Unraveling the secrets of rhizobacteria signaling in rhizosphere

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Abstract

Signaling among rhizobacteria and other soil microorganisms is an important mechanism to ensure a successful symbiotic relationship with their phytobionts. Quorum-sensing involves signaling molecules that provide essential networks for communication in the rhizosphere. These signaling molecules relay inter-and-intra-species information that coordinates and controls behavior in mixed communities, and the expression of these signaling molecules changes in response to the chemical cues. The diverse signaling molecules released in the rhizospheric zone affect the structural and physical heterogeneity of the soil and the quantity and identity of rhizobacteria. In general, rhizospheric signaling mechanisms can be categorized into three major types (i) plant to microorganisms signaling through low molecular weight molecules secreted by plants; (ii) interspecies and intraspecies microbial signaling, chiefly through quorum-sensing molecules; and (iii) microorganisms to plant signaling by microbially produced compounds. This review presents knowledge on the signaling molecules of the rhizosphere based on the above three mechanisms. The chemical nature of root exudates and their roles in attracting metabolically active rhizobacteria; the chemical properties of autoinducers secreted by rhizobacteria and their functions in intra- and inter-species interactions, including biofilm formation in the rhizosphere; and influence of quorum sensing on the root architecture, plant defense and biotic and abiotic stress responses, and gene expression are examined. The review provides a thorough understanding of rhizobacteria signaling and will help to develop novel strategies for agriculture, such as the novel use of plant growth-promoting rhizobacteria to enhance crops growth and quorum quenching technique to fight against plant pathogens.

Keywords: Rhizobacterium, root exudate, signaling molecules, quorum sensing, AHL

1. Introduction

The rhizosphere is a narrow yet highly complex and dynamic zone consisting of nutrient-rich soil. It is influenced by plant roots and its diverse microbial community, such as plant growth-promoting rhizobacteria (PGPR), plant growth-promoting fungi (PGPF), nematodes, mycorrhizal fungi, mycoparasitic fungi, and protozoa. Through their diverse communications as symbionts, these microorganisms have acquired an evolutionary relationship with their phytobionts (Venturi and Keel, 2016; Mondal and Baksi, 2019; Mathesius and Costa, 2021). Plants roots exude a variety of primary metabolites (sugars, nucleic acids, amino acids, carbohydrates, lipids, and organic acids) and secondary metabolites (phenolics, alkaloids, sterols, steroids, terpenoids, lignin, and essential oils). The release of these metabolites in the rhizosphere constitutes a significant amount of nitrogen and reduced carbon that benefits the plant by attracting and encouraging the growth of beneficial microbes while inhibiting pathogenic ones (Olanrewaju et al., 2019). Thus, these root-derived materials play an important role in shaping and establishing a mutualistic association between the symbiotic partners as well as inducing plant defense mechanisms (Canarini et al., 2019).

The rhizospheric signaling mechanisms can be categorized into three major types (i) plant to microorganisms signaling through low molecular weight molecules secreted by plants, which are involved in numerous complex plant-microbes interactions; (ii) interspecies and intraspecies microbial signaling, which takes place chiefly through quorum-sensing (QS) molecules permitting microorganisms to shape and contemporize their behavior; and (iii) microorganisms to plant signaling by microbially produced compounds that influence the root architecture, plant defense and biotic and abiotic stress responses, and gene expression (Altaf et al., 2017; Venturi and Keel, 2016). The communication of rhizobacteria with the host plant is a dynamic and interdependent relationship that involves both interacting partners and biotic-abiotic factors of the rhizosphere (Hassan et al., 2019). However, the abiotic factors, particularly environmental factors that moderate rhizospheric structure, are relatively unclear. It has been hypothesized that various abiotic elements may play a crucial role in modulating soil microbes' variability, including those colonizing in the rhizosphere (Santoyo et al., 2017). Indeed, in several cases, the soil or rhizosphere microbiome is affected by two or more abiotic factors, thereby complicating the analysis of the specific effects of single factors. Some abiotic modulating factors are pH, type of soil, soil moisture, soil water content, dissolved organic matter, temperature, atmospheric CO2, etc. (Santoyo et al., 2017).

A diverse variety of QS networks have been identified among soil bacterial species involving a number of signaling molecules, including acylated homoserine lactones (AHLs), diketopiperazines (DKPs), diffusible signaling factor (DSF), secondary metabolites, phytohormone- like molecules, and other small organic compounds (Venturi, and Keel 2016; Mondal and Baksi, 2019). Among the signaling molecules, AHLs are the most extensively studied in bacteria (Ostroumova et al., 2015a, b), cyclodipepetides and their derivative diketopiperazines have also been shown to modulates auxin signaling in plants (Ortiz-Castro et al., 2011). In general, to recognize its rhizospheric associated microbes, plants use pattern recognition receptors (PRRs) which are membrane-associated receptor-like kinases or receptor-like proteins, reflecting the prevalence of apoplastic colonization of plant-infecting microbes. In addition, there are various precise microbe-associated molecular patterns (MAMPs) which are molecular signatures that are highly conserved in whole classes of microbes, but they are yet to be fully characterized (Rashid et al., 2017). The signaling molecules also play a vital role in signal transduction both in inter- and intra-species interactions. They evoke a range of effects on different plant growth phases and other local and systemic immune responses, namely induced systemic resistance (ISR) and systemic acquired resistance (SAR) (Mhlongo et al., 2018; Shrestha et al., 2020). QS is also involved in the production of biofilm in the rhizosphere that facilitates colonization of the plant roots (Noirot-Gros et al., 2018; Zboralski and Filion, 2020). While several rhizobacteria can develop biofilms as multicellular communities, some develop into distinct morphotypes (Olanrewaju et al., 2017; Backer et al., 2018). These synchronized developmental dynamics are often controlled by cell-to-cell contact mediated by QS signals, as various strains isolated from the rhizosphere have been reported to produce andsecrete small molecules that act as autoinducers (AIs). For example, N-acyl homoserine lactones (AHLs) are used as AIs by Gram-negative bacteria, although AHLs are not exclusive to Gram-negative bacteria (Schikora et al., 2016).

QS plays an essential role in maintaining and improving crop production in agriculture. Several commercial products, such as Sudoz-P, Early green *Pseudomonas fluorescens*, Abtec, ROM, PMCS, Pangoo Plant grower, Green dual, Panther-PF, etc. are marketed as biofertilizer inocula, consisting chiefly of *Serratia* spp. or *Pseudomonas*, *Bacillus,* and other specialized fertility enhancer bacteria that are responsiblefor enhancing nitrogen fixation, colonization, and the transmission of phytopathogenic response (Jnawali et al., 2015). However, recently it has been realized that some microorganisms used as biofertilizers behave as opportunistic pathogens and belong to the biosafety level 2 (BSL-2) classification. Evidence presented in various scientific forums is increasingly favoring the merits of using BSL-2 microorganisms as biofertilizers (Keswani et al., 2019).

This review provides updated knowledge on the chemical nature and significance of the signaling compounds involved in plant-microbe interactions; it will help to develop further understanding of rhizobacteria communications and their applications in agricultural practices.

2. Plant to microorganisms: root exudates chemical compositions and influence of soil physico-chemical properties

The ability of plants to select specific bacteria may ensue directly from its chemical signals and their effects on its colonizing rhizobacteria (Doornbos et al., 2012). Root exudates secreted by plant roots serve as chemical attractants for numerous metabolically active microbial communities (Wang et al., 2021; Massalha et al., 2017). Several researchers found that plants establish a favorable environment by recruiting specific rhizospheric bacteria via root exudates (Dennis et al., 2010; Rudrappa et al., 2008; Loyola-Vargas et al., 2007; Fang et al., 2013). The stability of colonization is greater for specific regions of the root, presumably because these sites release abundant root exudates (Scharf et al., 2016). The rhizospheric bacterial community residing within the root vicinity use these soluble materials to mediate positive or negative interactions between plants and microbes. These signaling molecules can act as substrates for rhizobacteria, as plant pheromones to stimulate or antagonise other microorganisms. Once the rhizobacteria sense the signaling molecules, communication and interaction commence (Bhattacharya et al., 2010). The constituents of root exudates can modify microbial dynamics, favoring PGPR growth and preventing microbe growth considered hazardous to the associated plant (Dutta et al., 2013; De Coninck et al., 2015). Root exudates can also mediate tripartite signaling in the rhizosphere, among the host plant, pathogens, and the beneficial rhizobacteria (Liu et al., 2014).

2.1. Chemical composition of root exudates

Root exudates are rich in carbon and nitrogen sources, and therefore, are highly complex and difficult to classify. Although several constituents of root exudates have been identified and characterized (Ahmad et al., 2018; Scharf et al., 2016), but still a large proportion of root exudates are unidentified till date. The structural compositions of these root exudates (Table 1) alter soil physico-chemical properties to favor the colonization of rhizospheric bacteria (Godheja et al., 2017; Kumar et al., 2006; Dakora and Phillips, 2002). The compositions of the root exudates depend upon the physiological status of microorganisms, plants and soil (Hassan et al., 2019). For example, alterations in plant exudation of amino acids are regulated by microbial metabolites such as zearalenone, 2,4-diacetylphloroglucinol (DAPG, 5), and phenazine (Phillips et al., 2004).

Basically, root exudates can be categorized into low and high molecular weight signaling molecules. Low-molecular-weight exudates comprise various signaling molecules, i.e., sugars, organic acids, phenolics, amino acids, and other secondary metabolites. High molecular weight signaling molecules primarily include proteins and mucilages (as mucopolysaccharides). They are not diverse, but they constitute a substantial proportion of root exudates (Chapparo et al., 2014). Several compound types are exuded by plant roots, particularly amino acids and carbohydrates; they serve as general pheromones for various microbes, while others connect to more specific interactions (More et al., 2019). In non-pathogenic, i.e., a mutualistic or commensal interaction, the host is likely to distinguish analogous non-self, non-cultivar-dependent determinants known as SAMPs (Symbiont Associated Molecular Patterns). Hosts in commensal and mutualistic relationships are just as likely to recognize non-self as are hosts in pathogenic/parasitic interactions (McFall-Ngai, 2002).

Protein molecules released as root exudates are essential for antagonism against and rapport with bacteria (Pascale et al., 2020). Lectins are the most studied protein because of their role in biological recognition; they assist in both defense and symbiosis responses (Reyes-Montano and Vega-Castro, 2018). Plants also exude several protein molecules with consistent enzymatic defense activities (Prasannath, 2017). Many mucopolysaccharides released into the rhizosphere from the plant's root apex contain arabinogalactans that interact between plant roots and the rhizospheric microbes, attracting PGPR and repelling pathogens (Nguema-Ona et al., 2013; Cannesan et al., 2012; Xie et al., 2012).

The exact mechanisms utilized by plants to form/regulate their microbiome are still not fully understood. However, hormones involved in provoking immunity within plants, especially salicylic acid, are believed toplay a role in shaping the rhizospheric microbiome (Lebeis et al., 2015). Similarly, when the plant's jasmonic acid defense pathway is induced, the rhizospheric bacterial community leading to enrichment in microbes enhances plant defense mechanisms (Carvalhais et al., 2013). Phytochemical secretion occurred through active and passive processes by utilizing various transport mechanisms in plants (Loyola-Vargas et al., 2007). Passive exudation generally releases low-molecular-weight signaling molecules. Direct passive diffusion depends upon multiple factors such as permeability of the membrane, pH of the cytosol, and compound polarity (Badri and Vivanco, 2009). Other root exudates, such as secondary metabolites, proteins, and mucopolysaccharides, are exuded by active mechanisms that involve proteins embedded in a membrane (Huang et al., 2014). For instance, ATP-binding cassette transporters (ABC transporters) are linked with several transport mechanisms in plants, including root exudation (Wilkens, 2015; Hwang et al., 2016; Kang et al., 2011). The major facilitator superfamily (MFS) and the multidrug and toxic compound extrusion family (MATE) export several compounds across the plant cell membranes (Reddy et al., 2012). Moreover, proteins from the aluminum-activated malate transporter family (ALMT) have also been reported to act as key molecular actors in GABA (γ-aminobutyric acid) signaling that functions as a signal transducer in plants (Palmer et al., 2016).

Table 1: Various root exudates released by plants in rhizosphere and their functions

Root Exudates	**Compounds**	**Functions**
Enzymes	Amylase, proteases, invertase, peroxidase, phenolase, acid phosphatases, alkaline phosphatase, polygalacturonase, lectins, hydrolases, lipase	catalysts for P release from organic molecules, biocatalysts for organic matter transformation in soil
Organic acids	Acetic, succinic, laspartic, l-glutamic, salicylic, shikimic, isocitric, chorismic, sinapic, *p*-hydroxybenzoic, gallic, tartaric, protocatacheuic, *p*-coumaric, mugineic, oxalic, citric, piscidicaconitic, ascorbic, butyric, caffeic, citric, *p*-coumaric, ferulic, fumaric, glutaric, glycolic, glyoxilic, malic, malonic, oxalacetic, oxalic, *p*-hydroxy-benzoic, propionic, succinin, syringic, tartaric, valeric, vanillic	nutrient source, chemoattractant signals to microbes, chelators of poorly soluble mineral nutrients, acidifiers of soil, detoxifiers of Al, nod gene inducers
Phenolic acid and coumarin	Caffeic acid, benzoic acid, cinnamic acid, coumarin, ferulic acid, salycilic acid, syringic acid, vanillic acid	act as defense elements, antioxidant properties
Amino acids	α-Alanine, l-hydroxyproline, homoserine, mugineic acid β-alanine,γ-aminobutyric, arginine, aspartic, citrulline, cystathionine, cysteine, cystine, deoxymugineic, 3-epihydroxymugineic, aminobutyricacid, glutamine, glutamic, glycine, homoserine, isoleucine, leucine, lysine, methionine, mugineic, ornithine, phenylalanine, proline, serine, threonine, tryptophane, tyrosine, valine and all proteinogenic amino acids	nutrient source, nutrient acquisition from the rhizosphere
Vitamins	Thiamine, riboflavin, niacin, pantothenate, biotin	promoters of plant and microbial growth nutrient source
Polysaccharides and sugars	sucrose, pentose, arabinose, fructose, galactose, glucose, maltose, mucilages of various compositions, oligosaccharides, raffinose, rhamnose, ribose, sucrose, xylose, mannitol	Enhance root colonization
Lignin derivatives	Catechol, nicotinic acid, benzoic acid, phloroglucinol	Increases rhizospheric soil fertility
Nucleosides (purines)	Adenine, guanine, cytidine, uridine	nutrient source
Growth factors	*p*-Amino benzoic acid, biotin, choline, *N*-methyl nicotinic acid, niacin, pantothenic, vitamins B1 (thiamine), B2 (riboflavin) and B6 (pyridoxine)	coenzyme in metabolic pathways and central metabolism
Fatty acids	Linoleic, palmitic, stearic,linolenic, oleic	transport activities across the plasma membrane
Sterols	sitosterol, stigmasterol, Campesterol, cholesterol	regulate the fluidity and the permeability of phospholipid bilayers
Flavonoids and flavonols	Kaempferol, quercetin, rutin, naringenin, myricetin, strigolactone, genistein	inhibit root pathogens, stimulate mycorrhizal spore germination and hyphal branching, mediate allelopathic interactions between plants, affect quorum sensing, and chelate soil nutrients, helps in symbiotic nitrogen fixation
Inorganic ions and Volatile molecules	H^+, OH^-, HCO_3^-, CO_2, H_2,	influences many of the chemical and biological activities of soil
Mescellaneous	Auxins, scopoletin, hydrocyanic acid, glucosides, unidentified ninhydrin-positive compounds, unidentified soluble proteins, reducing compounds, ethanol, glycinebetaine, inositol and myo-inositol-like compounds, Al-induced polypeptides, dihydroquinone, sorgoleone	responsible for several functions like regulating growth and development of plant while some act as negatively for both plant and soil biota.

Compiled from Godheja et al., 2017; Kumar, et al., 2006; Dakora and Phillips, 2002.

Chemotaxis is a crucial mechanism for recruiting soil bacteria to the rhizospheric zone; it establishes the bacterial association with the plant's root (Parales and Ditty, 2018; Feng et al., 2021). The amount and concentrations of root exudates are dependent on the microbial activities in the rhizosphere which affect the root distribution/pattern and the availability of nutrients for uptake by the plant. The exudates that adhere to root surfaces induce chemotactic responses via methyl-accepting chemotaxis proteins (MCP), for example, McpA, McpB, McpC, TlpA, TlpB, TlpC, HemAT, YfmS, YvaQ, and YoaH (Feng et al., 2018). The MCP are bound to chemoreceptors (e.g., Tar, Tsr, Tap, Trg, and Aer in *E. coli*; Sourjik, 2004) in response to concentration gradients of amino acids, dipeptides, and sugars. The chemoreceptors are composed of a methyl-accepting (MA) domain, a cytosolic signaling domain, a HAMP (histidine kinase, adenyl cyclase, methyl-accepting chemotaxis protein [MCP] and phosphatase) linker (Aravind and Ponting 1999), and a ligand-binding domain (LBD), which is frequently located in the extracytoplasmic space and is responsible for extracellular binding compounds (Baker et al., 2006). The binding of the ligand to the LBD modulates the autophosphorylation of the histidine kinase CheA, which in turn transfers the phosphoryl groups to the response regulator CheY. The resulting CheY-Pinteracts with the flagellar motor to control cell swimming or tumbling that ultimately responsible for chemotaxis (Sourjik and Wingreen 2012).

2.2. Effect of soil physiological status on rhizobacteria and root exudates

Root exudate includes primary and secondary metabolites, enzymes, water, free oxygen, polysaccharides, and ions (Hayat et al., 2017). The nature and composition of root exudates are determined by various factors, including other micro-biota in plant roots, environmental factors, plant species, and their developmental stage (Doornbos et al., 2012; Hassan et al., 2019). Biotic factors, such as the uptake of root exudate by the microbes, influence the soil's physiological status. Plant roots are constantly exposed to an array of microbes and must interact and defend according to the type of biotic stress. It has also been demonstrated that plants release host-specific flavonoids in response to compatible rhizobia strains. Research evidence showed that microbes can modulate plant root exudation of proteins (De-la-Peña and Loyola-Vargas, 2014). The study of De-la-Peña and Loyola-Vargas (2014) established the compositions of proteins present in the root exudates varied depending on its microbial neighbor, and that the exudation of proteins by a given bacterium is modulated by the presence of a specific plant neighbor. The signaling between soil bacteria and plant roots is frequently based on root exudates eliciting variable responses from specific receptors. Chemical constituents of signaling molecules may reduce levels of one type of microorganism while attracting another. In fact, biological processes and nutrient availability to rhizobacteria are strongly affected by changes in soil chemistry. This could be a direct effect of signaling molecules, which for instance, could lead to resource competition (McNear, 2013). Competition among the subtypes in response to variation in chemotaxis to signaling molecules has been an essential factor in the colonization of roots. Rhizosphere acidification also plays a crucial role in determining the microbial environment. Bacteria are among the single-celled organisms most able to adapt to and thrive under harsh environmental pH conditions. The most sensitive component of the cell to pH changes is the protein (Hyyryläinen et al., 2001). Acidic soils are dominated by *Acidobacteria* and *Aphaproteobacteria* (Shen et al., 2019), while *Actinobacteria* abundance increases toward alkalinity (Jeanbille et al., 2016). Low rhizosphere pH increases phosphorus as well as those of micronutrients such as zinc, iron, and manganese availability in calcareous soils (Lei et al., 2015; Rengel, 2015). These alterations in nutrient content and the physical condition of the rhizosphere influence the habitat of PGPR.

3. Microorganisms to microorganisms: chemical properties of quorum sensing signaling molecules in rhizobacteria and their functions

3.1. Chemical properties of QS signaling molecules

Quorum sensing provides a significant competitive benefit to bacteria, increasing their probability of surviving while exploring difficult habitats. In bacterial communication, QS is related to the generation and release of signaling molecules into its rhizosphere, referred to as autoinducers (AIs). There are many QS network types; regulatory mechanisms result in the synthesis and expression of several signaling molecules, and their gene expressions have been reported by various workers (Papenfort and Bassler 2016; Rosier et al., 2018). The homoserine lactones signaling molecules range from those with short (C4-, C6-, and C8-) carbohydrate side chains to long (C12-, C14-, or even longer) side chains and can contain un-substituted groups in addition to OH- and oxo-C3-replaced compounds. Although AHLs are the ubiquitous AIs for Gram-negative bacteria, arrangements like AI-2 (furanosyl borate diester; alternative autoinducer), AI3, and quinolones (PQS) and a range of additional small compounds are recognized as signaling molecules (Effmert et al., 2012). A new group of Gram-negative bacteria signals (e.g., dialkylresorcinols and pyrones) that are mediatedby LuxR proteins werefound to be closely linked to the AHL-responsive LuxR family (Brameyer et al., 2015); however, it is not clear whether rhizobacteria release these signaling molecules.

Several bacteria identified from the rhizosphere are known to secrete QS signal molecules and interact withvolatile organic compounds (VOCs). For example, species of *Sinorhizobium, Pseudomonas*, *Burkholderia,* and *Rhizobium* are shown in Table 2, and the effect of QS on plant-microbe interactions is shown in Fig. 1. VOCs are presumed to play an important role in long-distance interaction within microbial populations, microbe-microbe, and plant-microbe associations within the rhizosphere (Bitas et al., 2013). VOCs have also been known to function as inter-and intra-species signals by affecting microbial function such as biofilm formation, stress tolerance, virulence, and gene expression (Audrain et al., 2015).

The diffusible signal factor (DSF) family (cis-2unsaturated fatty acids) is a group of QS signals in Gram-negative rhizobacterial species such as *Stenotrophomonas maltophilia* and *Burkholderia* spp. (Ryan et al., 2015). Interestingly, rhizobacterial DSF signaling molecules have also been shown to generate innate immunity in plants, thereby acting as inter-kingdom signal molecules (Kakkar et al., 2015). Furthermore, cyclic compounds such as diketopiperazines (DKZ) and 2-heptyl-3-hydroxy-4-quinolone (PQS) also have been reported as QS signaling molecules of pseudomonads (McKnight et al., 2000).

Various Gram-positive rhizobacterial root colonizers use peptides as QS signaling molecules; possibly, these molecules take part in interactions regulating inter- and intra-species functions (Monnet et al., 2016). Lipid compounds, namely 3-hydroxy-palmitate methyl ester (3OH-PAME) and cis-11-methyl- 2-dodecenoic acid (also referred to as diffusible signal factor or DSF), have been detected as QS-mediating molecules (Achari and Ramesh 2015). In Gram-positive bacteria, several incomplete cyclic peptides, butyrolactone, and AI-2, control various cellular activities and functions by perceiving the cell quantity. AI-2 was anticipated to be a “ubiquitous” QS signal in bacteria, but it might just be an exuded product of a common metabolic network of signaling (Winzer et al., 2002; Lyon and Novick 2004).

3.2. Functions and effect of bacterial signaling compounds in the rhizosphere

QS signaling molecules help rhizobacteria colonize plant-root surfaces or rhizospheric associated regions via QS-mediated gene expression (Rutherford et al., 2012; Nazzaro et al., 2013). The bacterial subfamily proteins LuxRs interact with small compounds and molecules but not with QS. The response of LuxRs to various plant signals involves a complex communal signaling mechanism (Venturi and Fuqua 2013; Gonzalez and Venturi 2013).

The interactions take place both outside and inside the plants (van der Burgh and Joosten, 2019). Quorum-imitating AHLs are synthesized and released in the vicinity by various plant species ranging from seedlings to mature plants (Teplitski et al., 2011). Based on differential proteome analysis, Mathesius et al. (2003) found that protein-related defense, stress, flavonoid metabolism, hormones, and several regulatory proteins were differentially expressed in plants treated with AHLs, indicating that AHLs modulate plant physiology. A recent study suggests that plants have the enzymatic machinery to degrade AHLs (Aziz and Chapman, 2020; Billot et al., 2020).

Researchers have reported the genes responsible for upregulation of auxin and downregulation of cytokinin and the ratio of auxin and cytokinin in a model plant inoculated with C6-homoserine lactone (C6- HSL) (von Rad et al., 2008); several workers have proposed the dual functions of AHL signaling molecules in *Arabidopsis thaliana* (Hartmann and Schikora, 2012; Schenk et al., 2012). The first study reporting the impact of AHLs on root biology was published ten years ago (Ortiz-Castro et al.2008). Short acyl chain AHLs, such as C4 or C6, was demonstrated to enhance plant growth rate, primarily in elongating the roots (Bai et al., 2012; Schenk et al., 2012), in contrast to signaling molecules with longer acyl chains (e.g., C12 or C14). Hartmann et al. (2014) examined the effect of AHLs on plant growth and found it was more complicated as the interactions may be very specific. For example, root nodulation in *Medicago truncatula* was increased by the production of long-chain 3-oxo-C14-HSL by *Sinorhizobium meliloti* (Veliz-Vallejos et al., 2020). Interestingly, the increased nodule number occurred only after a treatment with 3-

oxo-C14-HSL, which is the main AHL component of *S. meliloti.* but when treated with other AHLs, there was no effect. Whereas, in *Vigna radiate* only 3-oxo-C10-HSL induced adventitious roots but not the unsubstituted C10-HSL or C12-HSL (Bai et al., 2012).

Several plant genes were upregulated, related to secondary metabolism (e.g., phenols), which resulted in a pathogen challenge. Consequently, those plants amass phenolic and callose compounds (Schenk and Schikora 2015), indicating the effect of QS molecules of the AHL group on plant physiology and its importance in developing stress tolerance regulations in plants against stressors (Fig. 1).

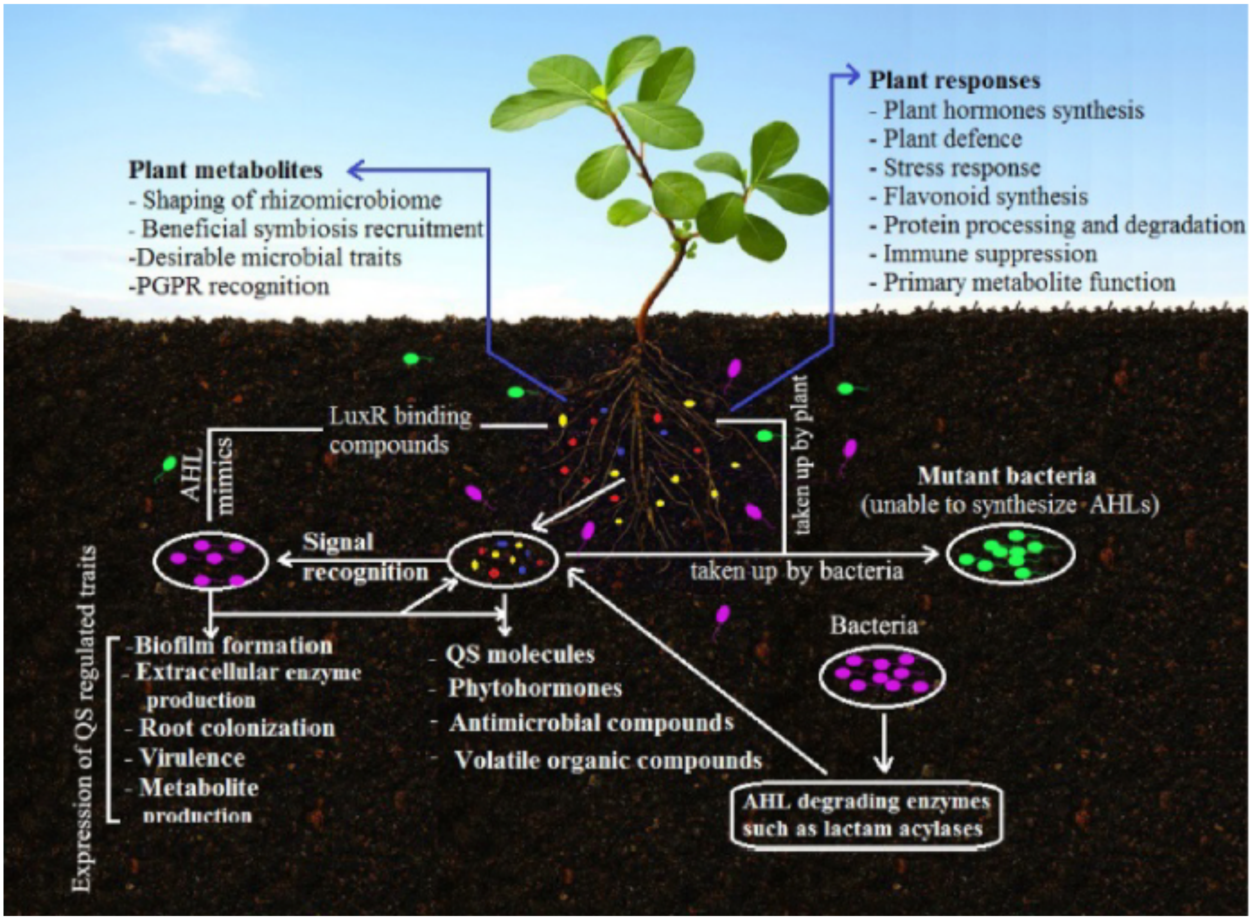

Fig. 1. Role of quorum sensing in plant-microbe interaction: Their impact and importance in developing stress tolerance in plants against stressors.

Table 2: PGPR and the signaling molecules

PGPR	Signaling molecules	References
S. meliloti Rm1021	C14-HSL	Chen et al., 2003
	3-Oxo-C14-HSL	Teplitski et al., 2003
	C16:1-9 cis-(L)-HSL	Marketon et al., 2002
	C18-HSL	Marketon et al., 2002
	C12-HSL	Marketon et al., 2002
S. meliloti AK 631	C10-HSL	Teplitski et al., 2003
S. meliloti Rm41	C8-HSL	Marketon et al., 2002
	3-Oxo-C8-HSL	Teplitski et al., 2003
	C16-HSL	Teplitski et al., 2003
Agrobacterium vitis	C14:1-9-cis-(L)-HSL	Li et al., 2005
Agrobacterium vitis	3-Oxo-C16:1-11cis- (L)-HSL, long-chain AHLs	Hao and Burr, 2006
Pseudomonas aeruginosa	C4-HSL	Pearson et al., 1995
P. aeruginosa	3-Oxo-C12-HSL	Pearson et al., 1994
Sinorhizobium meliloti AK 631	C6-HSL	Teplitski et al., 2003
Ochrobactrum sp. Pv2Z2	3O-C7-HSL; 3OHC7-HSL	Imran et al.,2014
Burkholderia cepacia	C8HSL	Antunes et al., 2010
Burkholderia pseudomallei	C8HSL, C10HSL, OHC8HSL, OHC10HSL,3OC14HSL, C8HSL, 3OHC8HSL, 3OHC10HSL	Antunes et al., 2010
Sinorhizobium meliloti	C14HSL to C18HSL	Marketon et al., 2002
Rhizobium leguminosarum	OHC6HSL, 3OC6HSL, C7HSL, 3OHC14HSL	Antunes et al., 2010
Erwinia carotovora	3OC6HSL	Antunes et al., 2010
Bacillus cereus	Peptide PapR	Van Delden et al., 1998
Staphylococcus aureus	Autoinducing peptide	Grenha et al., 2013
Burkholderia sp.	cis-11-Methyl-2-dodecenoic acid diffusible signal factor (DSF); N-acyl-L-HSL; N-(3-oxoacyl)-LHSL; N-(3-hydroxyacyl)-L-HSL	Schmid et al. (2012), Chapalain et al. (2013), Suppiger et al. (2013), and Ryan et al. 2015
Mesorhizobium Huakuii	C8-HSL	Wang et al. (2004) and Braeken et al. (2008)
Stenotrophomonas Maltophilia	cis-11-Methyl-2-dodecenoic acid diffusible signal factor (DSF)	Alavi et al. (2013); Ryan et al. (2015)
Bacillus subtilis	Peptides	Duanis-Assaf et al. (2016)
Ochrobactrum sp. Pv2Z2	3O-C7-HSL; 3OHC7-HSL	Imran et al. (2014)
Pseudomonas aeruginosa	N-(3-Oxododecanoyl)-homoserine lactone (OdDHL); N-butyrylhomoserine lactone (BHL); 2-heptyl-3-hydroxy-4- quinolone (PQS); 2-(2-hydroxyphenyl)-thiazole-4- carbaldehyde (IQS)	Lee and Zhang (2015)
Pantoea agglomerans YS19	N-3-Oxooctanoyl-L-homoserine lactone	Jiang et al. (2015)
Pseudomonas sp.	N-Acyl-L-HSL; N-(3-oxoacyl)-LHSL; N-(3 hydroxyacyl) - L-HSL; 2-heptyl-3-hydroxy-4-quinolone (PQS)	Williams and Camara (2009) and Hartmann and Schikora (2012)
Acinetobacter sp.	N-Acyl-L-HSL; N-(3-oxoacyl)-LHSL; N-(3-hydroxyacyl)-L-HSL	Atkinson and Williams (2009)
Pseudomonas fluorescens	3-OH-C6-HSL;3-OH-C7-HSL; 3-OH-C8-HSL; 3-OH-C10-HSL, C 6-HSL, C8-HS	Khan et al. (2005)
Rhodopseudomonas sp.	N-(p-Coumaroyl)-HSL; R = OH (pC-HSL)	Atkinson and Williams (2009)
Rhizobium sp.	N-Acyl-L-HSL; N-(3-oxoacyl)-LHSL; N-(3-hydroxyacyl)-L-HSL	Sanchez-Contreras et al. (2007)
Bradyrhizobium sp.	N-(p-Coumaroyl)-HSL; R = OH (pC-HSL)	Sanchez-Contreras et al. (2007)
Sinorhizobium Meliloti	C14HSL to C18HSL, 3-Oxo-C16	Marketon et al., 2002; Mathesius et al. 2003 and Hartmann et al. (2014)
Mesorhizobium huakuii	C8-HSL	Wang et al. (2004) and Braeken et al. (2008)
Bacillus subtilis	Peptides	Duanis-Assaf et al. (2016)
Pantoea agglomerans YS19	N-3-Oxooctanoyl-L-homoserine lactone	Jiang et al. (2015)
Serratia plymuthica HRO-C48	3-Oxo-C6	Pang et al. (2009)
Gluconacetobacter diazotrophicus PAL5	C6-, C8-, C10-, C12-, C14-HSL; 3-oxo-C10-, C12-, C14-HSL	Nieto-Penalver et al. (2012)
Prevotella intermedia	AI-2	Frias et al., 2001
Pseudomonas aeruginosa	OdDHLg	Wilder et al., 2009
Vibrio campbellii	AI-2, OH-BHLg, CAI-1	Defoirdt et al., 2008
Vibrio harveyi	CAI-1, AI-2, OH-BHLg	Defoirdt et al., 2008
Vibrio salmonicida	AHL	Bruhn et al., 2005
Vibrio vulnificus	AI-2	Kim et al., 2003
Porphyromonas gingivalis	AI-2	Frias et al., 2001
Photobacterium Phosphoreum	OH-OHLg	Flodgaard e al., 2005
Fusobacterium Nucleatum	AI-2	Frias et al., 2001
Erwinia amylovora	AI-2	Mohammadi and Geider, 2007
Burkholderia vietnamiensis	HHLg	Poonguzhali et al., 2007
Aeromonas salmonicida	BHL and HHLg	Bruhn et al., 2005

3.3. Inter- and intra-species signaling and signal interference

Upon identifying the signaling molecules at a particular concentration, transcription of specified genes directed by this mechanism is stimulated in the rhizobacteria. Several rhizobacterial mechanisms are controlled by the QS signals, which involve DNA transferase by siderophore production, biofilm formation, bioluminescence, conjugation, and stimulating potential of some rhizobacteria, often known as "swarming" (Barriuso et al., 2008b; Bramhachari, 2019). These signals can also be engineered in plants on trans-kingdom level in order to control gene expression in rhizospheric bacteria (Geddes et al., 2019).

The production of AHLs by diazotrophs such as *Rhizobium leguminosarum* suggests QS promotes signaling in the mature nodule (Daniels et al., 2002). Moreover, it is hypothesized that QS also affects rhizobacterial flow linked with host plants. For example, flavonoids produced by legumes enhance synthetic AHL gene' expression in rhizobia (Perez-Montaño et al., 2011). As anticipated, signaling among various microbes also occurs and certainly has consequences for plant-microbe interactions. During interspecies interaction, AIs secreted by any species can alter the behavior of its competitors. AHLs are also reported to act as interkingdom signaling molecules that affect plant gene expression, initiate systemic plant resistance, and influence plant growth (Venturi and Fuqua 2013) (Fig. 2). The process of hindrance in QS signaling is termed quorum quenching (QQ) (Lareen et al., 2016a,b). Plants can use several approaches to avert bacterial QS signaling, including the inhibition of AI biosynthesis and/or secretion, enzymatic degradation of these molecules, and disruption of their binding, receptors, and regulator site (Koh et al., 2013) (Fig. 2). For instance, plants produce cytokinins and IAA that affect QS. Beneficial bacteria can also protect plants by interfering with QS that disrupts pathogen signaling and plant colonization. For instance, microbes may utilize enzymes like acylase and lactonase, which degrade AHLs or release VOCs that impede bacterial AHL production (Hong et al., 2012; Aziz and Chapman, 2020).

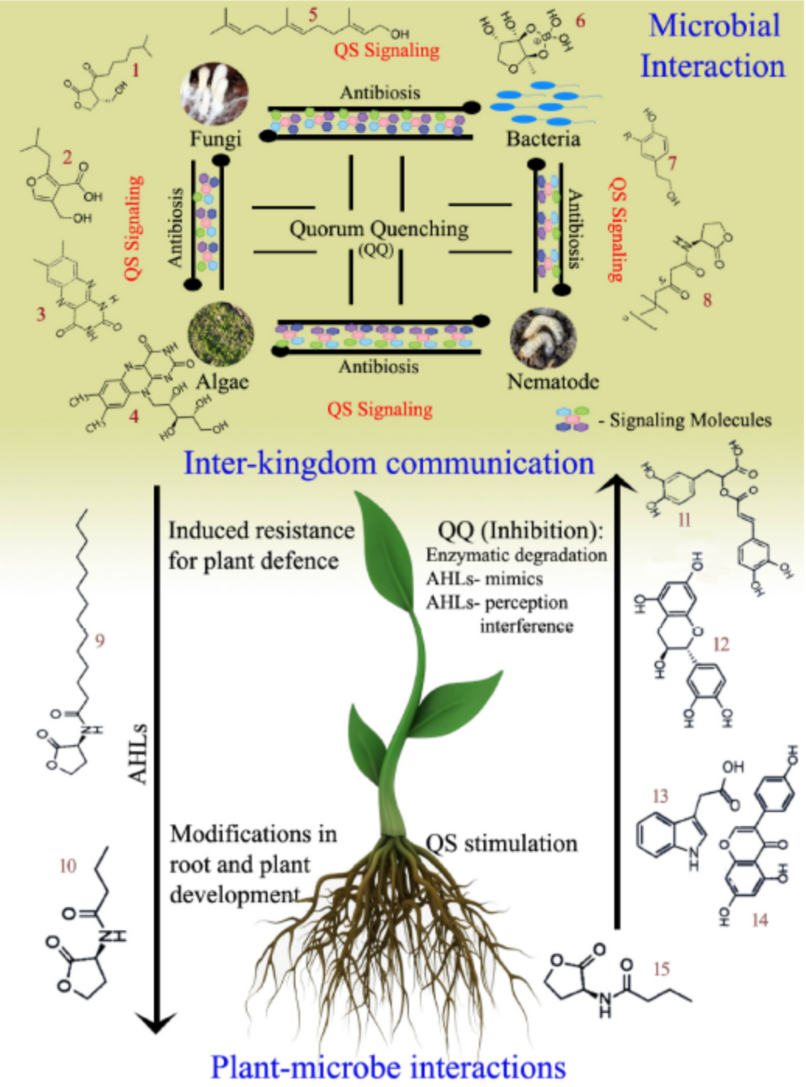

Fig. 2. Interkingdom communication between microbe-microbe and Plant-microbe interactions. Various microbes dwelling in the soil like fungi, bacteria, algae, and nematodes, etc. releases several quora sensing molecules (**1**-A-factor; **2**- MMF1; **3**- lumichrome; **4**- riboflavin; **5**- farnesol; **6**-AI-2; **7**-tyrosol; **8**–3′-O-C6-HSL = AI-1) between species including antagonist molecules to surpass in a competitive situation. Moreover, microbes also show interference between competitors via the quorum quenching (QQ) mechanism. Molecules like N-acyl homoserine lactones (AHLs) are used for both intraspecies and interkingdom communication (**9**- C14- HSL6, for plant defense; **10-** C14-HSL1, for plant development). Sometimes, plants produce molecules for interfering with bacterial QS signaling by reducing AHL interactions (**12**- genistein) or by mimicking AHL (**11**- rosmarinic acid). Plants may also activate microbial QS (**13**- IAA; **14**- D-(+)-catechin).

3.4. Biofilm formation through signaling by rhizobacteria

Biofilm formation under various stress conditions is an effective technique used by bacterial strains to ensure their survival in the plant rhizosphere. Rhizospheric biofilms can be both beneficial and pathogenic. The natural QS-driven beneficial biofilms that occur in rhizosphere suppress the plant pathogens and can be used as biocontrol agents, an alternative to chemicals (Harjai and Sabharwal, 2017). Pérez-Montaño et al. (2014) examined the bacterial surface components, especially mucopolysaccharides, and revealed that the formation of biofilm allows rhizobacteria to colonize their vicinity and remain vital under ecological stresses such as nutrient limitation and drought. This condition is often crucial for regular existence in bacteria of the genera *Bradyrhizobium*, *Mesorhizobium*, *Rhizobium,* and *Sinorhizobium.* For example, biofilm production makes the conditions more favorable for root inhabitation and symbiosis among *Glycine max* cv *Osumi* and *Sinorhizobium fredii* SMH12. In *S. fredii*, nod gene-stimulating flavonoids and the NodD1 protein are responsible for developing the biofilm configuration from monolayer to microcolony. The expression of the *NodD1* gene has been linked to flavonoids production, which induced specific QS regulations of the symbiotic biofilm (Pérez-Montaño et al., 2014). Paungfoo-Lonhienne et al. (2016) established the function of QS in the inhabitation and formation of biofilm by Burkholderia Q208, a PGPR of Australian sugarcane; it was found to have an extremely conserved QS regulation, designated BraI/R, programmed by three genes (braI, rsaL and braR) for synthesis of, and reaction to, N-AHLs. In the biofilm formation by Burkholderia, rsaL and braR are downregulated while braI is upregulated (twofold).

4. Microorganisms to plants signaling: quorum sensing in plant growth-promoting rhizobacteria

AHLs have been reported to contribute as signaling molecules in inter-species communication among rhizobacteria (Bukhat et al., 2020). Nevertheless, there is a dearth of knowledge regarding inter-species communication in the natural habitat of microbes. Recent studies also found that these bacteria produce the cyclodipeptides cyclo (L-Pro-LVal), cyclo (L-Pro-L-Phe), and cyclo (L-Pro-L-Tyr), which modulates auxin-responsive gene expression in roots (Ortiz-Castro et al., 2020). Mathesius et al. (2003) reported the root exudates of *Medicago truncatula* contained substances that mimic a AHL function that regulate AHL-regulated response in bacteria. The chemical constituent of such active QS-acting signaling molecules is not yet characterized and requires further study (Chen et al., 2002; Podile et al., 2013). A recent hypothesis reveals that alkamides and N-acylethanolamines (NAEs) are excellent candidates to act as AHL mimics, regarding their structural, chemical identity (Aziz and Chapman, 2020). Expression of QS appeared to be based not only on signaling molecules but also on the bacterial population density (Papenfort and Bassler, 2016).

As QS is used in the communication between a plant with its rhizobacteria, only a low concentration of the primary inoculum of PGPR is needed to promote plant growth (Persello-Cartieaux et al., 2003). The most effective PGPR inoculation was expected in organic and mineral poor soils or stressed soils, when development of the resident microflora was inhibited. This research was evaluated by using mathematical modeling and computer-based simulations (Strigul and Kravchenko et al., 2006). Particularly under field conditions, inoculation is not always successful due to the low survival rate of the inoculum. The balancing mechanism of QS and AIs may permit endophytic isolates to communicate with other linked endophytes and plant hosts, thus protecting mutualistic associations and habitat inside the plant tissues. PGPR can respond to QS-similar signaling molecules released by plants and other rhizospheric bacteria and even inactivate the QS signaling molecules released by other rhizobacterial species (Dong et al., 2002). For example, *Bacillus* releases various enzymes to inactivate or cleave the AHL produced by other Gram-negative bacteria. The AHL-cleaving enzyme, *aiiA*, allows *Bacillus* strains to break the lactone bond of AHLs through hydrolysis, expressing a procedure for an autoinducer-cleaving activity that permits these bacteria to co-exist with other Gram-negative bacteria (Lee et al., 2002). Therefore, the rhizobacteria's role can be directly or indirectly altered by plants and other microbial community members via QS signaling molecules (Podile et al., 2013).

4.1. QS and its role in regulating plant response

Besides regulating microbial functions, the QS molecules secreted by PGPR also evoke plant responses that are beneficial to those host plants (Kusari et al., 2015). For instance, plants may respond more adeptly to biotic alterations when exposed to QS molecules (Lareen et al., 2016a,b; Schenk and Schikora et al., 2016). AHLs can alter plant physiology; when treated with N-(butanoyl)-L-homoserine lactone (C4-HSL) and N-(hexanoyl)-L-homoserine lactone (C6-HSL), the auxin/cytokinin ratio in *Arabidopsis thaliana*was altered which affected the root growth (von Rad et al., 2008).The dual function of AHLs in *Arabidopsis thaliana* has been examined; the short acyl chain AHLs enhance the growth rate and primary root elongation, whereas the long acyl chain AHLs, such as N-(tetradecanoyl)- L-homoserine lactone (C14-HSL) or N-(dodecanoyl)-L-homoserine lactone (C12-HSL) stimulate pathogen resistance (Palmer et al., 2014). This process is called the AHL-priming or AHL-induced resistance method (Fig. 2). Additionally, the effect of AHLs may vary among plant species. The response of plants to AHLs depends on AHL structures, the amount released and plant species. As already indicated, AHLs can stimulate plant pathogen resistance, and jasmonic acid/salicylic acid-dependent pathways were suggested as part of this response (Schenk and Schikora, 2015). In addition to causing changes in plant's physiological and stimulation of pathogen resistance, QS bacterial compounds also evoke the formation and secretion of compounds that imitate bacterial QS molecules in their effects on plants (Fig. 2) (Teplitski et al., 2000; Corral-Lugo et al., 2016; Hartmann et al., 2014; Pérez-Montaño et al., 2013). AHL imitates and regulates QS at several levels, particularly inducing or repressing the AHL receptor of bacteria involved in symbiotic or pathogenic associations with their host plants (Rasmussen and Givskov, 2006). A study also concluded that a plant secreted rosmarinic acid when infected by *Pseudomonas aeruginosa.* The natural ligand of the bacterial QS activator RhlR induces QS-mediated biofilm formation and secretion of virulence factors. Thus, rosmarinic acid was released as a plant defense mechanism to impede QS by *P. aeruginosa* and thus reduced its pathogenicity (Corral-Lugo et al., 2016). In addition, D-(+)-catechin impedes the recognition of C4-HSL negatively via RhlR of *P. aeruginosa,* leading to a reduction in the secretion of QS signals and virulence factors (Vandeputte et al., 2010).

4.2. Examples of QS in endophytes

Endophytes are often documented in enhancing plant defense mechanisms by quorum-averting methods. Intriguingly, endophytes are frequently observed to have a QS mechanism that facilitates their colonization of host plants and thwarts plant pathogens (Khare et al., 2018). For example, *Burkholderia phytofirmans* strain PsJNT is reported to enhance endophytic association with various plants and promote a favorable plant-rooting structure with enhanced vascular arrangements, an improved quantity of phytohormones and chlorophyll, and provides resistance to phytopathogens. It was documented to exude a quorum autoinducer, i.e., 3-hydroxy-C8-homoserine lactone (Sessitsch et al., 2005). *Serratia plymuthica*, with extensive biological control ability, was reported as retaining copious amounts of homoserine lactone (HSL), videlicet, C4-HSL, C5-HSL, C6-HSL, C7-HSL, C8-HSL, and 3-hydroxy derivatives (3-hydroxy-C6-HSL, 3-hydroxy-C8- HSL), and 3-oxo derivatives (3-oxo-

C6-HSL, 3-oxo-C7-HSL, 3-oxo-C8 HSL) (Liu et al., 2011). *Pantoea agglomerans*, the olive plant epiphyte, and an endophyte (*Erwinia toletana*) associated with olive knot infection were found to secret signals similar to AHLs. This study is an example of tripartite associations among plants and associated microbes (Hosni et al., 2011). The genome sequencing of endophytic *Gluconacetobacter diazotrophicus* PAL5 associated with *Saccharum officinarum* showed the mechanism of QS and recognition of five AHLs, namely C6, C8, C10, C12 and C14-HSL (Nieto-Penalver et al., 2012). Dourado et al. (2013) described the misuse of quorum signaling molecules for *Methylobacterium* interaction with plants. A gene sequence was modified in plants and *Methylobacterium,* simultaneously initiating symbiotic interaction and colonization, showing the mutualistic association on QS mechanisms.

5. The role of quorum sensing signaling molecules in agriculture

The growing demand for food and the concern related to food quality are leading to the demand for novel and effective sustainable agricultural practices. PGPR is one of the most promising tools used in the agricultural industry. These beneficial microorganisms can act as biofertilizers to promote plant growth and stress tolerance, as well as combat plant pathogens. They boost plant resistance to infections via ISR and SAR. PGPR are an effective, sustainable, and environmentally friendly alternative to chemical fertilizers to be used in agriculture. For example, the use of nitrogen-fixing rhizobia (e.g., *Sinorhizobium meliloti*), with enhanced release of specific AHLs, might increase bacterial benefits and improve plant species effects not linked with specific strains (Zarkani et al., 2013; Hernandez-Reyes et al. 2014).

During the infection period, QS molecules direct the bacterial potential to produce biofilms and other density-regulated traits. Those molecules participate in the crucial role of QS among plant and bacterial cells. Several researchers have reported the role of QS molecules in controlling plant disease and the transmission of phytopathogens. Barriuso et al. (2008a) documented AHLs QS signaling compounds' functions in promoting plant growth and enhancing defense against salt stress. Johnson and Walcott (2013) documented that *Acidovorax citrulli* transformed from saprobic to pathogenic growth, causing bacterial fruit blotch (BFB) from seed-to-seedling in cucurbits; they concluded that QS was involved in the regulation of this transition. The role of QS in regulating genes was involved in the transmission of BFB to seedlings. Alavi et al. (2013) documented the DSF QS system's function in regulating the progressive impact of *Stenotrophomonas maltophilia* on plants. Oilseed rape seeds modified with the wild-type strain showed a significant improvement in growth rate compared to those coated with the mutant that lacks the gene rpfF for the regulation of DSF. They concluded that the QS molecule DSF is responsible for directing phenotypes in pathogenic Stenotrophomonas. Zúniga et al. (2013) reported the importance of AHLs in mediating QS in well-organized colonization of Arabidopsis thaliana and the coordination of beneficial interactions using suitable mutant strains of Burkholderia phytofirmans PsJN. These researchers also concluded that rhizobacterial reduction of the auxin indole-3-acetic acid (IAA) participates in promoting plant growth characters and is important for successful root inhabitation. A recent study supports that the critical role of auxin degradation by enzymes encoded in bacterial operons to modulate the behavior of synthetic bacterial communities and affect root growth have been examined (Finkel et al., 2020). Moreover, Jiménez-Vázquez (2020) demonstrated that an Achromobacter strain drives discrete root movements interfering with auxin transport and gravitropism. In addition, the interruption of QS via quorum quenching offers an interesting strategy to combat bacterial pathogens in agriculture. The use of enzymatic degradation of AHL have been reported to reduce the virulence of several plant pathogens (Rodríguez et al., 2020; Helman and Chernin, 2015; Faure and Dessaux, 2007).

6. Conclusions

Significant advances in understanding chemical signaling associated with plant-microbe interactions have contributed to clarifying the mechanisms involved in their associations. In this review, we have summarized the chemical signaling in the rhizosphere, the role of QS molecules in plant-microbe and microbe-microbe interactions, and their potential applications in agriculture. Investigation of symbiotic relationships provided valuable knowledge for the understanding of plant and microbe chemical signaling. However, in order to provide functional knowledge regarding the role of plant-microbe interaction, molecular entities involved in both plant and microbe signals must be interconnected. Moreover, each biological system's distinctiveness needs to be examined in depth as the interactions between specific signaling molecule and their targets are highly complex and difficult to generalize. There is a knowledge gap in rhizospheric signaling that require further research and scientific attention. A better understanding in the metagenomic of the rhizosphere would provide further insight into the interactions of rhizobacteria and the host plants. Currently, only a small percentage of the genomes of rhizobacteria have been sequenced. A better understanding of QS molecules and the QQ process would also help to develop novel strategies for agriculture in future.

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Declaration of competing interest

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