the phytomicrobiome stimulating plant growth has been illustrated in Fig. 14.1.
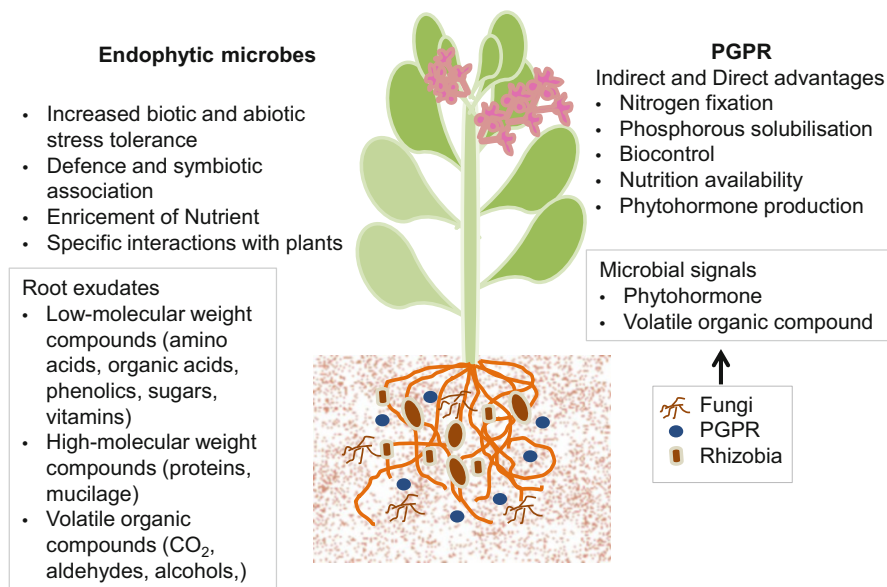
Endophytic microbes

- Increased biotic and abiotic stress tolerance
- Defence and symbiotic association
- Enricement of Nutrient
- Specific interactions with plants

Root exudates
- Low-molecular weight compounds (amino acids, organic acids, phenolics, sugars, vitamins)
- High-molecular weight compounds (proteins, mucilage)
- Volatile organic compounds (CO_2, aldehydes, alcohols,)

PGPR
Indirect and Direct advantages
- Nitrogen fixation
- Phosphorous solubilisation
- Biocontrol
- Nutrition availability
- Phytohormone production

Microbial signals
- Phytohormone
- Volatile organic compound

- Fungi
- PGPR
- Rhizobia

Fig. 14.1 Cross talking of plants and microbes through signaling pathways for promotion of plant growth

14.2 Plant Signal: Root Exudates

During the various stages of plant growth, seed germination to flowering the plant interacts with the surrounding soil which has a wide variety of microorganisms. Plant roots release various organic compounds in its surrounding soil, known as root exudates that lead to the improvement of the soil environment (Sarkar et al. 2022). The physical, chemical, and biological nature of the soil changes during the plant growth because of root exudates and rhizodeposition (el Zahar Haichar et al. 2014). This phenomenon of change in nature of surrounding soil is known as the rhizosphere effect. Root exudates are mainly composed of amino acids, organic acids, water-soluble sugars, hormones, vitamins, amino compounds, phenolics, and sugar phosphate esters. It is estimated that around 20–40% of the carbon fixed during photosynthesis is released as exudates from the plant roots (Badri and Vivanco 2009). The nature of the exudates depends on the growth stage of the plant and the environment. Modern ecological theories correlate root exudation for the plants' benefit for stimulating the beneficial microorganisms, thereby facilitating nutrient acquisition eventually inducing plant growth (Ortiz-Castro et al. 2009).

Based on the chemical nature of the compound, root exudates are categorized into three main classes.

14.2.1   Low-Molecular-Weight Compounds

They contribute to a major portion of root exudates, comprising amino acids, organic acids, phenolics, sugars, vitamins, and several secondary metabolites. These are usually transported through passive transport along the concentration gradient between the root cells and the external (soil) solution.

14.2.2   High-Molecular-Weight Compounds

They include proteins and mucilage.

14.2.3   Volatile Organic Compounds (VOCs)

They include carbon dioxide (CO_2), aldehydes, alcohols, and secondary metabolites.

The composition of the root exudates usually varies with plant species, age, and growth stages of plants' life cycle. Several abiotic factors, including soil type, temperature, light, micro-, and macronutrients also impact the chemical nature and time of exudation (Chai and Schachtman 2021). These factors often increase the rate of the exudation, thereby affecting the membrane integrity. For instance, under nitrogen-deficient conditions, root exudates assist the associations of plants with nitrogen-fixing microbes. Under this circumstance root exudates also inhibit the nitrifying and denitrifying bacteria, thereby reducing soil nitrogen losses. Ramesh et al. (2015) have revealed the anions and γ-aminobutyric acid (GABA) at the root apex to regulate the malate efflux anions channel (ALMT) under abiotic stress. Dong et al. (2004) have found the exudation of organic acids (such as oxalic acid, malic acid, and citric acid) to be predominantly increased in soybean plants under phosphate-deficient and aluminum-contaminated soil conditions. The chemicals present in the root exudates either attract microbes or produce carbon providing nutrition to the microbes.

Ecosystem also influences the nature and signaling cascade of the plant exudates. For instance, microbial infection in the plant root system assists the production of defense-oriented root exudates. The molecular pattern and the concentration of root exudates in soil are complex phenomena, which have not been completely understood so far. These exudates attract soil microbes, thereby establishing the rhizosphere effect. The composition of exudates also affects the microbial populations and activities.

14.3 Rhizosphere

The term "rhizosphere" was coined by a German plant physiologist Lorenz Hiltner in 1904 (Hiltner 1904). Rhizosphere (Greek "rhiza," root and "sphere," surrounding area) is defined as the plant root-soil interface or the seed-soil interface (Harley and Russell 1979). It has been described as the area surrounding the plant root (2–80 mm distance from root system), inhabited by distinctive microorganisms inducing the root exudation. It is a region of increased nutrient concentration and biotic activity. Enhanced interactions between the plants and soil microbes can be perceived in this region and, therefore, described as the microbe storehouse. These interactions can be symbiotic (beneficial), pathogenic (harmful), or neutral. The present chapter has discussed the beneficial aspects of the soil microbial interactions and their impact on plant growth and development.

14.3.1 Zones of the Rhizosphere

The rhizosphere is categorized into three zones based on the relative distance from the root (Lynch and Whipps 1991). As the proximity decreases, the influence of the root and its exudates decreases.

14.3.1.1 Endorhizosphere

It is the innermost zone, which includes the cortex and endodermis (internal) where the microbes and cations can occupy the apoplastic space (free space between cells).

14.3.1.2 Rhizoplane

It is the medial zone, which includes the root epidermis and mucilage. It is the root surface directly adjacent to the soil.

14.3.1.3 Exorhizosphere

It is the outermost zone contiguous to the epidermis extending from the rhizoplane out into the bulk soil.

The rhizosphere cannot be defined with a definite area or size due to the diversity and complexity of the plant root system. It is a gradient of physical, chemical, and biological properties changing along the root both radially and longitudinally. The rhizosphere isolated from the bulk soil is termed as edaphosphere (non-rhizosphere), where the rhizosphere effect is negligible or absent. It has 10- to 100-fold less

microbial density than the rhizosphere. The rhizosphere is enriched in organic matter and generally more acidic than the edaphosphere. The soil in the rhizosphere is subjected to chemical changes caused by the presence of root exudates and metabolites of microbial degradation.

14.3.2 Rhizosphere Effect and R/E Ratio

The rhizosphere effect indicates enhanced microbial activity in the rhizosphere. It can be quantitatively expressed with R/E ratio, where "R" denotes the amount of root exudates in rhizosphere soil and "E" is the edaphosphere soil content. This ratio is determined from the number of microbes present in the rhizosphere to that of the edaphosphere. The value of R/E ranges within 5–20.

14.3.3 Microbiome in Rhizosphere

Rhizosphere harbors a variety of microbes like bacteria, fungi, actinomycetes, and algae (Campbell and Greaves 1990). Based on the nucleic acid analyses techniques of genomic molecules from soil, the samples have been revealed to exhibit a huge diversity in the rhizospheric microbial population (Basu and Kumar 2021a). Around 98% of the microbes in the soil cannot be cultured, and hence their identification, characterization, and their effect are still not known. Some microbes are in a close association with roots like mycorrhizal fungi. There are a variety of free-living microbes which include filamentous fungi of the genus *Trichoderma* and a variety of plant growth-promoting rhizobacteria (PGPR) (Prasad et al. 2015). Rhizospheric organisms that have been well studied for their beneficial effects on plant growth and health include the nitrogen-fixing bacteria, mycorrhizal fungi, plant growth-promoting rhizobacteria (PGPR), biocontrol microorganisms, mycoparasitic fungi, and protozoa (Basu and Kumar 2020a, b).

14.3.3.1 Plant Growth-Promoting Rhizobacteria (PGPR)

Plant growth-promoting rhizobacteria (PGPR) are various bacterial members of several taxonomic groups colonizing the rhizosphere. Natural PGPR commonly include various species of *Pseudomonas* sp. and *Bacillus* sp. colonizing different plants such as *Arabidopsis*, barley, and rice. Numerous studies have revealed the PGPR to promote growth and productivity of different agricultural crop species plant (Backer et al. 2018; Tsukanova et al. 2017). They have also been found to confer induced systemic resistance (ISR) and systemic acquired resistance (SAR) consequently reducing phytotoxic microbial populations (Bukhat et al. 2020). PGPR play an important role in the signaling, metabolism, and hormonal homeostasis in plants

(Tsukanova et al. 2017). They also produce antibiotic compounds as well as hydrogen cyanide that inhibit the growth of poisonous rhizospheric microbes, thereby promoting plant growth. The PGPR also increase the availability and uptake of nutrients and provide resistance to abiotic and biotic stresses leading to agricultural sustainability.

14.3.3.2 Beneficial Fungi

In the soil microbiome, fungi also play a crucial role in promotion of plant growth. Mycotic populations efficiently spread over the soil and rhizosphere and eliminate the pathogenic fungal strains by competitive inhibition. They also contribute in the antibiotic production and elicitation of defense responses. The beneficial plant fungal populations stabilize the pathogenic microbes by parasitizing their spore (mycoparasitism) and sclerotia, ultimately leading to biocontrol. They also produce chemical compounds and enzymes (e.g., chitinase, glucanase, and protease), which degrade the harmful mycotic populations.

The free-living fungi are beneficial inhabitants of the rhizosphere. *Trichoderma* sp. belongs to this class and possesses the mycoparasitic capabilities, which is a more predominant attribute of the free-living fungi (Harman et al. 2004). They promote the plant development without showing any detrimental effects on the plants. The root colonization of *Trichoderma* is associated with the induction of both the local and systemic resistance that is directly influenced by the production of a fungal protein elicitor molecule, designated as *small protein1* (*Sm1*), which lacks toxic activity in plants and microbes (Djonovic et al. 2006). The *Sm1* promotes the immunity-related gene expressions in plants. Several studies have shown *T. atroviride* and *T. virens* to induce plant growth by producing indole-3-acetic acid (Contreras-Cornejo et al. 2009).

14.4 Microbial Signaling Involved in Plant Growth

Development of plant is driven by multiple factors, including root microbial population as a major contributor. Previous workers have revealed the signaling process to be executed by certain classes of molecules, including phytohormones, N-acyl-l-homoserine lactones (AHLs), and microbial volatile organic compounds (MVOCs) (Mhlongo et al. 2018).

The MVOCs and the AHLs play a crucial role in the bacterial downstream signaling, by which the bacterial genes may express (Ortiz-Castro et al. 2009). The MVOCs are recognized by the plants further contributing in the improvement of plant development and defense mechanisms by upregulating different genes.

In addition, there are many soil bacterial populations that belong to the class of *Proteobacteria*, which help plants in the uptake of mineral nutrients and nitrogen fixation (Basu and Kumar 2020b). Endophytic microbes help in manipulation of

biotic and abiotic stresses in plants (Basu and Kumar 2021a). These evidences establish the existence of a feedback loop system (Mandal et al. 2010).

14.4.1 Phytohormones

Former studies have shown the rhizosphere to potentially contribute the chemical components, which are essential for maintaining the developmental cues in plants (Ortiz-Castro et al. 2009). Phytohormones have been shown to play a crucial role in the plant development, indirectly regulating the nutrient uptake and distribution (Basu et al. 2022). They are produced in root and shoot, but their effectiveness is spatial. Therefore, the shoot and root growth is completely distinct from each other in accordance to the auxin and cytokinin gradient. Fate of root and shoot development has been found to be decided by the auxin and cytokinin produced by the soil microbiota (Su et al. 2011).

Root bacterial and fungal populations produce different phytohormones such as cytokinin, auxin, and ethylene (Table 14.1). Phytohormones auxin and cytokinin possess antagonistic role in development of plants. Conversely, production of these phytohormones occasionally leads to diseased conditions in plants (e.g., infection caused by *Agrobacterium tumefaciens* or *Ustilago maydis*). Therefore, the equilibrium of auxin-cytokinin and site of hormone accumulation can determine the beneficial or detrimental role of the microbial interaction.

14.4.1.1 Cytokinin

Cytokinin positively regulates the growth of the whole plant, especially the shoot (Beck 1996). Several studies have revealed the involvement of different gene expressions to stimulate cytokinin production in plants. Signal perception of cytokinins involves three sensor histidine kinases—*CRE1/AHK4/WOL*, *AHK2*, and *AHK3*, which upregulate multiple response regulator expression depending on the concentration of cytokinin (Kakimoto 2003). The cytokinin receptors are also necessary for the viability and normal growth of plants. Furthermore, the cytokinin signaling upregulates the *CYCD3* gene that encodes a D-type cyclin leading to the cell cycle progression and cell division in the shoot (Riou-Khamlichi et al. 1999). Additionally, cytokinin gradient has been reported to drive the plant, microbe, and insect interactions, thereby contributing in the plant defense system (Giron et al. 2013).

Several studies have shown the PGPR to produce cytokinin, consequently promoting plant growth and biomass production (Bukhat et al. 2020). Liu et al. (2013) have shown the inoculation of *Platycladus orientalis* plants with the PGPR *Bacillus subtilis* AE016877 to stimulate the cytokinin production in shoots. Further, Tahir et al. (2017) have shown the inoculation of tomato plants with PGPR *B. subtilis* SYST2 to enhance the expression of gene for cytokinin synthesis (*SlCKX1*) with

Table 14.1 Microorganisms stimulate plant growth by producing phytohormones

Microorganisms	Plant growth stimulated	Reference
Cytokinin		
PGPR		
Bacillus subtilis SYST2	Tomato (*Solanum lycopersicum*)	Tahir et al. (2017)
Pseudomonas fluorescens G20-18	*Arabidopsis thaliana*	Großkinsky et al. (2016)
B. subtilis AE016877	Oriental thuja (*Platycladus orientalis*)	Liu et al. (2013)
B. megaterium UMCV1	*A. thaliana*	Ortiz-Castro et al. (2008a, b)
		Lopez-Bucio et al. (2007)
B. subtilis IB 22	Lettuce (*Lactuca sativa*)	Arkhipova et al. (2005)
Auxin		
PGPR		
Azospirillum brasilense Sp245	*A. thaliana*	Spaepen et al. (2014)
Aeromonas punctata PNS-1	*A. thaliana*	Iqbal and Hasnain (2013)
Burkholderia cepacia RRE25	Rice (*Oryza sativa*)	Singh et al. (2013)
Serratia marcescens 90-166	*A. thaliana*	Shi et al. (2010)
Enterobacter cloacae UW4	Canola (*Brassica napus*)	Li et al. (2000)
Fungi		
Trichoderma atroviride	Tomato	Gravel et al. (2007)
T. virens	*A. thaliana*	Contreras-Cornejo et al. (2009)
Ethylene		
PGPR		
Achromobacter xylosoxidans Cm4, *Pseudomonas oryzihabitans* Ep4, and *Variovorax paradoxus* 5C-2	Potato (*Solanum tuberosum*)	Belimov et al. (2015)
Variovorax paradoxus 5C-2	*A. thaliana*	Chen et al. (2013)
Azotobacter chroococcum AZO2	Sesame (*Sesamum indicum*)	Dubey et al. (2012)
Corynebacterium sp. Sb26, *Rhizobium* sp. Sb16	Rice (*Oryza sativa*)	Naher et al. (2008)
Pseudomonas brassicacearum 520-1, *P. brassicacearum* Am3	Tomato	Belimov et al. (2007)
Pseudomonas brassicacearum Am3, *Pseudomonas marginalis* Dp	Indian mustard (*Brassica juncea*), rape (*B. napus*), and pea (*Pisum sativum*)	Safronova et al. (2006)
Achromobacter piechaudii ARV8	Pepper (*Capsicum annuum*), tomato	Mayak et al. (2004)
Pseudomonas putida GR12-2	Canola	Penrose et al. (2001)
	Barley (*Hordeum vulgare*), oat (*Avena sativa*), wheat (*Triticum aestivum*), canola, lettuce, tomato	Hall et al. (1996)

increased cytokinin level. Another PGPR strain *B. megaterium* UMCV1 has also been found to promote the growth and biomass of *Arabidopsis* plants (Lopez-Bucio et al. 2007).

14.4.1.2 Auxin

Auxin concentration along with environmental factors plays an important role in determining the root architecture in plants. The root and shoot meristem size, lateral organ primordial position, and floral morphogenesis are regulated by auxin. It also drives the cell cycle, thereby releasing the bud dormancy in plants (Tsukanova et al. 2017).

Microbial interaction with plant root induces the synthesis of auxin, including indole-3-acetic acid (IAA), indole-3-butyric acid (IBA), phenylacetic acid, 4-chlorindole-3-acetic acid, or their precursors (Spaepen et al. 2007). The IAA, major naturally occurring auxin, reciprocates the signaling during the plant-microbiota interaction. The IAA has been found to be a positive regulator of plant growth. Therefore, IAA overproduction has been suggested to induce the formation of long hypocotyls with increased numbers of lateral roots and root hairs. The amount, localization, and direction of IAA movement in plants have been proved to be affected by the PGPR (Ahmed and Hasnain 2014). Spaepen et al. (2014) have reported the PGPR strain *Azospirillum brasilense* Sp245 to produce higher concentration of IAA, thereby promoting root growth in *A. thaliana*. The PGPR strains *Aeromonas punctata* PNS-1 (Iqbal and Hasnain 2013) and *Serratia marcescens* 90-166 (Shi et al. 2010) have also been revealed to induce growth of *Arabidopsis* plants. Singh et al. (2013) have reported the IAA overproducing PGPR strain of *Burkholderia cepacia* RRE25 to stimulate growth of rice plants.

Several studies have revealed the rhizospheric fungal population to produce IAA leading to enhanced plant growth. This is an interacting system that may have a role in the fungi and plant symbiosis, where the fungi can use IAA and related compounds to interact with plants as part of their colonization strategy, consequently stimulating plant growth. Gravel et al. (2007) have shown the inoculation of tomato plants with *T. atroviride* to stimulate plant growth and yield by inducing IAA production. Contreras-Cornejo et al. (2009) have reported the plant-beneficial fungi *Trichoderma virens* to promote lateral root growth with enhanced biomass production in *Arabidopsis* through the IAA-dependent mechanism. The study has also revealed the mutations in IAA transport or signaling genes (*AUX1*, *AXR1*, *BIG*, and *EIR1*) to suppress the root growth by diminishing the effects of *Trichoderma*.

14.4.1.3 Ethylene

Ethylene plays an active role in seed germination, leaf maturation, root elongation, nodulation, root branching, floral initiation, and fruit ripening at low concentrations. However, high concentrations of ethylene have been found to cause phytotoxicity

leading to inhibition of root growth, defoliation, and early senescence. Several studies have shown plants to produce 1-aminocyclopropane-1-carboxylate (ACC), the precursor of ethylene under different abiotic and biotic stresses including drought (Basu et al. 2021a), submergence (Basu et al. 2020b; Basu et al. 2021b), and pathogenic infections (Basu and Kumar 2021b).

The PGPR also synthesizes ACC deaminase that helps plants by converting it to α-ketobutyrate and ammonia, thereby regulating the concentration of ACC. Therefore, the PGPR also regulates plant growth under different stress conditions by limiting the toxic level of ethylene. Hall et al. (1996) showed *Pseudomonas putida* GR12-2 to induce growth in barley, oat, wheat, canola, lettuce, and tomato seedlings. Later Penrose et al. (2001) also showed *P. putida* GR12-2 to promote plant growth in canola. Mayak et al. (2004) revealed *Achromobacter piechaudii* ARV8 to stimulate growth of pepper and tomato plants. Different strains of *Pseudomonas* spp. *P. brassicacearum* Am3 and *P. marginalis* Dp have been revealed to promote plant growth in Indian mustard, rape, peas (Safronova et al. 2006), and tomato (Belimov et al. 2007). Naher et al. (2008) showed *Corynebacterium* sp. Sb26 and *Rhizobium* sp. Sb16 to induce growth of rice plants. Strain of *Azotobacter chroococcum* AZO2 has been found to promote growth of sesame plants (Dubey et al. 2012). Belimov et al. (2015) showed strains of *Achromobacter xylosoxidans* Cm4, *Pseudomonas oryzihabitans* Ep4, and *Variovorax paradoxus* 5C-2 to stimulate growth of potato plants.

14.4.2 N-Acyl-L-Homoserine Lactone (AHL)

Bacterial adaptation, proficiency, cellular communication, and reproduction are regulated by an essential strategy, known as quorum sensing (QS) (Basu and Kumar 2021a). N-Acyl homoserine lactones (AHLs) belong to a class of bacterial QS signals from gram-negative bacteria (Hartmann et al. 2021). These compounds enable bacterial cells to regulate gene expression depending on the population density. Accumulation of AHLs confers resistance against phytopathogens (Table 14.2). The AHL-producing bacterial strain *Serratia liquefaciens* MG1 has been reported to promote plant growth by inducing SAR against phytopathogenic fungus *Alternaria alternata* in tomato (Schuhegger et al. 2006). Newman et al. (2008) reported the bacteria *Bacillus* sp. and *Pseudomonas* sp. to promote SAR in plants against *Xylella fastidiosa* and *Xanthomonas* sp. by degrading the diffusible signal factor. Kusari et al. (2014) have shown endophytic bacteria associated with *Cannabis sativa* plant to regulate phytopathogenic *Chromobacterium violaceum* by inhibiting QS.

Table 14.2 Microbial resistance against phytopathogens mediated by accumulation of N-acyl homoserine lactones (AHLs)

Microbes	Phytopathogens	Plants	References
Endophytic bacteria	*Chromobacterium violaceum*	*Cannabis sativa*	Kusari et al. (2014)
Ensifer meliloti (*Sinorhizobium meliloti*)	*Pseudomonas syringae*	*Arabidopsis thaliana*	Zarkani et al. (2013)
Bacillus sp. and *Pseudomonas* sp.	*Xylella fastidiosa* and *Xanthomonas* sp.		Newman et al. (2008)
Serratia liquefaciens MG1	*P. syringae*	*Arabidopsis thaliana*	von Rad et al. (2008)
	Alternaria alternata	Tomato	Schuhegger et al. (2006)

14.4.3 Microbial Volatile Organic Compound (MVOC)

Microbial volatile organic compounds (MVOCs) are variable compounds formed through the bacterial and fungal metabolism (Korpi et al. 2009). The compounds usually have low molecular weight (e.g., hydrocarbon, alcohol, aldehyde, and ketone), distinct odour, low boiling point and high vapor pressure. MVOCs establish communication with plants by functioning as attractants, repellents, or cautioning signals. Lemfack et al. (2014) have reported approximately 350 bacterial and 69 fungal species to produce about 846 diverse MVOCs. Different MVOCs are represented in Fig. 14.2.

The roles of PGPR in stimulating plant growth through the production of diverse MVOCs are well documented (Park et al. 2015). Different species and strains of PGPR, including *Bacillus*, *Pseudomonas*, and *Serratia*, have been revealed to stimulate growth of different plant species. The PGPR or PGPR-derived products frequently require the physical contact with the plants for inducing plant growth. However, different studies have reported about the distant regulation of plant growth without direct interaction with plants, which suggests the possibility of the emission of MVOCs by the PGPR. Different MVOCs stimulating growth of various plant species have been listed in Table 14.3. Ryu et al. (2003) first revealed two MVOCs, 3-hydroxy-2-butanone (acetoin) and 2,3-butanediol produced by PGPR strains *B. subtilis* GB03 and *B. amyloliquefaciens* IN937a to induce growth in *A. thaliana*. Again Zou et al. (2010) showed the PGPR strain *B. megaterium* XTBG34 to promote the growth of *Arabidopsis* plants by producing 2-pentylfuran. Park et al. have reported MVOCs (2-methyl-n-1-tridecene, 2-butanone, and 13-tetradecadien-1-ol) produced by the PGPR strain *Pseudomonas fluorescens* SS101 to stimulate growth of tobacco plants. Xie et al. (2014) have shown the spermidine-producing PGPR strain *Bacillus subtilis* OKB105 to stimulate growth in tobacco plants. Further, Tahir et al. (2017) have shown another strain of *B. subtilis* SYST2 to promote growth of tomato plants by producing MVOCs (albuterol and 1,3-propanediole). Kai and Piechulla (2014) showed another PGPR *Serratia odorifera* to promote the growth of moss *Physcomitrella patens* by producing CO_2.
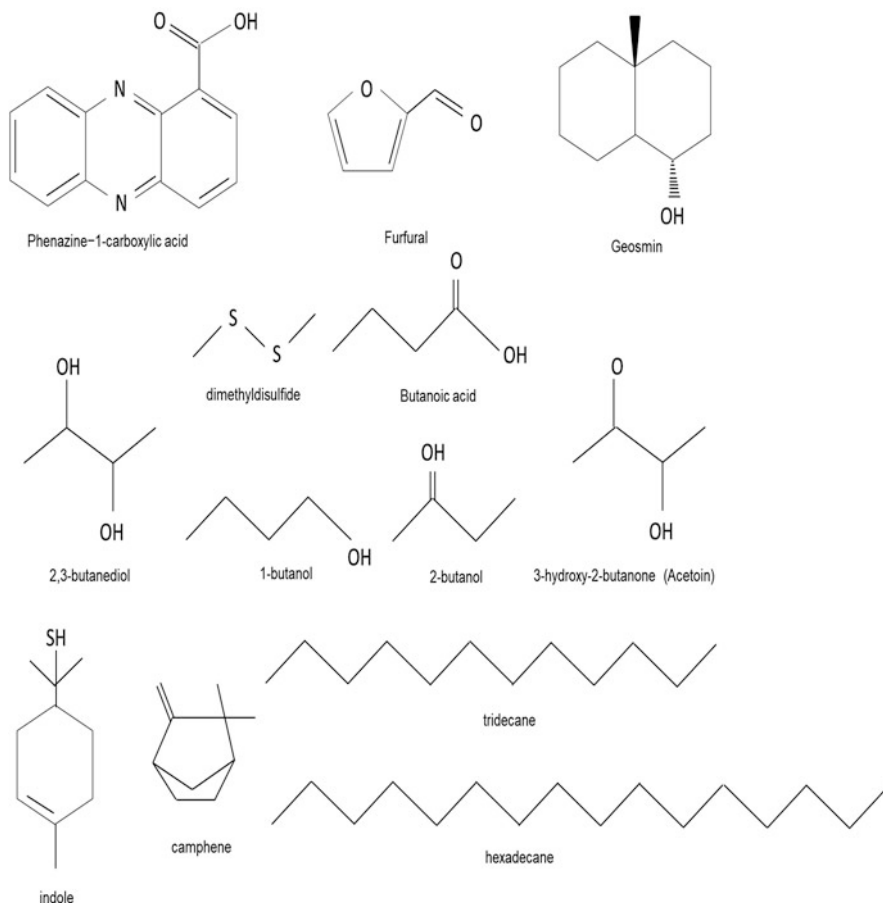
Fig. 14.2 Different microbial volatile organic compounds (MVOCs) responsible for establishment of communication with plants

Fungi being an important associate of the phytomicrobiome release abundant MVOCs playing a key role in plant-microbe interactions. A recent study showed beneficial fungal strain of *Trichoderma hamatum* FB10 to increase the growth and biomass of cowpea, small millet, maize, green gram, and black gram seedlings by synthesizing bioactive MVOCs (butanoic acid, ethanoic acid, hexadecanoic acid, butyrolactone, and hexadecane) (Baazeem et al. 2021). Another recent study showed the fungal strain of *Cladosporium halotolerans* NGPF1 to promote growth of tobacco (*Nicotiana benthamiana*) plants through the production of two MVOCs 2-methyl-butanal and 3-methyl-butanal (Jiang et al. 2021). Further, Paul and Park (2013) showed another strain of *Cladosporium cladosporioides* CL-1 to stimulate growth and fresh weight of tobacco seedlings by synthesizing MVOCs including dehydroaromadendrene, (−)-trans-caryophyllene, tetrahydro-2,2,5,5-

Table 14.3 Microbial volatile organic compounds (MVOCs) stimulating growth of different plant species

Microorganisms	MVOCs produced	Plant species with induced growth	Reference
Rhizobacteria			
B. subtilis SYST2	Albuterol and 1,3-propanediole	Tomato	Tahir et al. (2017)
Pseudomonas fluorescens SS101	2-Methyl-n-1-tridecene, 2-butanone, and 13-Tetradecadien-1-ol	Tobacco	Park et al. (2015)
Serratia odorifera	CO_2	*Physcomitrella patens*	Kai and Piechulla (2014)
Bacillus subtilis OKB105	Spermidine	Tobacco	Xie et al. (2014)
B. megaterium XTBG34	2-Pentylfuran	*Arabidopsis*	Zou et al. (2010)
B. subtilis GB03 and *B. amyloliquefaciens* IN937a	3-Hydroxy-2-butanone (acetoin) and 2,3-butanediol	*A. thaliana*	Ryu et al. (2003)
Fungi			
Trichoderma hamatum FB10	Butanoic acid, ethanolic acid, hexadecanoic acid, butyrolactone, and hexadecane	Cowpea, small millet, maize, green gram, and black gram	Baazeem et al. (2021)
Cladosporium halotolerans NGPF1	2-Methyl-butanal and 3-methyl-butanal	Tobacco (*Nicotiana benthamiana*)	Jiang et al. (2021)
Cladosporium cladosporioides CL-1	Dehydroaromadendrene, (−)-trans-caryophyllene, tetrahydro-2,2,5,5-tetramethylfuran, α-pinene, and (+)-sativene	Tobacco	Paul and Park (2013)
Phoma sp. GS8-3	2-Methyl-propanol and 3-methyl-butanol	Tobacco	Naznin et al. (2013)

tetramethylfuran, α-pinene, and (+)-sativene. Naznin et al. (2013) have shown the plant growth-promoting fungal strain *Phoma* sp. GS8-3 to induce the growth of tobacco plants by producing the MVOCs, 2-methyl-propanol and 3-methyl-butanol.

14.5   Future Prospects

The plant rhizosphere harbors a diverse reservoir of culturable microorganisms that can be exploited to benefit mankind. Interactions of plants and rhizospheric organisms influence plants' root functions, eventually altering their growth and

productivity. Therefore, understanding the soil-root and soil-seed interface is essential to manage the microorganisms for sustainable agriculture. Microbial activities and population numbers are often affected by the soil composition, which in turn has an impact on the nematodes and microarthropods that share this environment. Many rhizospheric microbes benefit crop production, reducing the dependence on chemical fertilizers to achieve high productivity. Some microbes also protect plants from the ravages of the severe disease-causing pathogens.

Exploration of rhizosphere may contribute in the enhanced application of plant growth-promoting organisms for sustainable plant growth and usage of the biocontrol agents for suppressing plant diseases and weeds. Rhizospheric organisms can also be used to enhance the formation of stable soil aggregates and as bioremediation agents of contaminated soils. Utilization of the beneficial microorganisms is fully consistent with sustainable agriculture, where the goal of paramount importance is to utilize the natural processes that promote the crops' output without irreparably damaging the natural resources. Progressive understanding of the ecology and biota in the rhizosphere may help in manipulating this zone of increased nutrients, biotic activity, and interactions to improve plant productivity and environmental quality.

Among the many recent discoveries in rhizosphere research, the ominous is finding that certain potential human pathogenic microorganisms are also successful inhabitants of this nutrient-enriched plant soil environment, and this ecology poses potential public health hazards for both producers and consumers who encounter them. An interesting thought for future exploration is the rhizosphere supports the populations of human health-promoting rhizobacteria (HHPR).

Rhizosphere bioremediation refers to the biodegradation of pollutants by microorganisms in the plant root zone. Plants play an important role to increase both microbial numbers and metabolism in soil, resulting in increased biodegradation activity. Several mechanisms elucidate the enhanced biodegradation in the rhizosphere: the root turnover increases soil organic carbon stimulating microbial activities, thereby metabolizing toxic pollutants; root exudates contain small organic acids, alcohols, and phenolic compounds that favor solubilization and bioavailability of hydrophobic pollutants; root tissues and microorganisms also secrete catabolic enzymes, such as peroxidases and laccases, involved in biodegradation mechanisms; specific compounds released by roots induce microbial enzymes and stimulate biodegradation; roots introduce oxygen in the rhizosphere, which is necessary for oxidative biodegradation by oxygenases.

In the near future, it could be expected that more studies will be conducted on this field, by which plant-microbe interaction will be more understandable. It will further open up new junctions to use microbial strains with a capability to produce the phytohormones for plant improvement under field conditions to sustain the agricultural production.

14.6   Conclusion

Microbes and plants have cohabited and coevolved for millions of years. The complicated interactions of plants with the rhizospheric microbial populations have not been completely understood so far. The microbial populations play a significant role in the nutrient uptake and assimilation. Additionally, they contribute in the plant development and immunity system. The cross talking of both the organisms through vibrant chemical signaling pathways indicates their symbiotic association. The present chapter has explored the potential role of the major signaling molecules in the plant-microbe interactions, which may improve the efficiency of the ecosystem. Therefore, the comprehensive analyses of microbial signaling may be effectively used to pave the way for the agricultural sustainability.

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