Quorum Sensing in Plant Growth-Promoting Rhizobacteria and Its Impact on Plant-Microbe Interaction

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Abstract

Quorum sensing is a widespread mechanism in enormous number of bacteria for regulating various gene expression in a cell density-dependent manner through production and recognition of small molecules known as autoinducer. Diverse kinds of quorum-sensing networks are found in different bacterial species. Among various signal molecules, acyl homoserine lactone (AHL) signal molecules are the most and widely studied in bacteria. A number of simple to advanced techniques are being used to identify and characterize signal molecules. Production of signal molecules in a number of rhizospheric bacteria is documented. Rhizosphere is an active atmosphere where microbe-microbe and microbe-plant interaction is highest due to rich availability of nutrients provided in the form of root exudates. Several ecological and interdependent key characters of bacteria, like antibiotic, siderophore, or enzyme secretion, virulence factors of phytopathogens, as well as plant-microbe communications, are coordinated through quorum sensing (QS). In this chapter, we have provided brief fundamental aspects of quorum sensing and then addressed the recent trends on the significance of quorum sensing and signal molecules in microbe-microbe and microbe-plant interactions in the rhizosphere with special reference to plant growth-promoting rhizobacteria and plant health.

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16.1 Introduction

Since ages, scientist believed that the single cell prokaryotic bacterium lacking true nucleus is not capable of establishing a fundamental form of community attitude as a consequence of chemical conversation between the members of a community. Interdependent behavior by means of autoinducer compounds was first discovered in bacteria which are living in symbiotic association with a marine squid (Kaplan and Greenberg 1985; Verma and Miyashiro 2013). The fundamental part of this molecular conversation, termed as "quorum sensing" (QS), and the signaling molecules implicated were established through an extremely basic test: via adding together a formally habituated supernatant of a heavily developed bacterial culture to a fresh, low concentration culture, the characteristics of the high density culture were conferred (Eberhard 1972; Waters and Bassler 2005). The signaling compounds implicated in this conversation are called as "autoinducers," as they were derived from within the bacterial cell and controlling their individual expression. The signaling compound can be perceived and reimported into these cells, consequently permitting the whole inhabitants to react to altering situation/necessities once a significant volume (equivalent to a particular cell density) or "quorum," i.e., the minimum number of bacterial cell accumulated in a given volume to make the "decision" to switch on gene expression of QS-regulated genes, is achieved as described by Ahmad et al. (2011).

The marine bacterium *Vibrio fischeri* was the first bacterium to be examined for quorum sensing. As a communication compound, N-(3-oxo)-hexanoyl-L-homoserine lactone (3oxoC6-HSL) was recognized to regulate bioluminescence as a readily assessable result of supportive action. Currently, numerous chemical signaling compounds of bacterial origin have been recognized. AHL served as a universal signal molecule within Gram-negative bacteria (Galloway et al. 2011). Molecules of AHL are created by *LuxI* homologues, and comprise, clearly with *LuxR* homologues, a transcriptional regulator. AHL comprises a conserved homoserine lactone ring with an uneven N-acyl chain (Ahmad et al. 2008). Bacteria belonging to both Gram-positive and Gram-negative groups use QS messaging pathways to control a different group of physiological behavior of bacterial cells which includes symbiosis, competence, virulence, antibiotic production, conjugation, motility, sporulation, and biofilm formation (Rutherford and Bassler 2012).

Universally, Gram-negative bacteria utilize acylated homoserine lactones as autoinducers, and Gram-positive bacteria exploit processed oligopeptides for interaction (Miller and Bassler 2001). Commonly studied autoinducer signals are N-acyl homoserine lactones (von Bodman et al. 2003), although half a dozen of other molecules, including diketopiperazines, 4-hydroxy-2-alkylquinolines (HAQs), and

autoinducer-3 (AI-3) in various Gram-negative bacteria (Jimenez et al. 2012), furanosyl borate diester in *Vibrio harveyi* (Chen et al. 2002), and c-butyrolactone in *Streptomyces*, have also been involved in quantity-based signaling (Yamada and Nihira 1998). While quorum-sensing peptides (QSPs) are especially reported from Gram-positive bacteria (Wynendaele et al. 2013), autoinducer-2 (AI-2) has been reported from both Gram-positive and Gram-negative bacteria (Pereira et al. 2013). Recently, Papenfort and Bassler (2016) have reviewed these aspects in much detail.

Various procedures and protocols used for finding and depiction of signal molecules are described by several authors as compiled by Rumbaugh (2011). Many simple techniques such as bioassays and chemical techniques such as thin-layer chromatography (TLC) and chromatographic and spectroscopic methods are regularly employed for recognition and classification of signal molecules (Gonzalez and Keshavan 2006; Kendall and Sperandio 2007). Fascinatingly, secretion of quorum-sensing interfering (QSI) molecules by eukaryotic microbes has created huge curiosity within the researchers because such molecules are capable of influencing the bacterial signaling system positively or negatively. In contrast, production of structural homologues to the many QS signal compounds has resulted in the improvement of additional QSI molecules that can be employed to manage pathogenic bacteria. Additionally, the construction of transgenic plants to facilitate the expression of bacterial QS genes until now is an effective approach to meddle with bacterial activities (Fray 2002; Hartmann and Schikora 2012).

The rhizosphere comprises an elevated amount of AHL-secreting bacteria in comparison to bulk soil, signifying their position in colonization (Elasri et al. 2001). This advocates that plants might be employing root-exuded molecules in the rhizosphere to obtain benefit of this bacterial information structure and control colonizing populations (Lugtenberg and Kamilova 2009; Lopez-Raez et al. 2012). Exudates from pea seedlings comprise compounds that impersonate components of QS molecules which advocate that plants are capable of selecting their microbial colleagues (Teplitski et al. 2000; Fatima et al. 2010). Perez-Montano et al. (2013) documented that *Oryza sativa* and *Phaseolus vulgaris* roots and seeds secrete molecules which exclusively meddle with the capability of plant-associated bacteria to develop biofilms, a crucial feature for bacteria-eukaryotic host communication. Plant host species have developed responses to AHLs. *Medicago truncatula* on contact to a broad concentration series of AHLs responded with a primary decline in different protein volume followed by increase of the same proteins afterward (Mathesius et al. 2003; Hartmann and Schikora 2012). A number of these proteins involved members of cytoskeleton structure/function, defense/stress response, isoflavone production, and metabolic enzyme families. This presents an interesting area of research as to how bacteria communicate among themselves and how plants have developed mechanisms to react to these signal compounds.

In the recent past, many articles and scientific literature have been published on the specific and general aspects of quorum sensing in plant pathogens and beneficial rhizobacteria (Singh et al. 2012; Hartmann and Schikora 2012; Hartmann et al. 2014; Kalia 2015; Schikora et al. 2016). In this chapter, we have reviewed extensive and updated literature to address the role of quorum sensing in plant

growth-promoting rhizobacteria (PGPR), possible interaction mechanisms, and signaling in the rhizosphere relative to plant-microbe interaction.

16.2 Diversity of Quorum-Sensing Signal Molecules and Its Detection

Various types of quorum-sensing network, its regulatory mechanism involved in production of signal molecules, and gene expression have been reviewed by various workers (Atkinson and Williams 2009; Papenfort and Bassler 2016) and are not the subject for discussion of this chapter. However, we have briefly summarized here important aspect. Among different Gram-negative bacteria, biosynthesis of N-acyl homoserine lactones (HSL) takes place in several deviations of the molecular structure. The range of HSL molecules varies from short (C4-, C6-, and C8-) carbohydrate side chains to long (C12-, C14-, or even longer) side chains and consists of unsubstituted in addition to OH- and oxo-C3-substituted compounds. Despite the fact that HSLs are the universal autoinducers in Gram-negative bacteria, arrangements like AI-2 (alternative autoinducer; furanosyl borate diester), AI3, and quinolones (PQS) and a range of extra minute compounds are known as signaling molecules (Effmert et al. 2012). Additionally, lipid compounds, like cis-11-methyl-2-dodecenoic acid (also called as diffusible signal factor or DSF) (Wang et al. 2004a) and 3-hydroxy-palmitate methyl ester (3OH-PAME) (Flavier et al. 1997), have been recognized as QS-mediating molecules. Moreover, cyclic compounds, such as 2-heptyl-3-hydroxy-4-quinolone (PQS) and diketopiperazines (DKZ), also have been recommended as QS signals of *Pseudomonads* (Holden et al. 1999; McKnight et al. 2000). In Gram-positive bacteria, a range of incomplete cyclic peptides, AI-2 and butyrolactone, control cellular functions and activities via perceiving the cell quantity. AI-2 was anticipated as a "universal" QS indicator in bacteria, but this task is still uncertain since it might just be a secreted product of a common metabolic network (Folcher et al. 2001; Winzer et al. 2002; Lyon and Novick 2004). Diverse types of quorum-sensing molecules and their corresponding producing bacteria are presented in Table 16.1.

Cell-to-cell communication between rhizosphere microbes probably takes place universally since several strains obtained from the rhizosphere have been documented to produce QS signals. For instance, it has become evident that a diversity of proteobacterial rhizosphere isolates secrete and/or react to N-acyl homoserine lactone (AHL) QS signals, together with strains associated to species or genera of *Pseudomonas chlororaphis*, *Pseudomonas putida*, *Pseudomonas syringae*, *Burkholderia*, *Serratia*, *Erwinia*, and *Ralstonia*, in addition to rhizobial species (Ferluga et al. 2008). AHLs have also developed to work as interkingdom messenger molecules affecting plant gene interpretation, the initiation of systemic plant resistance, and influencing plant growth and development (Venturi and Fuqua 2013). In recent times, new categories of signals (e.g., pyrones and dialkylresorcinols) secreted by Gram-negative bacteria have been revealed which are predicted by *LuxR* proteins and found to be strongly connected to the AHL-responsive LuxR

Table 16.1 Signal molecules of common PGPR

PGPR	QS network	Major signal molecules	References
Acinetobacter sp.	AHL	N-Acyl-L-HSL; N-(3-oxoacyl)-L-HSL; N-(3-hydroxyacyl)-L-HSL	Atkinson and Williams (2009)
Pseudomonas fluorescens	-Do-	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)
P. fluorescens CHA0	Non-AHL QS signal compounds		Kay et al. (2005)
Pseudomonas sp.	-Do-	N-Acyl-L-HSL; N-(3-oxoacyl)-L-HSL; N-(3-hydroxyacyl)-L-HSL; 2-heptyl-3-hydroxy-4-quinolone (PQS)	Williams and Camara (2009) and Hartmann and Schikora (2012)
Pseudomonas aeruginosa	-Do-	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)
Rhodopseudomonas sp.	-Do-	N-(p-Coumaroyl)-HSL; R = OH (pC-HSL)	Atkinson and Williams (2009)
Rhizobium sp.	-Do-	N-Acyl-L-HSL; N-(3-oxoacyl)-L-HSL; N-(3-hydroxyacyl)-L-HSL	Sanchez-Contreras et al. (2007)
Bradyrhizobium sp.	-Do-	N-(p-Coumaroyl)-HSL; R = OH (pC-HSL)	Sanchez-Contreras et al. (2007)
Sinorhizobium meliloti	-Do-	3-Oxo-C16	Mathesius et al. 2003 and Hartmann et al. (2014)
Mesorhizobium huakuii	-Do-	C8-HSL	Wang et al. (2004b) and Braeken et al. (2008)
Bacillus subtilis	LuxS	Peptides	Duanis-Assaf et al. (2016)
Pantoea agglomerans YS19	AHL	N-3-Oxooctanoyl-L-homoserine lactone	Jiang et al. (2015)
Stenotrophomonas maltophilia	Diffusible signal factor (DSF)	cis-11-Methyl-2-dodecenoic acid diffusible signal factor (DSF)	Alavi et al. (2013)
			Ryan et al. (2015)
Burkholderia sp.	Diffusible signal factor (DSF)/AHL	cis-11-Methyl-2-dodecenoic acid diffusible signal factor (DSF); N-acyl-L-HSL; N-(3-oxoacyl)-L-HSL; N-(3-hydroxyacyl)-L-HSL	Schmid et al. (2012), Chapalain et al. (2013), Suppiger et al. (2013), and Ryan et al. 2015
Ochrobactrum sp. Pv2Z2	AHL	3O-C7-HSL; 3OHC7-HSL	Imran et al. (2014)
Serratia plymuthica HRO-C48	AHL	3-Oxo-C6	Pang et al. (2009)
Gluconacetobacter diazotrophicus PAL5	AHL	C6-, C8-, C10-, C12-, C14-HSL; 3-oxo-C10-, C12-, C14-HSL	Nieto-Penalver et al. (2012)

family (Brameyer et al. 2015); it is at present unidentified whether these signals are formed by rhizobacteria. One more group of QS signals in Gram-negative bacteria is the DSF family (diffusible signal factor, which are cis-2-unsaturated fatty acids); more bacterial species are presently being identified which generate DSF, together with rhizosphere-inhabiting species such as *Burkholderia* spp. and *Stenotrophomonas maltophilia* (Ryan et al. 2015). Fascinatingly, bacterial DSF signal molecules have also been currently resolved to bring about innate immunity in plants, therefore performing as interkingdom signal molecules (Kakkar et al. 2015). Several Gram-positive bacterial inhabitants in the rhizosphere utilize peptides (also known as pheromones) as QS signaling compounds; probably these molecules participate in numerous regulatory functions both at the intra- and interspecies level (Bassler 2002; Monnet et al. 2016).

An accurate, exact, and responsive chemical examination of quorum-sensing autoinducer compounds was a necessary requirement for novel studies of quorum-sensing-associated regulation in bacteria. By employing these methods, a detailed tracking of these QS compounds in the habitat and inside eukaryotic cell, populated by HSL-producing bacteria, was made possible (Gotz et al. 2007; Hartmann and Schikora 2012). In case of quorum-sensing compounds pertaining to N-acyl homoserine lactone group, it has been proved lucky for the progress of study in this area that the first accessible chromatographic tools were soon aided by extremely sensitive and specific biosensors. These biosensors get benefit of the careful establishment of promoters of HSL-regulated genes by autoinducer molecules. Different existing operon fusion constructs of HSL-activated genes with the *lux-casette*, *gfp*, *rfp*, or *lacZ* have been evaluated by Fekete et al. (2010b). Additionally, the quorum-sensing-controlled violacein secretion by *Chromobacterium violaceum* can be utilized effectively to initiate HSL production or deterioration, respectively (McClean et al. 1997). The indicated constructs are also present on plasmids and can be transmitted to other bacteria. On the other hand, HSL-biosensor bacteria should contain their personal HSL-secreting genes deleted or inactivated to circumvent self-activation. The constructs generally have different precision for both short and long side chain HSLs, but there are also reporter plasmids that permit recognition of most HSLs with comparable sharpness (Thomson et al. 2000; Andersen et al. 2001). However, one has to be cautious in the utilization of these biosensors, as their report may be somewhat partial and has to be incremented with other resources of chemical or immunological metabolite analysis. The existence of HSLs in definite environments and their ecological importance have been encouraged by the use of green fluorescent protein (GFP) or red fluorescent protein/DsRed (RFP) stuck to HSL-regulated promoters. The potency of HSL down to 20 nmol l^{-1} can be identified by means of these bioreporter constructs. However, this recognition is relatively discriminatory, because, for example, in the case of the reporter strain *Pseudomonas putida* F117, the confined reporter plasmid pAS-C8 is 100 times extra susceptible to 3-oxo-C12-HSL than C12-HSL (Steidle et al. 2001). Using these constructs, the in situ secretion of HSL compounds can be, for example, discovered on the surface of roots, consequently ensuing in the regulation of "landscapes" of HSLs on occupied surfaces (Gantner et al. 2006).

In microcolonies or polymer matrix-surrounded biofilms, where the dispersion is limited, the local concentration of HSLs can reach high peak values. By using mathematical models for the computation of the autoregulated HSL secretion in bacteria and restricted dispersion (Muller et al. 2006), local concentrations in the mmol l^{-1} range can be calculated, accepting just a volume of a 5-μm cube with enclosed *Burkholderia cepacia*. This fact can have ecological importance for communication with eukaryotic hosts inhabited by HSL-producing bacterial microcolonies or biofilms that could also add to compensate the potential deterioration of HSL by quorum-quenching reactions. With reference to chemical analysis, GC-based methods of HSL quantification were established first. To amplify the sensitivity of the technique, for example, selective ion monitoring of the mass spectrometry (MS) detection or derivatization of the ß-oxo group to an oxime was applied (Charlton et al. 2000). As analyzed by Fekete et al. (2007), reversed-phase HPLC coupled with MS for selective detection has been useful in nearly all cases (Morin et al. 2003). Frommberger et al. (2004) established a micro-electrospray interface to MS after nano-LC separation of the HSLs. Electrokinetic chromatography (MEKC) also has been employed effectively for the recognition of HSLs and detection by MS. The most effective separation of HSLs is with UPLC analysis, as described in detail by Li et al. (2006). The classification of enantiomers of HSLs in biological matrices also is achievable by means of an optimized GC-MS approach (Malik et al. 2009). The maximum precision of molecular mass detection of HSLs has been completed by using the positive ion Fourier transform ion cyclotron resonance mass spectrometry (FTICR-MS) with mass errors of the peaks less than 0.1 ppm, as described by Fekete et al. (2007).

Nevertheless, still after employing this highly resolving analytical instrument, it is suitable to use two independent analytical approaches (e.g., UPLC and FTICR-MS) to clearly recognize HSL molecules, particularly when the recognition is from very complex matrices, such as nutrient broth medium, frequently used in microbiology (Hartmann and Schikora 2012). One more autonomous technique for the examination of HSL molecules is based on immunochemistry. From several labs, monoclonal antibodies (MAB) have been produced against several HSL molecules (Kaufmann et al. 2006, 2008; Chen et al. 2010a, b). These MABs not only allow the research of the biological impact of scavenging HSL but also the investigation of reduced sample sizes and the localization of the allocation of HSL secreted by bacteria connected with eukaryotes (Park et al. 2007; Hartmann and Schikora 2012). For more details, readers are being suggested to read specific review article on the subject (Rumbaugh 2011).

16.3 Quorum Sensing in Plant Growth-Promoting Rhizobacteria

Quorum sensing provides a great competing benefit to bacteria enhancing their likelihood to stay alive, while they can explore more difficult habitats. QS in bacterial conversation is connected with the manufacturing and discharge of signal

molecules, termed autoinducers, into the surrounding medium. On recognition of the signal compounds at a given concentration, transcription of definite genes controlled by this system is stimulate or withdrawn in the bacteria. There are different microbial mechanisms regulated by QS which include DNA transferase by conjugation, bioluminescence, siderophore production, biofilm formation, and moving ability of some bacteria, also termed as "swarming" (Fray 2002; Barriuso et al. 2008b). Streptomycetes, with high G+C-content, have been shown to control spore development as well as antibiotic manufacturing by a quorum-sensing indicator called A-factor. The separation of AHLs from bacteroids of *R. leguminosarum* advocates that quorum sensing might play a role in the mature nodule (Daniels et al. 2002). It is hypothesize that quorum sensing influences population flow in connection with host plants. Both siderophores and HSLs have been recommended to participate as chemical signal molecules for interspecies conversation among bacteria (Guan and Kamino 2001). However, insufficient information is available related to interspecies conversation in the natural microbial habitat. Mathesius et al. (2003) documented better discharge of AHL mimics in exudates of *Medicago truncatula*. The chemical composition of such active quorum sensing mimicking secondary metabolites is presently unidentified and also needs additional explanation (Teplitski et al. 2000; Chen et al. 2002; Podile et al. 2014).

QS-regulated gene expression is based not only on signal compounds but also on bacterial population thickness (Williams 2007). The requirement for a minimum level of the primary PGPR inocula to promote plant growth considerably sustains the thought that quorum sensing by microorganisms participates in plant-rhizobacteria communications (Persello-Cartieaux et al. 2003). Bacteria can respond to QS-like molecules secreted by other rhizospheric bacteria (Steidle et al. 2001) and by plants (Teplitski et al. 2000) and even eradicate the QS signal compounds secreted by other bacterial species (Dong et al. 2002). Other than producing regulatory peptides, *Bacillus* secretes enzymes to degrade the AHL moieties produced by Gram-negative bacteria. Genes encrypting for AHL-degrading enzymes, *aiiA*, have been established in *B. thuringiensis* and different subspecies (Lee et al. 2002). The occurrence of such proteins permits *Bacillus* strains to split the lactone bond of AHLs via hydrolysis, signifying a method for autoinducer-degrading activity, permitting these bacteria to struggle with other Gram-negative bacteria. Bacterial functions in the rhizosphere can, therefore, be changed directly by plants or other microorganisms via QS molecules (Podile et al. 2014).

In addition to motility and QS, bacterial major outer membrane protein (MOMP) also performs a crucial task in initial host identification. The MOMP of *Azospirillum brasilense* demonstrated better adhesion factor to exudates of cereals than exudates of legumes and tomatoes and could work as a bond implicated in root adsorption and cell accumulation of the bacterium (Burdman et al. 2001). Bacterial lipopolysaccharides (LPS), particularly the O-antigen chain, can also cooperate in root habitation (Dekkers et al. 1998a, b). On the other hand, it is strain related since the O-antigenic side chain of *Pseudomonas fluorescens* WCS374 does not help in potato root attachment (De Weger et al. 1989), while the O-antigen chain of

P. fluorescens PCL1205 is implicated in tomato root colonization (Dekkers et al. 1998b). Several workers (Simons et al. 1996; Dekkers et al. 1998a; Compant et al. 2010) also reported that high bacterial growth rate and capability to produce vitamin B1 and secrete NADH dehydrogenases help in plant colonization.

Endophytes comprising a vital constituent of plant structure are frequently reported assisting in plant defense reactions by quorum-preventing methods. Fascinatingly however, endophytes are repeatedly observed to have quorum-sensing mechanisms that permit them to sustain their own inhabitation in host plants and counteract plant pathogens. For instance, strain PsJNT is described to set up endophytic relations with different plants and acknowledged to develop plant-rooting structure with improved vascular arrangements, enhance quantity of chlorophyll and phytohormones, and offer resistance to phytopathogens. Fascinatingly, *Burkholderia phytofirmans* strain PsJNT was reported to secrete quorum autoinducer 3-hydroxy-C8-homoserine lactone (Sessitsch et al. 2005). In addition, endophytic *Serratia plymuthica* with enormous biological control capability was found to hold high amount of homoserine lactone (HSL), namely, C4-HSL, C5-HSL, C6-HSL, C7-HSL, C8-HSL, 3-oxo derivatives (3-oxo-C6-HSL, 3-oxo-C7-HSL, 3-oxo-C8 HSL), and 3-hydroxy derivatives (3-hydroxy-C6-HSL, 3-hydroxy-C8-HSL). These AHL molecules were due to two quorum-sensing mechanisms in *S. plymuthica* (Liu et al. 2011). Additionally, the olive plant epiphyte (*Pantoea agglomerans*) and endophyte (*Erwinia toletana*) linked with olive knot infection were observed for the discharge of signals analogous to AHLs. This chemical communication changed the virulence of pathogen *Pseudomonas savastanoi* pv. *savastanoi* blamed for olive knot. This work is an illustration of tripartite connections among plant and connected microbes (Hosni et al. 2011).

The genome sequence of endophytic *Gluconacetobacter diazotrophicus* PAL5 based on *Saccharum officinarum* exposed the existence of quorum-sensing mechanisms and identification of eight AHLs, viz., C6, C8, C10, C12, and C14-HSL (Nieto-Penalver et al. 2012). A current description from Dourado et al. (2013) demonstrated the exploitation of quorum-sensing compounds for *Methylobacterium* (famous for displaying endophytic lifestyle) communications with plants. A series of genes were up- and downregulated in *Methylobacterium* and host plant at the same time facilitating colonization and symbiotic relations, presenting the reliance of plant-endophyte relations on quorum-sensing mechanisms. Rhizobacteria are extensively recognized to improve production of plants by nitrogen fixation and production of siderophores and phytohormone, decrease plant stress, induce systemic resistance, and have capability to attenuate phytopathogenic signals (Liu et al. 2012). Thus, maintaining quorum-sensing mechanisms and autoinducers may allow the endophytic isolates to talk with other connected endophytes in addition to the host plant, thus preserving symbiotic relationship and habitation inside the inner tissues of plants. Surely, there is a deficiency of information on such organization, which needs to be examined in deepness to search for the possible plant physiological modifications and resistance reactions such as release of ethylene, salicylic acid, and defense proteins during the initial stages of colonization.

16.4 Recent Reports on Quorum-Sensing-Associated Functions in Plant Growth-Promoting Bacteria

The rising demand for food and the apprehension related to food quality are the compelling activities advancing to new approaches in agriculture. An effective plant protection mechanism possesses a huge potential to make certain an adequate and high-quality food delivery. Biocontrol agents are well recognized and widely used; however their potential is not yet fully exploited. These days numerous products based on bacterial inoculum, primarily consisting of *Bacillus*, *Pseudomonas*, or *Serratia* spp., arrived at the market. The use of N_2-fixing *Rhizobia* (e.g., *Sinorhizobium meliloti*), with improved secretion of specific AHLs, might augment the useful effects of bacteria and increase the effect to plant species generally not connected with the specific strain (Zarkani et al. 2013; Hernandez-Reyes et al. 2014). Further, a better comprehension of the communication among bacterial quorum-sensing compounds and eukaryotic host cells can unlock novel strategies in agriculture. Throughout the infection procedure, QS molecules administer the bacterial capability to form biofilms and other density-regulated traits. Those compounds participate in key role in the communication among bacterial and plant cells. Several workers documented the role of quorum sensing in plant disease control and phytopathogen transmission. Some of the reports are summarized briefly.

Barriuso et al. (2008a) reported the role of N-acyl-homoserine lactone (AHL) quorum-sensing signaling compounds in plant growth promotion and the initiation of defense against salt stress. They utilized two Gram-negative, plant growth-promoting rhizobacteria, designated as M12 and M14, and were identified by 16S rDNA sequencing as *Burkholderia graminis* species. Both strains were found to produce a diversity of N-acyl-homoserine lactone (AHL) quorum-sensing signaling compounds. AHL generation was examined in vitro by thin-layer chromatography by applying AHL biosensors, and the characteristic of the AHLs produced was decided by liquid chromatography-tandem mass spectrometry. The in situ secretion of AHLs by M12 and M14 in the rhizosphere of *Arabidopsis thaliana* plants was distinguished by co-inoculation with green fluorescent protein-based biosensor strains and confocal laser scanning microscopy. To establish both plant growth promotion and defense against salt stress, these PGPRs were examined on wild-type tomato plants, in addition to their matching transgenics expressing *YenI* (short-chain AHL producers) and *LasI* (long-chain AHL producers). In wild-type tomato plants, it was found that only M12 improved the plant growth and this result vanished in both transgenic lines. On the opposing, M14 did not encourage development in wild-type tomatoes but did so in the *LasI* transgenic line. Resistance to salt stress was stimulated by M14 in wild-type tomato, but this outcome vanished in both transgenic lines. The strain M12, however, did not stimulate salt resistance in wild-type tomato but did so in *LasI* tomato plants. These outcomes disclose that AHL QS signaling compounds decide the capability of both PGPR strains M12 and M14 to enhance plant growth and to activate protection against salt stress.

Johnson and Walcott (2013) reported that *Acidovorax citrulli* convert from saprobic to pathogenic growth for seed-to-seedling distribution of bacterial fruit blotch

(BFB) of cucurbits; they speculate that quorum sensing was implicated in the regulation of this procedure. Using *aacI* (*luxI* homologue) and *aacR* (*luxR* homologue) mutants of AAC00-1, they examined the task of QS in watermelon seed colonization and seed-to-seedling distribution of BFB. *aacR* and *aacI* mutants of AAC00-1 inhabited germinating watermelon seed at wild-type levels; on the other hand, BFB seed-to-seedling distribution was influenced in a cell thickness-attached approach. There were no important distinctions in BFB seedling transmission among watermelon seed penetrated with approximately 1×10^6 CFU of AAC00-1, the *aacR* or *aacI* deletion mutants (95.2, 94.9, and 98.3% BFB occurrence, correspondingly). On the contrary, when seed inoculum was decreased in the order of $1x10^3$ CFU $seed^{-1}$, BFB seed-to-seedling transmission dropped to 34.3% for the *aacI* mutant, which was considerably low than the wild type (78.6%). Fascinatingly, BFB seed-to-seedling distribution for the *aacR* mutant was not significantly unusual to the wild-type strain. This information advocates that QS takes part in the regulation of genes implicated in seed-to seedling spreading of BFB.

Alavi et al. (2013) accounted the role of DSF quorum-sensing system in controlling the progressive impact of *Stenotrophomonas maltophilia* on plants. They reported that the quorum-sensing molecule DSF (diffusible signal factor) is accountable for the directive of phenotypes in pathogenic *Stenotrophomonas*; to date, no helpful results were documented to be managed by it. They examined the role of DSF in the plant growth-promoting model strain *S. maltophilia* R551-3 using functional and transcriptomic analyses. For this intention, these workers correlated the wild-type strain with a mutant deficient in the *rpfF* (regulation of pathogenicity factors) gene that is necessary for the synthesis of DSF. Oilseed rape seeds coated with the wild-type strain demonstrated a statistically significant enhancement in germination rate compared with those coated with the *rpfF* mutant. Likewise, the wild-type strain displayed improved plant growth promotion and a better effectiveness in colonizing oilseed rape compared to the mutant strain. Furthermore, only the wild type was competent of establishing organized cell masses both in vitro and in the rhizosphere, a quality decided by DSF. Gene transcription analyses revealed that many genes documented to participate in plant inhabitation (e.g., cell motility, chemotaxis, multidrug efflux pumps, biofilm formation) are controlled by the *rpf*/DSF system in *S. maltophilia.* Additionally, these workers discovered novel prospective traits of spermidine, mainly for both growth enhancement and stress protection. In general, these results elucidated an association among the regulation of DSF and the constructive communication outcome with the plant host.

Zuniga et al. (2013) evaluated that by using appropriate mutant strains of *Burkholderia phytofirmans* PsJN, data can be acquired showing the significance of N-acyl homoserine lactone-mediated quorum sensing in well-organized inhabitation of *Arabidopsis thaliana* plants and the organization of an advantageous communication. These workers also noticed that bacterial deterioration of the auxin indole-3-acetic acid (IAA) takes part in plant growth-promoting characters and is crucial for successful root colonization.

Perez-Montano et al. (2014) found that bacterial surface components, particularly exopolysaccharides, in association with bacterial quorum-sensing molecules

are vital for the formation of biofilms within the majority of species as examined until now. Biofilm formation permits soil bacteria to inhabit their neighboring territory and stay alive under frequent ecological stresses such as drought and nutrient limitation. This form of life is regularly important for continued existence in bacteria of the genera *Mesorhizobium*, *Sinorhizobium*, *Bradyrhizobium*, and *Rhizobium*. They also established that biofilm construction is essential for a most favorable root colonization and symbiosis among *S. fredii* SMH12 and *Glycine max* cv Osumi. In this bacterium, nod gene-activating flavonoids and the NodD1 protein are necessary for the evolution of the biofilm configuration from monolayer to microcolony. QS mechanisms are also essential for the complete growth of both types of biofilms. In fact, both the *nodD1* mutant and the lactonase strain (the lactonase enzyme stop AHL buildup) are imperfect in soybean root inhabitation. The destruction of the lactonase strain in its colonization capability results in the decline of the symbiotic parameters. Fascinatingly, NodD1 jointly with flavonoids induces certain quorum-sensing mechanisms involved in the growth of the symbiotic biofilm. Therefore, *S. fredii* SMH12 through distinctive key compound, the flavonoid, competently forms biofilm, colonizes the legume roots, and induces the production of Nod factors, necessary for fruitful symbiosis. Oslizlo et al. (2015) demonstrated that *Bacillus subtilis* isolated from tomato rhizosphere displayed variety of the ComQXPA quorum-sensing mechanisms. This QS mechanism controls the secretion of antipathogenic and biofilm-activating compounds, for example, surfactins, which are responsible for the biocontrol activity of this bacterium.

Paungfoo-Lonhienne et al. (2016) established the role of quorum sensing in colonization and biofilm formation by *Burkholderia* Q208. They accounted that *Burkholderia* strain Q208, a PGPR of Australian sugarcane, exhibits an extremely conserved quorum-sensing mechanism, nominated as BraI/R, which is programmed by a cluster of three genes (*braI*, *rsaL* and *braR*), the results of which create and react to *N*-dodecanoyl-3-oxo-homoserine lactone. In the biofilm *Burkholderia braI* is upregulated (twofold), while, strangely, *rsaL* and *braR* are downregulated (to 0.35- and 0.45-fold of reference levels, respectively). The absolute counts of raw reads of *rsaL* (16,000) and *braR* (15,500) are higher than the mean (700) read number over all expressed genes, signifying that even though these genes are downregulated, BraI/R quorum sensing by *Burkholderia* Q208 continues to be effective in the sugarcane rhizosphere.

16.5 Role of Quorum Sensing in Rhizosphere Signaling and Plant-Microbe Interactions

The rhizosphere is a highly complex microecological niche rich in nutrient released by plant root and provides suitable environment for growth and multiplication of an array of soil microbial populations. Primary and secondary metabolites released in the form of plant root exudates are believed to shape, signal, and interfere with rhizosphere microflora by attracting beneficial microflora and combating pathogenic microflora. In a review by Venturi and Keel (2016) described various issues related

to signaling in rhizosphere and divided the process in three groups: (i) signaling between microbes, (ii) from plants to microbes, and (iii) microorganisms to plants. Two major groups of small signaling molecules are recognized. First is the QS molecules released by bacteria and volatile organic compounds (VOCs) released by various bacteria and fungi. VOCs are assumed to play significant task in long-distance communication within microbial populations, microbe-microbe, along with plant-microbe cooperation within the rhizosphere (Bitas et al. 2013). VOCs are also known to also work as intra- and interspecies signals by influencing gene expression and microbial functions such as biofilm, virulence, and stress tolerance (Audrain et al. 2015). Various rhizobacteria isolated from rhizosphere are known to produce QS signal molecules, and respond to these molecules. For example species of *Burkholderia*, *Pseudomonas*, *Rhizobia*, and *Sinorhizobium* as depicted in Table 16.1, and impact of QS on plant-microbe interaction is presented in Fig. 16.1.

Phytocompounds secreted by plant roots promote microbial interaction and also influence plant-microbe interactions (Zhang et al. 2015). Plant-produced signals have been studied only in well-established association such as legume-rhizobia symbiosis and mycorrhizal associations as reviewed by other workers and are not topic of discussion here (Downie 2010; Oldroyd 2013). The role of QS in

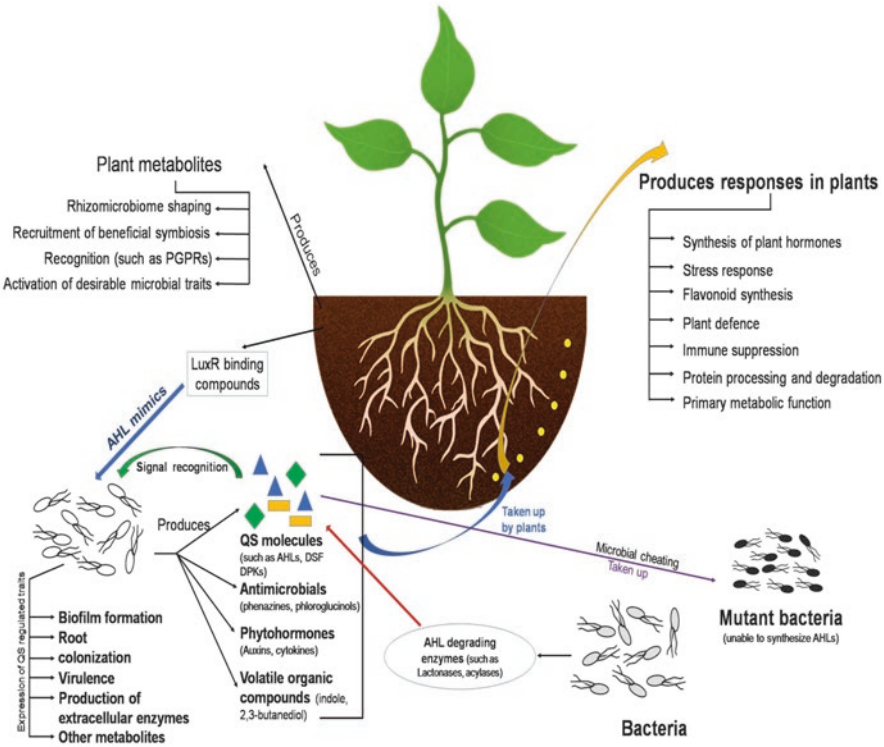

Fig. 16.1 Role of quorum sensing in microbe-plant interactions and rhizosphere signaling

plant-microbe association is now becoming more evident, since many rhizobacteria employ QS molecules to colonize plant surface or plant-associated environment through QS-mediated gene expression (Von Bodman et al. 2003; Newton and Fray 2004). On the other hand, plant-derived compounds are reported to interfere in bacterial quorum sensing. Recently a bacterial subfamily of LuxRs proteins produced by bacteria interacts with plant small molecules and not with QS. LuxRs is expected to respond plant signals indicating a more complex interkingdom signaling mechanism (Venturi and Fuqua 2013; Gonzalez and Venturi 2013). Various signals produced by PGPR are now characterized, and the best studied AHLs are found to influence plant physiology and plant-microbe interaction such as induction of plant defense against pathogens, pest, and abiotic stressor, which results in promotion of plant growth and development (Shoresh et al. 2010; Zamioudis and Pieterse 2012; Cameron et al. 2013; Pieterse et al. 2014).

Terrestrial plants related to different genera are recognized to generate AHL-mimic molecules for defense system in opposition to pathogen and communication with connected bacterial communities, both inside and outside the plant tissues (Perez-Montano et al. 2013). Quorum-mimicking AHLs are synthesized and secreted in close proximity by different plant species varying from seedlings to a mature plant (Teplitski et al. 2011).

Mathesius et al. (2003) have reported the modulatory role of signaling molecules, AHLs, on plant physiology based on differential proteome analysis and found that protein-related defense, stress, flavonoid metabolism, hormones, and many regulatory proteins were differentially expressed in plants treated with AHLs. von Rad and his colleagues have reported the upregulation of auxin and downregulation of cytokinin genes and influence the ratio of auxin and cytokinin in the treated model plant with C6-HSL (von Rad et al. 2008). Hartmann and Schikora (2012) and Schenk et al. (2012) proposed a double role of the AHL molecules in *Arabidopsis thaliana.* Short acyl chain AHLs, like C4 or C6, were revealed to increase the growth rate, primarily elongating the roots (von Rad et al. 2008; Bai et al. 2012; Liu et al. 2012; Schenk et al. 2012), in contrast to molecules with longer acyl chains (e.g., C12 or C14).

Recently, Hartmann et al. (2014) described the impact of AHLs on plant growth in plant species and found that it is more complex. However, in some studied cases, it may be very specific such as in mung bean and *Medicago truncatula* plants. Long-chain 3-oxo-C14-HSL produced by *Sinorhizobium meliloti* showed increase in root nodulation in *Medicago truncatula* (Veliz-Vallejos et al. 2014). It was interesting to note that the increased number of nodules was observed only after a treatment with 3-oxo-C14-HSL, the predominant AHL of *S. meliloti*, and treatment with other AHLs showed no effect. In mung bean plants, only the 3-oxo-C10-HSL, but not the unsubstituted C10-HSL or C12-HSL, was able to induce adventitious roots (Bai et al. 2012).

In a study conducted on barley treated with C6-, C8-, and C10-HSLs indicated modulatory role in the activity of glutathione *S-transferase* and *dehydroascorbate reductase*. On the other hand, in yam bean, no influence was measured (Gotz-Rosch et al. 2015). Yet another interesting example is the modification of plant cell walls

in AHL-primed plants. In this primed stage, plants upregulated the transcription of numerous genes pertaining to secondary metabolism (e.g., phenols). In consequence, upon a challenge with pathogens, those plants accumulate callose and phenolic compounds (Schenk and Schikora 2015). In a recent review article, Schikora et al. (2016) described the effect of quorum-sensing molecules of the N-acyl homoserine lactone group on plant physiology and significance in the development of stress tolerance mechanism in plants against stressors (Fig.16.1).

16.6 Conclusion and Future Direction

Research carried out in the last decades has shown that quorum sensing is a widespread global regulatory mechanism of gene expression in a density-dependent manner among several bacteria including both pathogenic and beneficial species. Plant-associated bacteria such as PGPR, both free living and symbiotic, have been investigated, which use QS to regulate specific traits. Some of these are important in the interaction with other bacteria or the host plant. These bacteria produce small molecules called autoinducer. Various types of complex QS network are present in bacteria, but the most commonly studied system in Gram-negative bacteria is found to possess AHL-based LuxR/LuxI homologous systems. The signal molecules contribute not only in signaling within bacterial population in the rhizosphere but also contribute in plant-microbe interactions.

Interestingly plants are able to react or hamper bacterial QS which clearly indicated its significance in plant-bacteria interactions. Many bacteria in rhizosphere produce AHL-degrading enzymes, thus exhibiting phenomenon of quorum quenching. On the other hand, plant metabolites can also inhibit QS thus showing QS-mimic activity. Recent reports indicated that bacteria produce compounds which act as receptor for plant signals. Researchers have provided evidences that the treatment of plant with AHLs results in plant response which induces resistance to pathogens and stressor. Studying the dynamics of AHL production and degradation and response of plant-associated microbial biome will certainly help to fully explore the role of QS in plant-microbe interaction.

Now it has been established that plant is able to control the recruitment of root microbiome and to select specific microbes of desired function. Therefore, there is a greater need to understand how plant root-associated bacteria such as free-living PGPR are recruited by plants. Further, the role of QS-mediated signaling and other signaling mechanisms in the rhizosphere contributing in the establishment and maintenance of dynamic root microbiome needs to be studied. It is expected that an enhanced understanding on all these aspects will open new avenues to modulate root microbiome through the use of appropriate consortium of beneficial microbes for improved crop productivity and soil health.

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