Chapter 4
The Role of Phytohormones in Cross-communication Between Plants and Rhizo-Microbes

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Abstract Plants in their ecological niches establish multiple interactions with arthropods and rhizosphere microorganisms. Plant growth-promoting rhizobacteria (PGPR) and soil-borne fungi can establish molecular dialogues with plants by producing powerful molecules such as ethylene (ET), auxins (IAA), cytokinins (CKs), and gibberellins (GAs) that activate specific molecular mechanisms that subsequently modulate specific physiological processes such as cell division, expansion, or cellular differentiation, whereas abscisic acid (ABA) or enzymatic components as the 1-aminocyclopropane-1-carboxylate deaminase (ACCase) have the ability to induce resistance to different kinds of abiotic stresses as salinity and drought. The microbial root interaction might activate defense responses mediated by the phytohormones salicylic acid (SA) or jasmonic acid (JA) that result effectives against the attack of plant pathogenic microorganisms (hemi- and biotrophic or necrotrophic pathogens) or chewing and piercing sucking insects. This chapter highlights the role of several microbial metabolites that impact on the molecular mechanisms modulated by phytohormones that regulate defense responses and the growth and development of plants.

Keywords Phytohormones · Plant-microbe interactions · Rhizobacteria · Secondary metabolites · Soil microbes

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4.1 Introduction

Plants and microorganisms interact in practically all the ecosystems and their presence is essential to maintain life on earth due to the ecosystemic services that both provide (Herrera-Paredes and Lebeis 2016). Because plants are anchored to the soil through the roots, it is through this system that plants interact with myriads of rhizosphere microorganisms, such as bacteria, ectomycorrhizal, arbuscular mycorrhizal fungi (AMF), and free-living fungi (Reboutier et al. 2002; Splivallo et al. 2009). Some microorganisms can be found associated with the seeds, stems, leaves, and fruits of plants (Romero et al. 2014; Coleman-Derr et al. 2016; Ramírez-Ordorica et al. 2020). These microorganisms induce on plants a broad range of effects that can be negative, neutral, or beneficial for the host (Newton et al. 2010; Zúniga et al. 2017). Beneficial interactions involve communication among the two organisms through signaling metabolites that are exuded by plant roots and microorganisms. These compounds subsequently are perceived by the epidermal cells of the host plant, and in turn impact on the endogenous signaling programs of the cells (Ortíz-Castro et al. 2008; Baetz and Martinoia 2014). Interactions between plants and microorganisms can be through physical contact such as root colonization or interactions without physical contact that involve the exchange of low molecular weight compounds that function as specific signals to modulate some physiological, biochemical, or molecular processes in the recipient organism (Ryu et al. 2003; Contreras-Cornejo et al. 2009; Rasmann and Turlings 2016). Rhizosphere bacteria and fungi produce a number of metabolites that when perceived in the target cell can function as phytohormones in plants (Splivallo et al. 2009; Shi et al. 2017). To date, the number of microbial metabolites identified is broad and several of them have plant growth modulatory activity that resembles the function of the canonical phytohormones but such compounds have very different chemical structure, thus the molecular mechanisms through which the plants perceive and respond to them are hot topics at this moment (Contreras-Cornejo et al. 2015a, b, c; Garnica-Vergara et al. 2016).

On the other hand, some compounds of microbial origin can also activate defense responses. Under starvation, rhizosphere microorganisms can release low molecular weight compounds or peptidic compounds that stimulate plant immunity. Such defensive priming has been found to be effective to resist the attack of plant pathogen microorganisms or even herbivorous insects (Battaglia et al. 2013; Coppola et al. 2019a, b; Contreras-Cornejo et al. 2020a, b). In order to illustrate the biological, ecological, and agricultural importance of the microorganisms in the rhizosphere, this chapter describes the most recent scientific advances that highlight some secondary metabolites of microbial origin that are perceived by plants and modulate different aspects of growth, development, and defense under different environmental conditions.

4.2 Microorganisms in the Rhizosphere

Soil microorganisms include various genera and species of bacteria, fungi, oomycetes, nematodes, and amoebae (Newton et al. 2010; van Dam and Bouwmeester 2016). The composition of the microbial communities in the rhizosphere differs between plant species (Hardoim et al. 2008; Redford et al. 2010). For example, *Arabidopsis thaliana* rhizosphere community is mainly associated with bacterial phyla Acidobacteria, Actinobacteria, Bacteroidetes, Cyanobacteria, Firmicutes, Gemmatimonadetes, and Proteobacteria (Lundberg et al. 2012). Plant root exudates, soil pH, nutrients availability, soil humidity, and other abiotic factors participate in the modulation of the microorganism populations (Kim and Lee 2020; Juan-Ovejero et al. 2020). Microorganisms have important roles for the optimal functioning of the ecosystem, for example: mobilization and stabilization of carbon, organic matter decomposition, nutrient mineralization and biocontrol of pathogenic microorganisms, and the different types of interactions with plants (Mitchell et al. 2003).

Microbial community structure is dependent on temperature variations (Manzoni et al. 2012). The depth in the soil can affect the location of microorganisms; the microbial population is found to be more in aerated soils (Liu et al. 2016). Additionally, the edaphic properties of the soil, for example, the concentrations of electron donors or acceptors in bulk soil, agricultural practices as the utilization of organic nitrogen fertilizers, and plant vegetation cover species, can largely modulate impact in microbial communities assemblage (Caradonia et al. 2019; Yuan et al. 2019). In a recent report it was shown that the microbiota of tomato (*Solanum lycopersicum*) is constituted mainly by members of Actinobacteria, Bacteroidetes, Alpha-, Beta-, Gamma-, and Deltaproteobacteria and Verrucomicrobia (Caradonia et al. 2019). However, in the peatland rhizosphere, the phyla Ascomycota and Basidiomycota are fungal communities present at 46% and 40%, respectively (Thormann et al. 2007). Otherwise, the lifestyles of the microorganisms determine if they can live freely in the rhizosphere, or if they form endophytic associations with plants (Akiyama et al. 2005; Bae et al. 2011).

4.3 Plant-Microorganism Interaction

The microorganisms in the rhizosphere may have no apparent effect on plants, be harmful if they cause disease, or can be beneficial for plants. Beneficial microorganisms can stimulate plant growth through: (1) direct mechanisms, by the production of growth regulating molecules, and processes that improve the acquisition of macronutrients (N, K, Ca, Mg, P, and S) and micronutrients (Fe, B, Mn, Zn, Cu, Mo, and Ni), and (2) indirect mechanisms, mainly by the biocontrol of phytopathogen microorganisms (Contreras-Cornejo et al. 2016; Ramakrishna et al. 2019). It has often been observed that beneficial soil microorganisms stimulate plant immunity

and promote resistance to different types of abiotic stress such as those caused by water deficit, salinity, or soil contamination by heavy metals (Martínez-Medina et al. 2019; Kim and Lee 2020).

Root exudates are an important source of compounds to enrich the rhizosphere near to the plants with nutrients, and as a consequence the microorganisms in close association with the root increase their population density and association with the plants (Zúniga et al. 2017; Sasse et al. 2018). Plant metabolites or those of microbial origin, depending on their physicochemical characteristics, can be diffused through the rhizosphere or towards the atmosphere (Tyc et al. 2017). Plants release the root compounds that are exuded through passive processes such as diffusion, channels, vesicular transport, or more complex processes as ATP-binding cassette (ABC) transporters (Baetz and Martinoia 2014). Some compounds derived from plants function as signaling molecules to attract the beneficial microorganisms towards the root, and later root colonization takes place (Akiyama et al. 2005).

In the case of associations established by AMF, host plants initiate the interaction through the production and release of stringolactones that are carotenoid-derived compounds of low molecular weight less than 500 Da (Rasmann and Turlings 2016). These metabolites, when perceived by the fungal spores, promote the growth of the hyphae towards the host plant. Specifically, root exudates from *Lotus japonicus* plants release 5-deoxy-stringol, which at concentrations of 30 pg to 100 ng is a branching factor for *Gigaspora margarita* hyphae (Akiyama et al. 2005). It is known that plants growing in phosphorus limitation are forced to increase their ratio of root exudation, which favors the exudation of agents that promote the branching of AMF hyphae (Nagahashi and Douds 2000). In the rhizosphere, there are some species of fungi that also establish associations with plants and colonize the roots without apparent participation of signaling molecules that favor interaction; such is the case of the endophytic fungus *Piriformospora indica* that colonizes the root tissue of barley (*Hordeum vulgare* L.) (Waller et al. 2008).

Soil microorganisms can perceive the components present in root exudates (De Weert et al. 2002). More recently it was shown that during plant-*Trichoderma* interactions, plants release oxylipins and carbohydrates through root exudates that are perceived by the fungus and function as chemotactic agents for the attraction of the microorganism towards the root (Lombardi et al. 2018; Macías-Rodríguez et al. 2018). In the particular case of tomato plants inoculated with *Trichoderma atroviride* IMI 206040, it was observed that before physical contact between the two organisms, the plants mainly exude the monosaccharides arabinose, xylose, glucose, myo-inositol, and fructose. Later, when *T. atroviride* grew towards the root, the levels of carbohydrate exudation were slightly reduced and the exudation of sucrose that served as a nutritional and as a carbon source for the fungus increased its levels (Macías-Rodríguez et al. 2018).

In regard with the associations of rhizobia with roots, it is known that plants release flavonoids which are chemotactic agents for nitrogen-fixing bacteria and in response such bacteria release molecules named "nod factors," which are substances structurally related to acylated chitin oligomers (Bisseling and Geurts 2020). It has been assumed that plants in the cell membrane possess a receptor for nod factors,

which is a heterodimeric receptor that in *Medicago truncatula* is composed of the kinases LYSM DOMAIN-CONTAINING RECEPTOR LIKE KINASE 3 (MTLYK3) and NOD FACTOR PERCEPTION (MtNFP) (Zipfel and Oldroyd 2017). Then, in order to activate this mechanism, bacteria approach the proximity of the root hairs, and such structures cover the bacterial cell, thus forming the nodule where the fixation of atmospheric nitrogen will occur (Oldroyd et al. 2011; Podlešáková et al. 2013).

4.3.1 Root Perception of Microbial Signals

Changes in the shape and structure of the root are often the result of the perception of microbial signals by the host plant cells (Gutiérrez-Luna et al. 2010). Table 4.1 shows the physicochemical properties of the canonical phytohormones. Some of them can be produced by rhizosphere microorganisms. Depending on the type of signal, microbial molecules can induce changes in the plasticity of the root system, which implies an increase in the formation of secondary roots and root hairs (Contreras-Cornejo et al. 2009, 2015b; Garnica-Vergara et al. 2016). These changes in the root system allow the plants a more vigorous anchoring to the soil, improved uptake of water and nutrients and a greater contact surface with the microorganisms of the rhizosphere (Ortíz-Castro et al. 2009). Figure 4.1 shows the impact of the inoculation of *Bacillus amyloliquefaciens* M496 on the growth of maize and *Medicago truncatula* plants grown in MS medium. Bacterial inoculation enhances both shoot length growth and root branching, which suggests that such strain uses an

Table 4.1 Physicochemical properties of phytohormones

Name	Molecular formula	Molecular mass (g/mol)	Density (g/cm^3)	Appearance	Class of compound
Indole-3-acetic acid (IAA)	$C_{10}H_9NO_2$	175.19	1.4 ± 0.1	White solid	Indolic compound
Ethylene (ET)	C_2H_2	28.05	1.138[a]	Colorless gas	Hydrocarbon
Abscisic acid (ABA)	$C_{15}H_{20}O_4$	264.32	1.2 ± 0.1	Colorless solid crystals	Isoprenoid-derived compound
Zeatin (CK)	$C_{10}H_{13}N_5O$	219.24	1.4 ± 0.1	Yellowish to off-white crystals	Adenine-derived compound
Jasmonic acid (JA)	$C_{12}H_{18}O_3$	210.27	1.1 ± 0.1	Off-white oil	Oxylipin-derived compound
Salicylic acid (SA)	$C_7H_6O_3$	138.12	1.4 ± 0.1	White solid	Phenolic compound

Partial information in this table was taken from Contreras-Cornejo et al. (2009, 2015a, b)
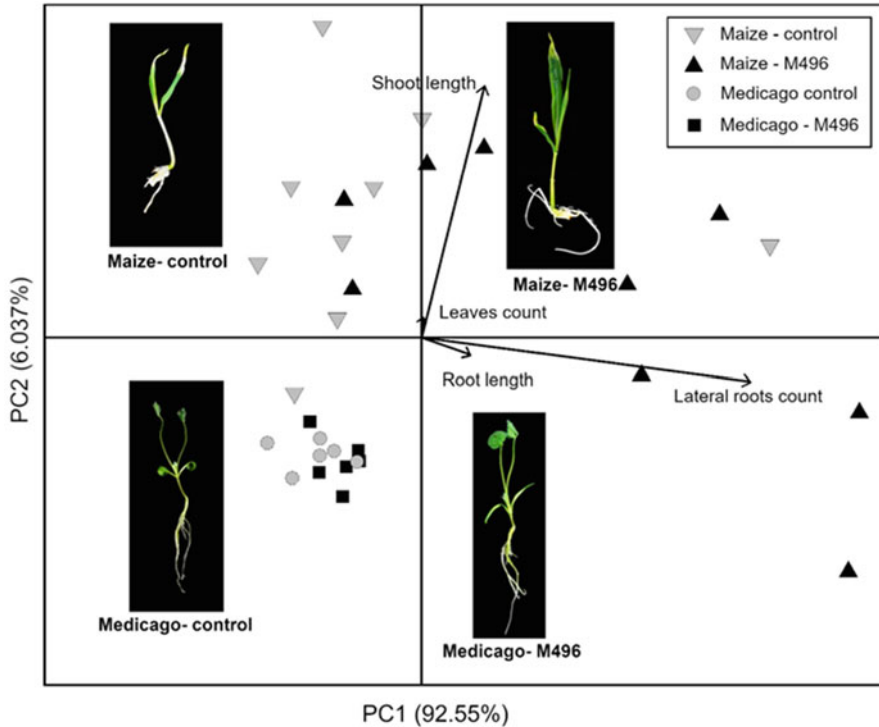[a] This property is in kg/m^3 at 25 °C

Fig. 4.1 Principal component analysis (PCA) that highlights the effects of *Bacillus amyloliquefaciens* M496 on maize and *M. truncatula* plants. Notice that the main effect of this microorganism is promoting shoot growth and lateral root formation. This pattern suggests a plant species-independent response to the same bacterial strain

efficient mechanism to induce beneficial effects on mono- and dicotyledonous plants.

Some bacteria and fungi in the rhizosphere can produce metabolites that directly impact some signaling pathways, modulated by canonical phytohormones, thus producing the typical hormonal effects at the physiological level (Splivallo et al. 2009; Contreras-Cornejo et al. 2014a, b; Garnica-Vergara et al. 2016; Gouda et al. 2018). Figure 4.2 shows the chemical structure of some phytohormones. However, there are some microbial compounds that can antagonize the effect of phytohormones (Reboutier et al. 2002). For example, the basidiomycetous fungus *Pisolithus tinctorius* that establishes ectomycorrhizas with *Eucalyptus globulus* releases an indole alkaloid metabolite called hypaphorine that reduces the root hair elongation and counteracts the activity of the auxin IAA (Ditengou and Lapeyrie 2000; Reboutier et al. 2002). Below are described some rhizospheric microorganisms, microbial metabolites, and the molecular mechanisms that are modulated in plants when both kind of organisms cointeract.
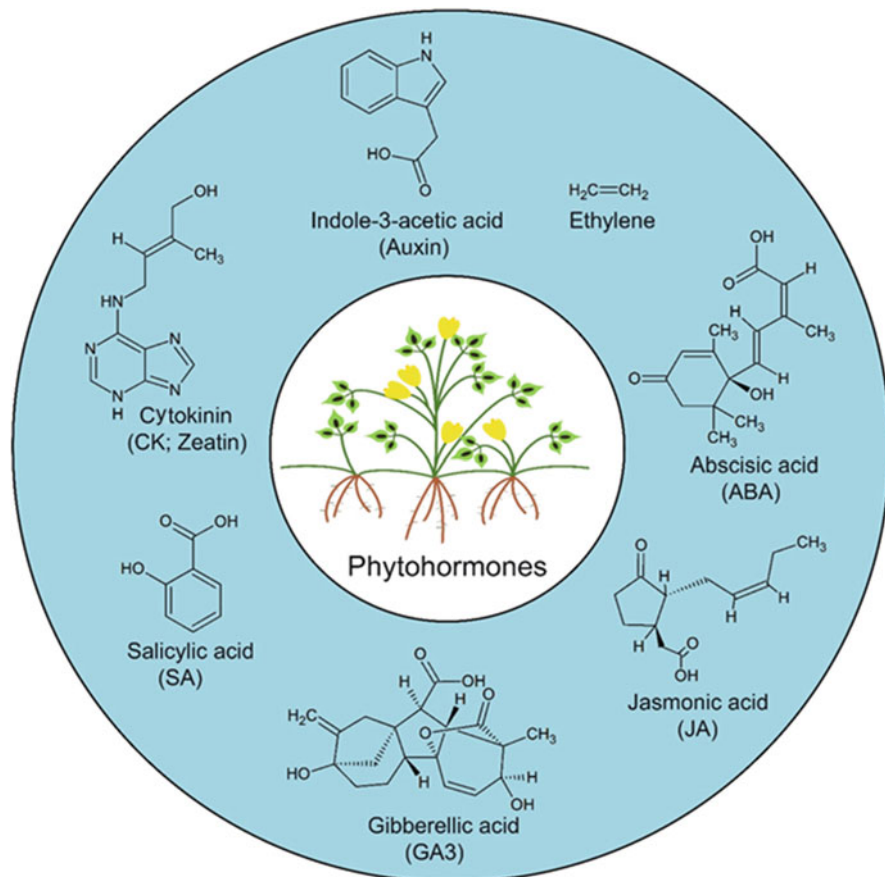
Fig. 4.2 Molecular structures of the seven canonical phytohormones. Rhizosphere microorganisms as bacteria or fungi can produce this class of compounds. To the best of our knowledge JA has not been identified in microorganisms but beneficial plant microorganisms activate its signaling mechanism. Notice differences among chemical structures

4.3.1.1 Auxins

Auxins are a group of compounds whose main chemical characteristic is that they have the indole molecule as structural base. It is known that a large number of pathogenic and beneficial soil bacteria and fungi produce auxins (Contreras-Cornejo et al. 2020b). The main auxin in plants that participates in multiple development processes is indole-3-acetic acid (IAA). The IAA biosynthesis pathway starts from chorismate from which anthranilate results, and then the amino acid tryptophan (Spaepen et al. 2007). In bacteria, several routes have been proposed for IAA biosynthesis that use the following metabolites as precursors: (1) indole-3-acet-amide, (2) indole-3-pyruvate, (3) tryptamine, and/or (4) indole-3-acetonitrile

(Spaepen et al. 2007). It has been speculated that IAA released to the environment is present in its protonated form because the rhizosphere is considered a weakly acidic environment (Hinsinger et al. 2003).

The IAA signaling mechanism starts when the molecule is perceived by influx transporters (i.e., AUX1) and these internalize the phytohormone within the cell (Swarup et al. 2001). Also involved in auxin transport are the efflux transporters PIN FORMED 2 (PIN2, also named EIR1) (De Billy et al. 2001). Subsequently, IAA binds to the nuclear receptor TIR1 (a F-box protein transport inhibitor 1) (Kepinski and Leyser 2005). In *Arabidopsis thaliana*, three other auxin receptors, named AFB1, AFB2, and AFB3, have also been identified (Dharmasiri et al. 2005; Parry and Estelle 2006). TIR1 is part of the SCF^{TIR1} complex that participates in the ubiquitination of proteins that will later be degraded. When IAA binds to the TIR1 receptor, part of the SCF^{TIR1} ubiquitination molecular complex, the degradation of Aux/IAA proteins which repress the expression of auxin response genes is promoted (Spaepen et al. 2007). Auxins modulate different genes that are classified into the following families: *Gretchen Hagen 3* (*GH3*), *auxin/indole-acetic acid-inducible* (*AUX/IAA*), and *small auxin up RNA* (*SAUR*) genes (Zhao et al. 2014). There is another family of genes different from those described above and it is named as *auxin-repressed proteins* (*ARP*) whose expression is also modulated by IAA (Lee et al. 2013). The modulation of the auxin signaling pathway during the plant-microorganism interaction has been shown in the case of poplar (*Populus tremula* × *Populus alba*) inoculated with the ectomycorrhizal fungus *Laccaria bicolor* which induced the formation of lateral roots and increases of the auxin levels at the root tips. Treatments of plants with 1-naphthylphthalamic acid, an auxin transport blocker, affected the accumulation of auxins and the development of lateral roots. An oligoarray analysis in plants that perceived the metabolites released by the fungus revealed important changes in the expression of several genes belonging to the molecular mechanism of auxins as *PtaPIN* and *PtaAUX* of the auxin transport, *PtaGH3* involved in auxin conjugation, and *PtaIAA* genes involved in the signaling of auxins (Felten et al. 2009). In vitro assays between *Arabidopsis thaliana* and *Trichoderma virens* Gv29-8 revealed that the fungus promotes plant growth. The beneficial effect on the accumulation of foliar biomass, induction of lateral roots, and formation of root hairs was the result of the production of IAA (13.48 ± 0.97 μg/L), indole-3-acetaldehyde (59.40 ± 4.47 μg/L), and indole-3-ethanol (72.33 ± 1.41 μg/L). Genetic confirmation for the participation of IAA in the foliar growth promotion of *Arabidopsis thaliana* by *T. virens* Gv29-8 was supported by the phenotype observed in the plant due to the reduced response on growth promotion in the mutants *aux1-7*, *eir1-1*, and *axr1-3* inoculated with the fungus (Contreras-Cornejo et al. 2009).

IAA can also interact with the ET signaling pathway and modulate plant development as evidenced by the production of this volatile hormone and its release from the truffle mycelium and due to its hormonal activity on the host plant *Cistus incanus* and non-host *Arabidopsis thaliana* (Splivallo et al. 2009). In the case of the in vitro interaction between *Trichoderma atroviride* IMI206040 and *Arabidopsis thaliana*, it has also been observed that the fungus modulates plant growth by activating the IAA

and ET pathways, with cross talk between both hormonal response pathways. This complex signaling mechanism involves the activity of the MAP kinase MPK6, which is induced after 15 min by 1 μM of IAA and by high concentrations of indole-3-acetaldehyde and indole-3-ethanol produced by *T. atroviride* IMI206040. In this interaction, MPK6 possibly functions as a repressor element, which results in the activation of molecular events, leading to the negative regulation of the formation of lateral roots, root hairs, and the growth of the primary root (Contreras-Cornejo et al. 2015b). In the same work, it was found that the fungus activates the ET pathway through the production of this phytohormone; the developmental processes that ET regulates on the root system for the formation of lateral roots and root hairs involve the components of the ET pathway (ET RESPONSE 1) ETR1, ETHYLENE INSENSITIVE 2 (EIN2), and EIN3, probably using MPK6 and CTR1 as modulators of fungal signals between IAA and ET pathways (Contreras-Cornejo et al. 2015b). In the case of the plant-pathogen interaction a key role for *OsGH3.1* in the induction of rice resistance against *Magnaporthe grisea* was evidenced in experiments with the transformant plant overexpressing *OsGH3.1* because in such lines the resistance to the pathogenic fungus was higher (Domingo et al. 2009).

4.3.1.2 ACCase/Ethylene (ET)

Some rhizospheric microorganisms such as the bacterium *Burkholderia phytofirmans* PsJN can promote plant growth through the action of the enzyme called 1-aminocyclopropane-1-carboxylic acid deaminase [ACCase] (Sessitsch et al. 2005). This mechanism begins when the microorganisms that possess ACCase perceive the ACC exuded by the roots of the plants, and this organic acid is cleaved into α-ketobutyrate and ammonia (Santoyo et al. 2016). ACCase encoding gene has been identified in several microorganisms that include the yeast *Hansenula saturnus*, *Trichoderma asperellum* T203, and *Penicillium citrinum* (Minami et al. 1998; Jia et al. 1999; Viterbo et al. 2010).

It has been proposed that the amino acid L-methionine is used as a precursor for the production of α-keto-γ-(methylthio) butyric acid, and due to its photosensitive properties it releases ET (Splivallo et al. 2009). In microorganisms, there are at least two ET biosynthetic pathways involving the compounds 2-oxo-4-methylthiobutyrate (OMTB) or 2-oxoglutarate (Cristescu et al. 2002). The OMTB pathway has been found to exist in the fungi *Botrytis cinerea*, *Penicillium digitatum*, and the yeast *Saccharomyces cerevisiae*, and in the bacterium *Pseudomonas syringae* (Nagahama et al. 1994; Weingart et al. 1999; Cristescu et al. 2002).

ET is a gaseous molecule of very low molecular weight that coordinates different aspects of plant physiology such as development and defense (Jaroszuk-Ściseł et al. 2019). In *Arabidopsis thaliana*, at least five receptors of ET have been detected called: ET RESPONSE 1 (ETR1), ETR2, ET RESPONSE SENSOR1 (ERS1), ERS2, and ET INSENSITIVE 4 (EIN4) (Kazan 2015). The activation of these receptors causes repression of CONSTITUTIVE TRIPLE RESPONSE 1 (CTR1), that permits ETHYLENE INSENSITIVE 2 (EIN2) to relay the ET signal to the

transcription factors EIN3 and ETHYLENE-INSENSITIVE3-LIKE (EIL). Then, EIN3 activates ETHYLENE RESPONSE FACTOR 1 (ERF1), inducing the expression of ET-responsive genes (Huang et al. 2003; Kieber et al. 1993; Sánchez-Rodríguez et al. 2010). Nine genes encoding ACC synthetases (ACS) have been detected in *Arabidopsis thaliana* (Tsuchisaka and Theologis 2004). It is known that *Piriformospora indica* induces changes in the expression of the *ACS1* and *ACS8* genes in the tips of the roots of reporter plants that express the activity of β-glucuronidase (GUS) (Khatabi et al. 2012).

4.3.1.3 Cytokinins (CKs)

These types of compounds are derivatives of N_6-substituted adenine compounds (Wang et al. 2017). Some plant-mutualistic bacteria such as *Sinorhizobium meliloti* and *Mesorhizobium loti* have been detected to produce CKs (Lohar et al. 2004; Frugier et al. 2008). In *Streptomyces turgidiscabies*, the causal agent of potato scab, a biosynthetic pathway for this phytohormone has also been detected (Joshi and Loria 2007). For several decades, it has been known that *Agrobacterium tumefaciens* transfers to its host plants a specific fragment of DNA (transfer DNA [T-DNA]) that comes from a tumor-inducing (Ti) plasmid and among the genes that are encoded in such plasmid, a *trans*-zeatin synthesizing gene is found, which promotes the production of *trans*-zeatin in bacteria (Hwang et al. 2013).

In plants, CKs promote cell division but also participate in various processes associated with active growth, metabolism, and in modulating defense responses (Giron et al. 2013). CKs are active at the site of their synthesis, but also at distal sites where they are concentrated after being transported from other very distant parts (Zhao 2008). It has been detected in *Arabidopsis thaliana* that the transporter ABCG14 (an ATP-binding cassette) regulates the translocation of ^{14}C-*tZ* type CK from roots to foliages through the xylem (Ko et al. 2014).

In *Medicago truncatula*, the CK signaling mechanism is triggered when the phytohormone is perceived by the extracellular cyclase/histidine kinase-associated sensing extracellular domain in the CK response 1 (CRE1) transmembrane receptor (Gonzalez-Rizzo et al. 2006; Kundu and DasGupta 2018). On the other hand, the endophytic fungus *Piriformospora indica* can promote the growth of the model plant *Arabidopsis thaliana* by activating CKs signaling; importantly, increases in the content of *cis*-CKs were detected in the roots of the plant and there is evidence that shows that the combination of the CRE1/AHK2 receptors is necessary during the signaling mechanism (Vadassery et al. 2008).

It has been identified in rice plants (*Oryza sativa*) infected with the pathogen *Magnaporthe oryzae*, that there is a space-dependent hormonal modulation between components of the signaling pathway mediated by CKs and ABA. In the early stages of the infection by *M. oryzae*, a suppression of the immune system occurs in the plant, which is partly related to the activation of the signaling pathway mediated by ABA, which leads to activation of the signaling pathway modulated by CKs and the expression of genes that code for sugar transporters (Cao et al. 2016).

In *Arabidopsis thaliana* ecotype Columbia-0, an interesting effect on the modulation of the components of the CKs and auxins signaling pathways has been detected during the clubroot disease caused by the obligate biotrophic *Plasmodiophora brassicae*. During this disease, genes belonging to the *GH3* family and members involved in the auxin homeostasis were upregulated. In contrast, some components involved in the CK homeostasis were downregulated (Siemens et al. 2006). It is known that in early stages of the interaction, *Plasmodiophora* provides CKs to the host plant, which causes a re-initiation of cell division in the cortex, and consequently several signaling and metabolic events occur that will allow to maintain the plant pathogen and later the gall formation (Devos et al. 2006).

4.3.1.4 Gibberellins (GAs)

These compounds act in multiple processes of plant growth such as modulation of cell division in growing tissues, stem elongation, flowering, seed germination, fruit formation, and senescence (Yamaguchi 2008; Hamayun et al. 2009). GAs are tetracyclic diterpenoid molecules (Qin et al. 2013). These types of compounds are produced by various bacteria and fungi and a little more than 130 molecules structurally related to GAs have been identified (Contreras-Cornejo et al. 2015c).

Initially, these molecules were identified in the phytopathogenic fungus *Fusarium fujikuroi* (teleomorph *Gibberella fujikuroi*) which attacks rice plants (*Oryza sativa*), but also in other microorganisms such as the phytopathogenic bacterium *Xanthomonas oryzae* pv. *oryzicola* and *Mesorhizobium loti* MAFF303099 (Nett et al. 2017). These compounds have also been identified in *Sphaceloma manihoticola*, strains of *Phaeosphaeria* sp. (MacMillan 2002; Bömke and Tudzynski 2009). The main active molecule in plants of this group of compounds is gibberellic acid 3 (GA3), although there is evidence showing that GA4 is the most active in *Arabidopsis thaliana* (Contreras-Cornejo et al. 2015c). In the signaling mechanism, bioactive GA in the plant promotes the interaction of the GA-Insensitive Dwarf 1 receptor (GID1) with DELLA proteins (Hirano et al. 2008). The signaling mechanism of GAs is finely modulated through the inactivation of bioactive GAs by modifying the molecular structure through the epoxidation of the 16, 17 double bond of GAs by the enzymatic activity of a cytochrome P450 monooxygenase, or alternatively by the methylation of the molecule by the action of GA methyl transferases (Zhu et al. 2006; Varbanova et al. 2007). In bacteria the production of GAs is modulated by a cytochrome P450 (CYP)-rich operon. This group of enzymes in turn produces *ent*-kaurene which is the predecessor intermediate product of (*E,E, E*)-geranylgeranyl diphosphate, which will be the substrate of the *ent*-copalyl diphosphate synthase and the resulting product of this reaction will be the target of the *ent*-kaurene synthase (Morrone et al. 2009; Hershey et al. 2014). The operon that regulates the production of GAs has been identified in nitrogen-fixing rhizobacteria and in phytopathogenic microorganisms. There is evidence to suggest that GA9, which is inactive in plants and which is produced by rhizobia, is converted by the plant to its active form GA4, this probably in order to block further nodulation

(Tatsukami and Ueda 2016). The signaling mechanism of these phytohormones is also key in establishing symbiotic interactions. There is evidence showing that GAs and the GID1 receptor are components involved during the interaction of *P. indica* with roots (Schäfer et al. 2009). Similarly, gibberellin DELLA proteins are components that modulate arbuscular mycorrhizal symbioses (Foo et al. 2013).

4.3.1.5   Abscisic Acid (ABA)

This phytohormone is involved in modulating various physiological processes in plants such as abscission of leaves and stomatal opening to control transpiration and gas exchange that implies the entry of CO_2 that will be used during photosynthesis (Brodribb and McAdam 2011). ABA is also involved in the modulation of lateral root development and in the activation of mechanisms of resistance or tolerance to abiotic stress caused by water deficit or salinity (Achard et al. 2006). The ABA signaling mechanism occurs in the nucleus of cells. The phytohormone has a heterodimeric receptor made up of the RCAR protein (REGULATORY COMPONENT OF ABA RECEPTOR) and the PP2C protein (PROTEIN PHOSPHATASE TYPE 2C) that includes ABI1 (ABSCISIC ACID INSENSITIVE 1 [ABI1]). PP2Cs phosphatases have been proposed to regulate the ABA pathway by repressing the activity of the SUCROSE-NONFERMENTING KINASE1-RELATED PROTEIN KINASES (SnRKs) protein kinases. However, in the presence of ABA the activity of PP2Cs is inhibited. As a consequence, the repressed protein kinases are released, remaining active to phosphorylate the respective components of the ABA pathway, such as bZIP (basic leucine zipper) transcription factors such as ABI5 (Raghavendra et al. 2010). Two mutants insensitive to ABA, *abi1* and *abi2* have been isolated in *Arabidopsis thaliana*; such mutants have the characteristic that they do not close their stomata in response to the exogenous application of ABA (Allen et al. 1999). On the other hand, ABI4 is a transcriptional factor of the APETALA 2 (AP2) type that is modulated in response to ABA during plant development or in response to salt and sugar (Arroyo et al. 2003; Finkelstein et al. 2011). In vitro experiments to study the interaction between *Arabidopsis thaliana* and *T. virens* Gv29-8 and *T. atroviride* IMI206040 showed that both fungal species modulate the opening of stomata in leaves. This effect was correlated with the modulation of leaf transpiration. Interestingly, it was found that the *abi1-1* and *abi2-1* mutants did not close their stomata in response to the fungal inoculation, suggesting that modulation of stomatal activity by *Trichoderma* involves the ABA pathway. Chemical analysis revealed that *T. virens* Gv29-8 and *T. atroviride* IMI 206040 produce ABA, and that both species modulate the expression of the reporter gene *abi4:uidA* (Contreras-Cornejo et al. 2015a).

However, other types of metabolites of bacterial and fungal origin have been identified and they are not structurally related with the typical phytohormones but can also activate growth and development processes in plants. Below are described some of such compounds and the mechanisms that they activate when communicating with plants.

4.3.1.6 Homoserine Lactones

Different Gram-negative bacteria have a self-modulation system known as "Quorum-Sensing" (QS) through a group of metabolites identified as homoserine-lactones (HSL), and themselves regulate their population density, motility, biofilm formation, and biosynthesis of both exopolysaccharides and siderophores (Chalupowicz et al. 2008; Zúñiga et al. 2017). The QS system of bacteria is key in the establishment and colonization of these microorganisms on their host plant as revealed in *Arabidopsis thaliana* and maize (*Zea mays*) (Coutinho et al. 2013; Zúñiga et al. 2013). *Paraburkholderia phytofirmans* PsJN is known to have two different QS systems named BpI.1./R.1 and BpI.2/R2 (BraI/R-like QS system) that modulate HSL production (Zúñiga et al. 2017).

HSL have an acyl chain and when they are perceived by the roots of the plants they can be captured towards the interior of the root and modulate the root growth (Götz et al. 2007; Ortíz-Castro et al. 2008; von Rad et al. 2008). For example, it has been observed that the modulation of the growth of rice (*Oryza sativa*) plants by the *Pseudomonas aeruginosa* PUPa3 system is due in part to the regulation of QS by acyl-homoserine lactones (Steindler et al. 2009). The QS system has also been reported in the host-specific tumorigenic pathogen bacterium *Pantoea agglomerans* pv. *gypsophilae*. This microorganism mainly biosynthesizes *N*-butanoyl-L-homoserine lactone (C_4-HSL) and *N*-hexanoyl-L-homoserine lactone (C_6-HSL) in lower concentrations (Chalupowicz et al. 2009).

Interestingly, it has been observed that the modulation of galls induced by *P. agglomerans* is due to the modulation of the QS system, auxin levels, and CK (Chalupowicz et al. 2009). It is known that HSL *N*-decanoyl-homoserine lactone (C_{10}-HLS) can regulate the growth of *Arabidopsis thaliana* (Ortíz-Castro et al. 2008). Interestingly, *N*-3-oxo-hexanoyl-homoserine lactone (3OC_6-HSL) stimulates the elongation of the primary root of *Arabidopsis thaliana*. This effect on the roots was correlated with the increase in the expression of the *AtMYB44* gene that codes for a transcriptional factor involved in plant defense and saline stress. The effect of 3OC_6-HLS on root elongation was affected in the *atmyb44* mutant. It was detected that the modulation of root growth by 3OC_6-HSL was due in part to the regulation of the expression of genes *ARR15* and *ARR4* in response to CK and *IAA7*, *IAA14*, and *MAX2* in response to auxins, respectively (Zhao et al. 2016).

4.3.1.7 Polyamines

Polyamines are a class of low molecular weight compounds found in higher organisms, microorganisms, and plants. The most common are cadaverine, putrescine, spermine, and spermidine. It is known that *Azospirillum brasilense* Az30 can promote the root growth of rice plants in a mechanism partially mediated by the production of cadaverine (Cassán et al. 2009). Recently, Xie et al. (2014) reported that *Bacillus subtilis* OKB105 has the ability to promote the growth of *Nicotiana*

tabacum plants and spermidine was identified as one of the molecules responsible for regulating this phenotype in plants. The growth promotion of *N. tabacum* by *B. subtilis* involved the induction of the expression of cell expansion genes *Nt-EXPA1* and *Nt-EXP2* and the inhibition of the *Nt-ACO1* gene that encodes a 1-aminocyclopropane-1-carboxylic acid oxidase that participates in the biosynthesis of ethylene.

4.3.1.8 Volatile Organic Compounds

Soil microorganisms emit volatile metabolites that fulfill multiple functions in ecosystems and among the activities is the communication between the members of the microbial community and with the associated plants (Camarena-Pozoz et al. 2018). Although some rhizobacteria and rhizosphere fungi are grouped in the same genus, there may be differences at the metabolic level, and as a consequence they impact differently on the physiology of plants (Gutiérrez-Luna et al. 2010; Contreras-Cornejo et al. 2014a, b; Garnica-Vergara et al. 2016; Guo et al. 2020). Table 4.2 shows some particular cases of plant growth-promoting rhizobacteria and their chemicals that are bioactive on plants. It has been observed that volatile metabolites that alter plant growth have molecular masses of less than 300 Da and are of lipidic nature (Fincheira and Quiroz 2018; García-Gómez et al. 2019). However, there is still too much work to do on the role of microbial volatile metabolites in different interactions because ~2000 volatile compounds have been identified from 1000 microbial strains (Lemfack et al. 2018). It has been observed that the soil bacteria *Enterobacter cloacae*, *B. amyloliquefaciens*, and *B. subtilis* can promote plant growth through the emission of volatile compounds (Lugtenberg and Kamilova 2009).

In a study carried out by Gutiérrez-Luna et al. (2010) with several isolates of rhizobacteria to evaluate their effect on the growth promotion of *Arabidopsis thaliana* through the emission of volatile organic compounds, it was found that the isolates L254 and L272a, although both belong to the genus *Bacillus*, had a very different impact on the growth and development of the root system as evidenced by the different pattern of lateral root and root hair formation. When chemical analyses were performed to determine the profile of the volatiles emitted by the bacterial isolates L254, L255, L265a, L266, L270, and L272a, the following metabolites were found: 1-butanol, 6-methyl 2-heptanol, 2-nonenal, 1-octen-3-ol, benzaldehyde, butyrolactone, acetophenone, tridecanal, tetradecanal, 4-decanone, 6-undecanone, 5-tridecanone, cyclodecane, 3-tetradecanone, 2-pentadecanone, 1-tridecanol, 6,10,14-trimethyl 2-pentadecanone, 2-pentadecanol, 9-octadecanone, 4-octadecyl morpholine, cyclododecane, and 2-morpholinomethyl-1,3-diphenyl-2-propanol.

It has been determined that *T. virens* Gv29-8 releases a mixture of VOCs constituted in part by mono (C_{10})- and sesquiterpenes (C_{15}) that included camphene, 3-carene, β-myrcene, β-phellandrene, eucalyptol, *trans*-β-ocimene, β-terpinene, β-caryophyllene, τ-cadinene, δ-cadinene, α-amorphene, and τ-selinene. In experiments carried out in vitro in Petri dishes to test the effects of the *T. virens* VOCs on

Table 4.2 Microbial metabolites and their effect on plants

Strain	Chemicals	Plant	Effect	References
Arthrobacter agilis UMCV2	Dimethylhexadecylamine	*Medicago truncatula*	Growth promotion	Orozco-Mosqueda et al. (2013)
	Dimethylhexadecylamine	*Sorghum bicolor*	Iron uptake stimulation	Castulo-Rubio et al. (2015)
	Dimethylhexadecylamine	*Medicago sativa*	Growth promotion	Velázquez-Becerra et al. (2011)
	Pool of VOCs	*Medicago truncatula*	Iron deficiency stress response, brassinosteroid content increased	Flores-Cortez et al. (2019)
Azospirillum brasilense SP7	Pool of VOCs	*Mentha × piperita*	Growth promotion, monoterpene biosynthesis stimulated	Santoro et al. (2011)
Bacillus amyloliquefaciens FZB42	Pool of VOCs	*Arabidopsis thaliana*	Growth promotion, multiple transcriptional modifications related to stress responses	Hao et al. (2016)
Bacillus amyloliquefaciens strains	Pool of VOCs	*Arabidopsis thaliana*	Growth promotion and phytopathogens growth inhibition	Asari et al. (2016)
Bacillus megaterium XTBG34	2-Pentylfuran	*Arabidopsis thaliana*	Growth promotion	Zou et al. (2010)
Bacillus methylotrophicus M496	3-Hydroxy-2-butanone	*Zea mays*	Growth promotion	Pérez-Flores et al. (2017)
Bacillus methylotrophicus M4-96	3-Hydroxy-2-butanone	*Fragaria × ananassa*	Growth promotion	Vicente-Hernández et al. (2019)
Bacillus sp. B55	Dimethyl disulfide	*Nicotiana attenuata*	Sulfur assimilation	Meldau et al. (2013)

(continued)

Table 4.2 (continued)

Strain	Chemicals	Plant	Effect	References
Bacillus strains	Pool of VOCs	*Arabidopsis thaliana*	Growth promotion, root architecture modifications	Gutiérrez-Luna et al. (2010)
Bacillus subtilis SYST2	1,3-Propanediol	*Solanum lycopersicum*	Growth promotion	Tahir et al. (2017)
Bacillus subtilis	2,3-Butanediol	*Arabidopsis thaliana*	Growth promotion	Ryu et al. (2003)
GB03	Pool of VOCs	*Arabidopsis thaliana*	Growth promotion, inflorescence development, chlorophyll content	Xie et al. (2009)
	Pool of VOCs	*Ocimum basilicum*	Growth promotion, essential oil accumulation	Banchio et al. (2009)
	Pool of VOCs	*Arabidopsis thaliana*	Iron acquisition induction	Zhang et al. (2009)
	Pool of VOCs	*Mentha × piperita*	Growth promotion, monoterpene biosynthesis stimulated	Santoro et al. (2011)
Bacillus vallismortis EXT-1	3-Hydroxy-2-Butanone	*Nicotiana tabacum*	Growth promotion	Ann et al. (2013)
Burkholderia ambifaria	Dimethyl trisulfide, acetophenone, 3-hexanone	*Arabidopsis thaliana*	Growth promotion, fungi growth inhibition	Groenhagen et al. (2013)
Burkholderia pyrrocinia LMG 21822	Indole	*Arabidopsis thaliana*	Growth promotion	Blom et al. (2011)
Chromobacterium violaceum CV0	Indole	*Arabidopsis thaliana*	Growth promotion	Blom et al. (2011)
Escherichia coli	Indole	*Arabidopsis thaliana*	Growth promotion	Bailly et al. (2014)
Paenibacillus polymyxa E681	n-Tridecane	*Arabidopsis thaliana*	Induced systemic response (ISR)	Lee et al. (2012)
Proteus vulgaris JBLS202	Indole	*Arabidopsis thaliana*	Growth promotion	Bhattacharyya et al. (2015)

Pseudomonas fluorescens SS101	13-Tetradecadien-1-ol, 2-butanone, 2-Methyl-n-1-tridecene	Nicotiana tabacum	Growth promotion	Park et al. (2015)
Pseudomonas fluorescens WCS417r	Pool of VOCs	Mentha × piperita	Growth promotion, monoterpene biosynthesis stimulated	Santoro et al. (2011)
Pseudomonas simiae AU	Pool of VOCs	Glycine max	Growth promotion and induced systemic tolerance (IST) to salt stress	Vaishnav et al. (2015)
Streptomyces coelicolor	3-Octanone	Arabidopsis thaliana	Growth promotion	Dotson et al. (2020)

the growth of *Arabidopsis thaliana*, it was found that the blend of VOCs promoted both the shoot growth and lateral root formation (Contreras-Cornejo et al. 2014b). In other hand, although species of the phytopathogenic fungus *Verticillium* cause rot in different crops, it has been observed that natural mixtures of volatile compounds constituted in part by 2-methyl-1-propanol, 3-methyl-1-butanol, 2-methyl-1-butanol, 3-pentenol, 3-methyl-3-buten-1-ol, 3-octanone, acetoin, 1-hexanol, 4-methyl-5-hexen-2-ol, 3-octanol, 4-methyl-6-hepten-3-ol, 1-octen-3-ol, 3,5,5-trimethyl-2-hexene, 2,3-butanediol, 3-ethyl-4-methyl-3-penten-2-one, himachala-2,4-diene, β-caryophyllene, α-amorphene, azulene, and phenylethyl alcohol but their effects on plants have not been fully elucidated. Such compounds from fungi can promote the *Arabidopsis thaliana* growth and such effect is related in part with the manipulation of the auxin-mediated signaling pathway (Li et al. 2018).

However, few studies have shown that certain pure metabolites are biologically active to promote growth. Among the group of the sesquiterpenoid compounds, it is known that β-caryophyllene is a metabolite whose range of biological activity in *Lactuca sativa* plants is 25–100 μM (Minerdi et al. 2011). Among the different volatile metabolites produced by *Laccaria bicolor* the sesquiterpenoid compound (−)-thujopsene is present, which is responsible for stimulating the formation of lateral roots in *Arabidopsis thaliana* (Ditengou et al. 2015). In experiments performed in vitro, it has been found that some species of *Trichoderma* emit the lactone 6-pentyl-2*H*-pyran-2-one. Applied exogenously on *Arabidopsis thaliana* at concentrations of 50–175 μM, such metabolites are responsible for promoting the plant growth through the modulation of the auxin transporters expression (Garnica-Vergara et al. 2016).

The volatile metabolites 2,3-butanediol and 3-hydroxy-2-butanone (acetoin) are compounds produced by *Bacillus subtilis* GB03 and *Bacillus amyloliquefaciens* IN937a released in the soil and triggered towards the atmosphere by the plant growth-promoting bacteria (Ryu et al. 2003). In pharmacological tests with the pure compound 2,3-butanediol and *Arabidopsis thaliana* it was found that such volatile metabolite is active in the range of 1–100 μg as revealed by the increased growth of the leaf area (Fincheira and Quiroz 2018).

4.3.2 Root Colonization

Microorganisms of the rhizosphere can colonize root tissues and establish eventual, facultative, or obligate associations with their host (Santoyo et al. 2016). The processes of root colonization involve the production of hydrolytic enzymes of microbial origin that are used as tools to break the layers of root cells and penetrate the root tissue (Contreras-Cornejo et al. 2016). Cellulases and xylanases are fungal enzymes that degrade specific plant tissue constituents, and most likely are components involved in the root colonization process (Henrissat et al. 1985; Payne et al. 2015; Estrada-Rivera et al. 2019).

There are other types of non-hydrolytic enzymes that favor the binding or adhesion of fungal hyphae to root cells. For example, swollenin (Swo) produced by *T. asperellum* and other fungal strains (Brotman et al. 2008; Meng et al. 2019). Swo possesses a cellulose-binding module, and in turn disrupts the structure of the crystalline cellulose present in the plant cell wall. It has been demonstrated that during the plant-*Trichoderma* interaction Swo facilitates the expansion of the plant cell wall in roots and root hairs (Brotman et al. 2008). Once the physical interaction between the root and the microorganism occurs, a series of physiological, biochemical, and molecular events are triggered in the host plant.

4.3.3 Plant Growth Promotion

The promotion of plant growth and development regulated by rhizosphere microorganisms can occur at different stages of the interaction (Sevilla et al. 2001; Ryu et al. 2003; Real-Santillán et al. 2019). In nature, some plants and microorganisms establish specific associations, while there are microorganisms that have the ability to promote growth without host specificity (Ray et al. 2018). Figure 4.3 shows the dynamics among phytohormones and other microbial molecules that modulate multiple process of the plant physiology. It has often been observed that soil bacteria and fungi can modulate the growth and plasticity of the root system (Contreras-Cornejo et al. 2014a, b). These effects are the result of inducing the differentiation of epidermal cells for the formation of root hairs, the activation of the cells of the primary root pericycle to induce the formation of lateral roots, and by activating the cell cycle in the cells of the tip of the primary root (López-Bucio et al. 2007).

It is important to note that the modulation of the plant growth and development by microorganisms can vary because not all microorganisms impact in the same way (Reboutier et al. 2002; Gutiérrez-Luna et al. 2010; García-Gómez et al. 2019). This effect is because there are microorganisms that produce more than one growth regulating metabolite. For example, *Burkholderia phytofirmans* PsJN and *Pseudomonas putida* W619 produce IAA and ACCase, and *Enterobacter* sp. 638 produces siderophore, IAA, acetoin, and 2,3-butanediol (Santoyo et al. 2016). Figure 4.4 shows the kind of VOCs produced by some soil fungi and the roles of such metabolites in plant physiology remain to be determined.

It has been observed that bacteria that have the same 16S rRNA gene sequence may impact differently on the phenotype of the plants with which they interact (Blakney and Patten 2011; Haney et al. 2015; Timm et al. 2015; Herrera-Paredes and Lebeis 2016). While some microorganisms can impact on the formation of lateral roots, others can do so on the formation of root hairs or the growth of the primary root (Reboutier et al. 2002; Gutiérrez-Luna et al. 2010; Garnica-Vergara et al. 2016). Even a certain microorganism can modulate the development of the host plant depending on the type of interaction that can occur without physical contact or by establishing the colonization of the root tissue (Macías-Rodríguez et al. 2018). Frequently, the aerial zone of the plants is also altered after the microbial stimulus.
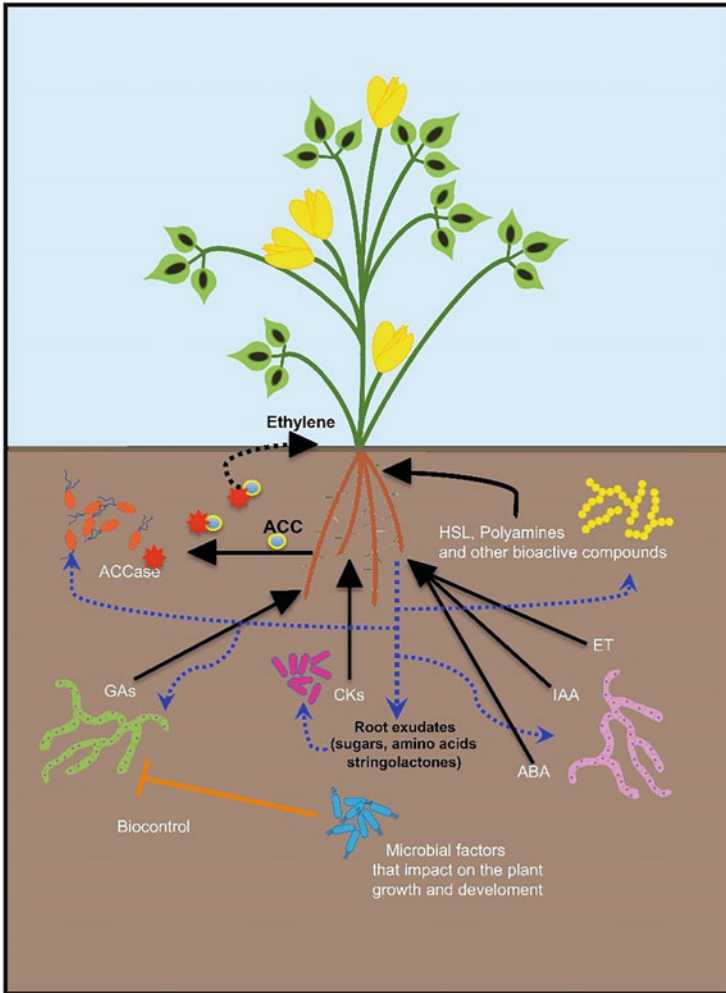
Fig. 4.3 A simplified model for a plant-microorganism interaction. In the rhizosphere detrimental or plant beneficial microorganisms produce several metabolites (black lines) with capacity to modulate the plant growth or induce defense responses. In addition, root exudates (blue lines) impact on the microbial communities and key plant-derived compounds are signaling molecules to coordinate specific interactions with rhizobia or mycorrhizal arbuscular fungi. Furthermore, sugar derived from roots can serve as nutritional source for soil microorganisms. *ABA* abscisic acid, *IAA* indole-3-acetic acid, *ET* ethylene, *CKs* cytokinins, *GAs* gibberellins, *ACCase* 1-aminocyclopropane-1-carboxylate deaminase, *ACC* 1-aminocyclopropane-1-carboxylic acid, *HSL* homoserine-lactones

Petioles, leaf size, and accumulation of foliar biomass generally increase (Flores-Cortez et al. 2019).

The opening of foliar stomata can also be modulated, which will have an impact on the transpiration of the leaves and the exchange of gases towards the atmosphere
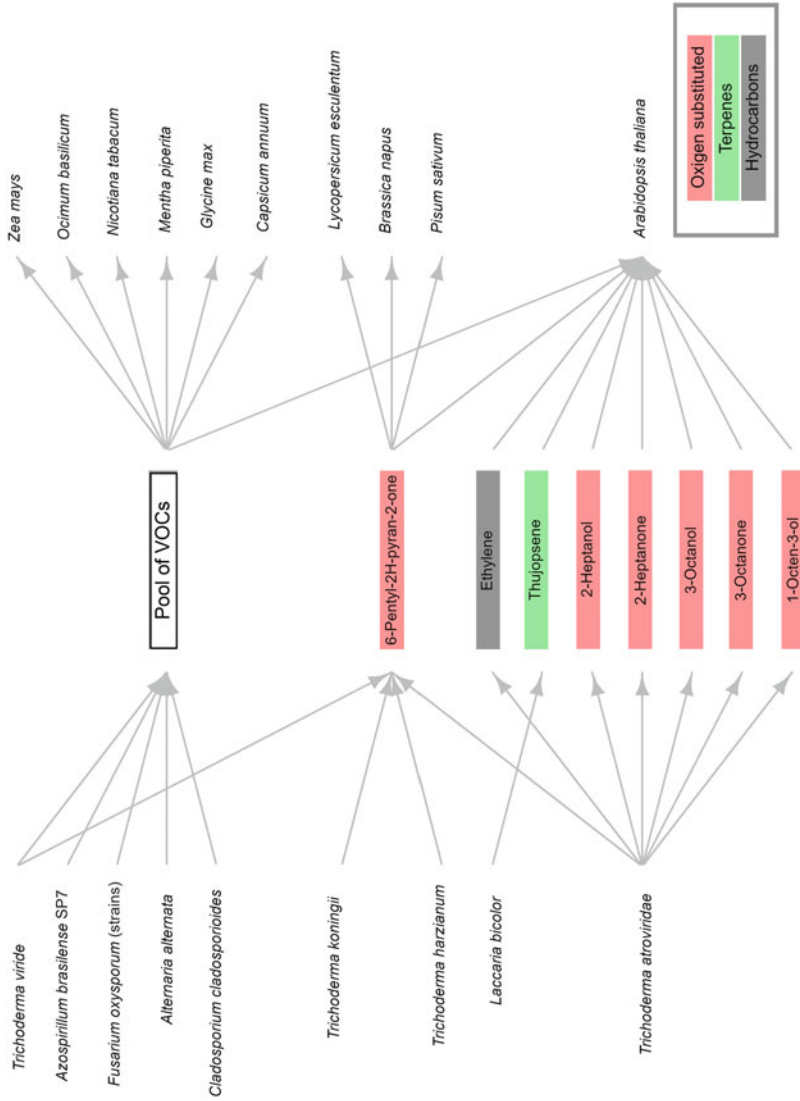
Fig. 4.4 Schematic representation of volatile compounds produced by soil fungi and plants in which have been investigated their effects

(Contreras-Cornejo et al. 2015b). The modulation of plant growth and development has been observed in different plants of agricultural interest and under different growing conditions. It has been observed that the rhizobacterium *Arthrobacter agilis* UMCV2 modulates in an organ-specific manner the expression of *FERRIC REDUCTION OXIDADSE (FRO)* genes *MtFRO1*, *MtFRO2*, *MtFRO3*, *MtFRO4*, and *MtFRO5* of *Medicago truncatula* involved in iron uptake in both conditions of sufficiency and deficiency (Montejano-Ramírez et al. 2018).

Another beneficial effect for sugarcane plants cultivar SP70-1143 induced by the colonization of the diazotrophic bacterium *Acetobacter diazotrophicus* (syn. *Gluconacetobacter diazotrophicus*) is the promotion of growth and the incorporation of nitrogen as revealed by a $^{15}N_2$ incorporation bioassay (Sevilla et al. 2001). *Azospirillum brasilense* is another diazotrophic bacterium whose effects on growth promotion are mainly attributed to the production of IAA (Barbieri et al. 1991; Okon and Labandera-Gonzalez 1994). Rhizosphere microorganisms can also promote the plant growth through the production and emission of volatile organic compounds. For example, in vitro experiments with bean plants (*Phaseolus vulgaris*) and *Arabidopsis thaliana* inoculated with the rhizobacteria *Bacillus megaterium*, it was found that compared with non-inoculated plants, the microorganism promoted the growth of both types of plant as shown by the accumulation of fresh biomass and the induction of lateral roots (López-Bucio et al. 2007).

4.4 Plant Defense Responses

One of the first events that occur during the plant-microorganism interactions is the activation of local or systemic defense responses, and it will depend on the type of microorganism detected (Stringlis et al. 2018). After the perception of the microbial signals by the host plant, there are increases in the cytoplasmic Ca^{2+} content, changes in the endogenous content of reactive oxygen species (i.e., H_2O_2, NO), and primary metabolites that include the phytohormones salicylic acid, jasmonic acid, and ethylene (Farag et al. 2013).

Defense responses can be induced after the perception of bacterial components such as low molecular compounds (AHLs), flagella, siderophores, and lipopolysaccharides (Lugtenberg and Kamilova 2009). The tomato mottle virus (ToMoV) which is transmitted by natural dynamics of viruliferous silverleaf whitefly *Bemisia argentifolii* adults. An experiment carried out in the spring of 1998 under field conditions to evaluate the effect of the inoculation of various plant growth-promoting bacteria on tomato plants infected with *Bemisia argentifolii* revealed that treatments with *Bacillus subtilis* 937b and *Bacillus pumilus* SE34 significantly reduced the rate of symptom severity (Murphy et al. 2000). Some microorganisms have the potential to control multiple plant diseases.

Liu et al. (2017) observed that the strains AP196, AP197, AP203, AP208, and AP298 of *Bacillus velezensis* showed some effectiveness in reducing postemergence damping off in pepper caused by *Rhizoctonia solani*, in cucumber caused by

Pythium ultimum, and in tomato caused by *Xanthomonas axonopodis* and *Pseudomonas syringae* pv. tomato in plants grown in controlled conditions. The rhizobacterium *Pseudomonas fluorescens* FPT9601-T5 isolated from tomato plants also induces defense responses that partially suppress the infection caused by *Pseudomonas syringae* pv. tomato DC3000 in *Arabidopsis thaliana*; these effects were related to increases in the expression of genes involved in signal transduction and metabolic processes. Among the genes that were downregulated, some are members of the family of transcriptional factors *ETHYLENE RESPONSE FACTOR* (*ERF*) and *MyB* belonging to the signaling pathway mediated by ET (Wang et al. 2005). Microorganisms that establish physical interactions with roots also often emit volatile organic compounds that can activate defense responses in plants (Farag et al. 2013).

For example, it was observed that some rhizobacteria can stimulate defense responses through the emission of VOCs (Farag et al. 2013). In an elegant work by Ryu et al. (2004) with *Arabidopsis thaliana* plants exposed to the VOCs of the bacteria *Bacillus subtilis* GB03, *Bacillus amyloliquefaciens* IN937a, and *Escherichia coli* DH5α and infected with the pathogenic plant bacterium *Erwinia carotova*, it was found that the strains GB05 and IN937a significantly reduced the foliar attack of the pathogen. This effect was due in part to the activity of 2,3-butanediol in the concentration range of 0.2 pg to 20 μg. In the same work, it was found that the VOCs of the GB05 strain induced changes in the expression of the reporter line *PDF1.2::GUS* in response to JA/ET, observed as increased activity of β-glucuronidase.

It was found that VOCs released by *T. virens* also induced changes in the expression of the transgenic line *LOX2::GUS*, a JA-responsive gene. Such priming on plant defense was correlated with accumulations in the contents of JA and H_2O_2. *T. virens* Gv29-8-elicited plant immunity was effective to restrict the attack caused by the necrotrophic fungus *Botrytis cinerea* on the shoot (Contreras-Cornejo et al. 2014b).

These data suggested that bacterial or fungal VOCs can modulate defense responses and confer protection against the attack of pathogenic microorganisms. On the other hand, the complex mixtures of VOCs emitted by plants in interaction with soil microorganisms generally have a strong impact on the third trophic level because they act as alarm signals, inducing indirect defense responses to attract natural enemies of herbivorous insects (Dicke et al. 2009; Schausberger et al. 2012). For example, maize plants constantly suffer the attack of the fall armyworm *Spodoptera frugiperda*, but in field conditions the insect is endoparasitized by female wasps of *Campoletis sonorensis* and during the maize root-*T. atroviride* association, the fungus releases in the soil 6-PP, which attracts *C. sonorensis* towards plants that are suffering herbivory. Endoparasitism is then stimulated, providing biocontrol of *S. frugiperda* at least in controlled conditions (Contreras-Cornejo et al. 2018a).

4.4.1   JA/ET Mediated Immunity

The induction of systemic resistance is a characteristic of plant beneficial microorganisms. This phenomenon was first detected in plant growth-promoting rhizobacteria and later identified in biocontrol and mycorrhizal fungi (Jaroszuk-Ściseł et al. 2019). Such microorganisms can induce increases in the content of JA, a metabolite derived from oxylipins (Wang et al. 2020). The production of JA occurs within the cell, in the chloroplast; there in the organelle linoleic acid (18:3) and hexadecatrienoic acid (16:3) through the corresponding catalytic activity of the enzymes lipoxigenase, allene oxidase synthase, and allene oxide cyclase are converted to 12-oxophytodienoic acid (OPDA) and dinor-OPDA. Subsequently, OPDA reductase 3 (OPR3) acts on OPDA and converts it to 3-oxo-2 (2-′-pentenyl)-cyclopentane-1-octanoic acid (OPC-8:0). This last compound is subjected to three cycles of β-oxidation resulting then in the production of JA (Al-Zahrani et al. 2020).

JA activates effective defense responses against necrotrophic pathogens or herbivorous chewing insects (Browse 2009). Recently, it was reported that *T. virens* Gv29-8 when associated with the roots of maize plants increases the content of 2-oxo-phytodienoic acid in the xylem (12-OPDA) and α-ketol of octadecadienoic acid (KODA); these oxylipins were shown to be key in the induction of ISR because the mutant line *lox10* of maize that is susceptible to the attack of the pathogenic fungus *Colletotrichum graminicola* and that was later transfused with sap that contained high concentrations of 12-OPDA restored the ISR in such mutant (Wang et al. 2020).

In multiple plant-microorganism interactions a cross talk can occur between phytohormones that simultaneously modulate plant growth and defense processes (Villalobos-Escobedo et al. 2020). In a more recent work, it was reported that during the interaction of *T. atroviride* with *Arabidopsis thaliana*, the fungal NADPH oxidase plays a key role in both plant growth promotion and defense responses enhanced by the fungus. In regard with the modulation of the root-system architecture by the fungus, important information was revealed by the Δ*noxR* mutant of *T. atroviride*. Such strain failed in modulating the developmental progress of lateral roots formation as observed with the wild-type strain. In contrast, Δ*noxR* efficiently activated JA-mediated plant defense, which was effective against the attack of the necrotrophic fungus *B. cinerea* (Villalobos-Escobedo et al. 2020). Modulations of the endogenous levels of JA in maize plants by *T. atroviride* IMI 206040 after 5 days of interaction with roots also resulted in an effective priming of plant defense to reduce the attack of the chewing insect *S. frugiperda* (Contreras-Cornejo et al. 2018b).

On the other hand, auxin has been shown to alter SA production and JA signaling, and ABA can act as a hormone antagonistic to ET/JA-mediated signaling (Ponzio et al. 2013). In a study carried out in tobacco plants (*Nicotiana tabacum*) infected with *Pseudomonas syringae*, it was found that resistance to the infection caused by this pathogen was due to the modulation of the ABA and kinetin (a CK) levels. In

this condition, CK decreased the ABA levels in tobacco plants. On the other hand, the decrease in ABA concentrations allowed the participation of CK to activate the resistance mechanism against *P. syringae* (Großkinsky et al. 2014).

4.4.2 SA-Mediated Immunity

It has been observed that some pathogenic bacteria and soil fungi can activate defense responses mediated by SA (Contreras-Cornejo et al. 2011). This type of defense is known as systemic acquired resistance (SAR) and is effective against biotrophic microorganisms (Vlot et al. 2009). The SA-mediated signaling mechanism results in the induction of the expression of *PATHOGENESIS-RELATED* (*PR*) genes and their subsequent translation into their respective defensin proteins (Barriuso et al. 2008). There is evidence, though, that the signaling routes of the JA and SA are antagonistic (Derksen et al. 2013). The activation of both routes simultaneously by some beneficial microorganisms has been reported (Contreras-Cornejo et al. 2011; Niu et al. 2011). For example, the rhizobacterium *Bacillus cereus* AR156 when inoculated in *Arabidopsis thaliana* ecotype Col-0 activates effective defense responses against the pathogenic bacterium *Pseudomonas syringae* pv. tomato DC3000. AR156 induced the expression of the *PR-1*, *PR-2*, and *PR-5* genes in response to SA and *PDF1.2* that encodes plant defensin in response to JA/ET, which suggests that the SA, JA, and ET pathways are simultaneously activated, probably involving the NPR1 component (Niu et al. 2011).

A similar effect in the activation of the JA and SA signaling pathways was found in *Arabidopsis thaliana* after the inoculation with *T. atroviride* IMI 206040 and *T. virens* Gv.29-8 because both markers *PR-1::GUS* of response to SA and *LOX2::GUS* of response to JA were activated after 6 days of inoculation when the root colonization was established. In such interactions, although both signaling pathways were activated, they were slightly primed one on the other as revealed by the activity of β-glucuronidase after GUS staining and the levels of SA and JA accumulated in shoot tissues (Contreras-Cornejo et al. 2011).

4.5 Conclusion

In the environment, plants interact with myriads of microorganisms. In the case of plant beneficial rhizobacteria or fungi, they impact on physiological responses modulating the plant growth, adaptation to resist abiotic stress caused by salinity, drought or soil contamination and the activation of defense responses. A plant-microorganism interaction can initiate with the emission of a certain metabolite derived from one of the involved organisms. Then such signaling molecule encodes a key message to coordinate and form a specific interaction; for example, arbuscular mycorrhizal associations are established after the rhizodeposition by the plant and

perception of strigolactones by the spores of the target fungus, which in turn will grow tropically towards the host root. In the case of nitrogen-fixing bacteria, plant roots release chemotactic agents to attract the rhizobia and after a complex signaling mechanism the nodule is formed.

In other interactions, microorganisms release volatile or soil diffusible signaling molecules that coordinate both plant growth and defense responses. In those cases, such plant responses are regulated after the activation of endogenous mechanisms modulated by phytohormones. For example, plant growth and development are coordinated by auxins, gibberellins, CKs, ET, and ABA. Cross talk among phytohormones can occur to efficiently coordinate some plant responses. For example, lateral root formation and root hair induction is a process that requires the participation of the MPK6, auxins, and ET. Depending on the kind of rhizosphere microorganism, plant immunity is primed by the canonical defense mediators SA, JA, and ET. This can occur due to the perception of microbial defense elicitors as peptides or flagellin or when the root colonization is established. In some interactions, plant defense involves the synergistic activity of JA and ET, but frequently antagonistic roles among JA and SA, SA and IAA, and CKs and ABA have been observed. Currently, there is a broad body of scientific literature that describes the role of rhizosphere microorganisms in plant performance. However, there is a need to investigate and generate more information about the role of unknown microbial signals that are released in the atmosphere and in the soil, and how they impact on plant performance under different changing environmental conditions or when plants are challenged simultaneously with more than one type of aggressor (i.e., pathogens and herbivores). This kind of information will be relevant to generate knowledge with potential application to manage crops in cultured lands with serious troubles of pests or disturbances caused by the climatic global change.

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