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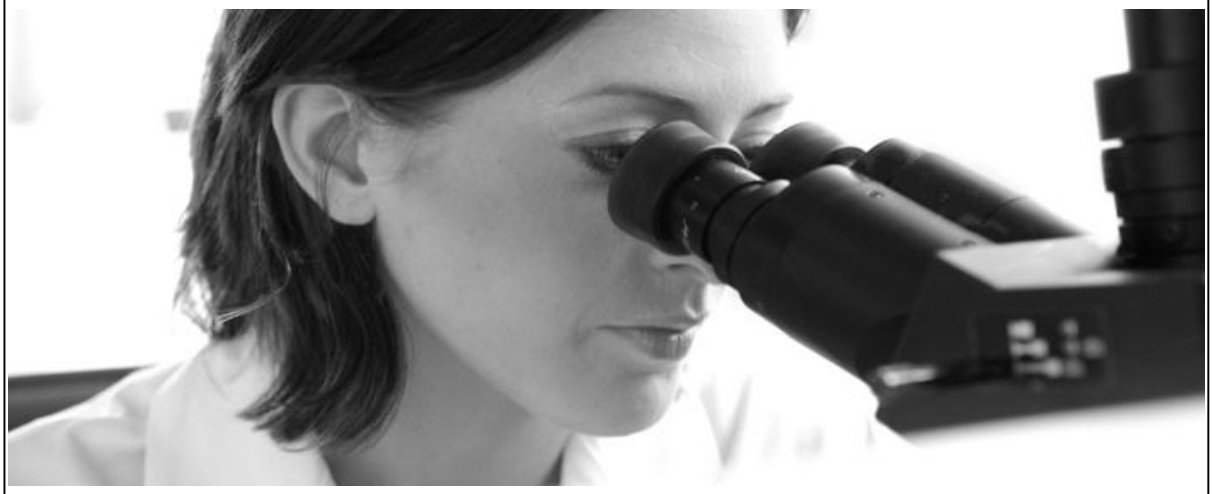

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**RESEARCH ARTICLE**

# QUORUM SENSING IN *RHIZOBIUM*

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## INTRODUCTION

***Quorum sensing:*** is cell to cell signaling mechanism that enables the bacteria to collectively control gene expression. This type of bacterial communication is achieved only at higher cell densities. Quorum sensing was discovered and described over 25 years ago in two luminous marine bacterial species, *Vibrio fischeri* and *Vibrio harveyi*. Quorum sensing is omnipresent in many known bacterial species. It has been reported that most of bacteria, not only free-living in various environments but also those associated with higher organisms (symbionts or pathogens), use a sort of quorum sensing mechanism for controlling different 'social' activities. Many human and plant pathogenic gram negative bacteria, including the genera *Agrobacterium*, *Brucella*, *Bukholderia*, *Erwinia*, *Enterobacter*, *Pseudomonas*, *Ralstonia*, *Serratia*, *Vibrio* and *Yersinia*, utilize the QS mechanism for regulation of the virulence factors synthesis. Symbiotic bacteria of legumes belonging to the *Rhizobium* genus mediate their physiological processes connected with nodulation efficiency, symbiosome development as well as nitrogen fixation by means of complex regulatory systems based on signal molecules and QS.

### *History*

Quorum sensing was first observed in *Vibrio fischeri*, a bioluminiscent bacterium present in the photophore of bobtail squid. Research into AHL based quorum sensing started in the late 1960s. The marine bioluminescent bacteria *Vibrio fischeri* was being grown in liquid cultures and it was observed that the cultures produced light only when large numbers of bacteria were present. It was later shown that the luminescence was initiated by the accumulation of an activator molecule or "autoinducer".

### *Why do bacteria talk to each other?*

QS enables bacteria to co-ordinate their behavior. As environmental conditions often change rapidly, bacteria need to respond quickly in order to survive. These responses include adaptation to availability of nutrients, defense against other microorganisms which may compete for the same nutrients and the avoidance of toxic compounds potentially dangerous for the bacteria. It is very important for pathogenic bacteria during infection of a host (e.g. humans, other animals or plants) in order to be able to establish a successful infection.

### *Quorum Sensing Mediated Processes*

- ***Bioluminescence:*** It occurs in various marine bacteria such as *Vibrio harveyi* and *Vibrio fischeri.* Takes place at high cell density.
- ***Biofilm formation:*** It is mass of differentiated microbial cells, enclosed in a matrix of polysaccharides. Biofilm resident bacteria are antibiotic resistant. Quorum sensing is responsible for development of thick layered biofilm.
- ***Virulence gene expression:*** QS upregulates virulence gene expression.
- ***Sporulation:*** QS upregulates spore-forming genes in *Bacillus subtilis.*
- ***Competence:*** It is ability to take up exogenous DNA. QS Increase competence in *Bacillus subtilis.*

### *Quorum Sensing Molecules*

Several classes of microbially-derived signaling molecules have now been identified. Broadly, these can be divided into two main categories:

***Acyl-homoserine lactones (AHLs):*** The structure of different microbial AHLs varies with the size and composition of the acyl chain, ranging from 4 to 14 carbon atoms; these contain double bonds, and often, an oxo-or hydroxyl group on the third carbon. Majority of AHLs identified to date have an even number of carbons in the acyl chain, which are regulated by two components Lux regulatory system. The type of AHL

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produced by a particular species is often strain-dependent. This reflects on the differing habitats in which the individual strains reside.

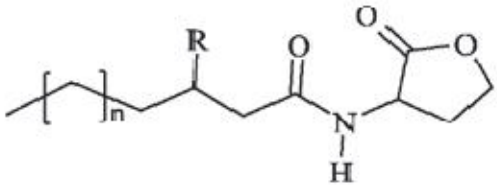


**Fig.1** *N*-acyl homoserine lactone (AHL)-the main QS signal molecule of gram negative bacteria

All AHLs are composed of the homoserine lactone ring and the acyl side chain that varies in length, oxidation state and presence of substituents. R-substituent at third carbon in the acyl side chain, hydrogen (H), oxygen (O) or the hydroxy group (HO) in the known AHLs.

***Autoinducer peptides (AIPs)****:* Only in gram positive bacteria. To date, acyl-HSL production has not been shown for any Gram positive bacterium, although the antibiotic-producing filamentous *Streptomyces* uses acylated-lactones (called *g*-butyrolactones) as signals. Aside from this specialized group, gram positive quorum-sensing systems typically make use of small post-transcriptionally processed peptide signal molecules. These peptides are usually secreted by ATP-binding cassette (ABC) transporters. Some peptides interact with membrane bound sensor kinases that transduce a signal across the membrane. Others are transported into the cell by oligopeptide permeases, where they then interact with intracellular receptors. While the Gram negative bacteria use LuxR-type proteins for autoinduction, Gram positive bacteria use two-component adaptive response proteins for the detection of the autoinducers. The signaling mechanism is a phosphorylation/ dephosphorylation cascade. The secreted peptide autoinducer increases its concentration as a function of the cell population density.

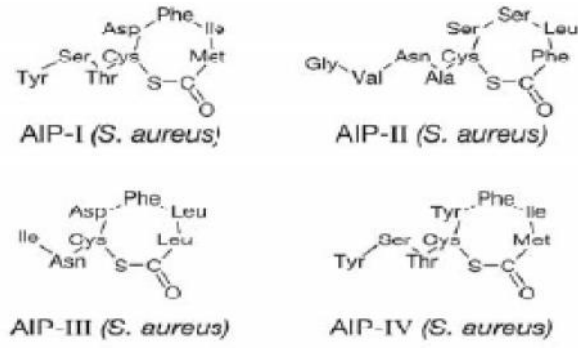
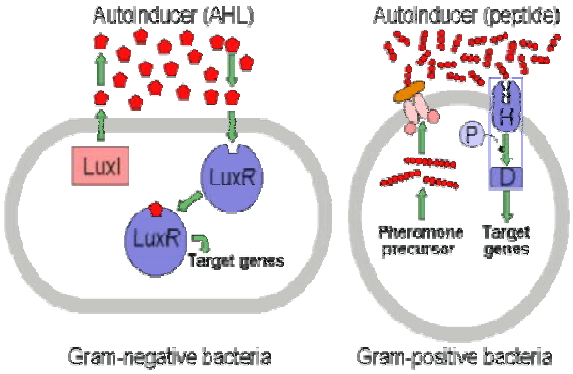



**Fig.2** Structures of some autoinducer peptides in *S. aureus*

***AHLs in the rhizobia****:* In the rhizobia, AHLs have been detected in *Rhizobium leguminosarum*, *Rhizobium etli* and *Rhizobium meliloti* and in many cases, multiple AHL molecules are detected. In *R. leguminosarum*, AHLs are required for activation of the *rhiABC* operon (a set of rhizosphere-expressed genes), *raiIR* and *cinIR* genes and is involved in root nodulation and growth inhibition. Until recently, AHL autoinducers had not been detected in *B. japonicum* the symbiont of soybean, a major agricultural crop.

***Qs System In Gram Positive And Gram Negative Bacteria***

Cell density-dependent gene expression, termed quorum sensing, is recognized as a widespread phenomenon in both gram negative and gram positive bacteria. AHL-mediated quorum sensing is employed by diverse gram negative proteobacteria belonging to α, β and γ subdivisions, but no AHL-producing gram positive bacteria have so far been identified. While gram negative bacteria employ hydrophobic low molecular weight signal molecules, post-translationally modified peptides are engaged by gram positive bacteria as quorum sensing signal molecules. These peptides, referred to as autoinducing peptides (AIPs), range from 5 to 34 amino acids in length and typically contain unusual chemical architectures.




***Quorum-Sensing Genes In Rhizobia***

The various genes signaling AHLs and associated phenotypes in different rhizobia are summarized in.

***Rhizobium leguminosarum*:** There are three different biovars of *R. leguminosarum*:

- bv. *viciae*, which nodulates peas, vetch and lentils,
- bv. *trifolii*, which nodulates clover,
- bv. *phaseoli*, which nodulates *Phaseolus* beans.

Most research has been done on *R. leguminosarum bv. viciae* and thus far four different LuxI-type AHL synthase genes have been identified in different isolates of *R. leguminosarum* bv. *viciae*. Each of these AHL synthase genes has a dedicated regulator encoded by a gene (usually) closely linked to the AHL synthase gene.

***cinI and cinR:*** Common to all the analyzed strains of *R. leguminosarum* are the *cinI* and *cinR* genes, which are located on the chromosome. CinR regulates the expression of *cinI* in response to CinI-made 3-OH-C14:1-HSL and there appears to be co-regulation of adjacent genes. Mutations in *cinI* or *cinR* reduce the expression of all other AHL synthase genes and it appears that the *cinI*/*cinR* system acts as an overall switch potentially influencing many aspects of rhizobial physiology.
***raiI and raiR:*** The *raiI* and *raiR* genes are located on a large (non-symbiotic) plasmid in *R. leguminosarum* bv. *phaseoli* strain 8002, but are absent from the genome of the sequenced strain of *R. leguminosarum* bv. *viciae* and appear to be absent from some other analysed strains of *R. leguminosarum* bv. *viciae*. RaiR regulates the expression of *raiI* in response to the

RaiI-made AHLs 3-OH-C8-HSL and C8-HSL, but other genes regulated by RaiR are yet to be identified.

***rhiI and rhiR:*** The *rhiR* gene was one of the earliest sequenced quorum-sensing regulators in the bacterial kingdom and was originally identified because it was very close to the genes (*nod*) required for legume nodulation and is required for the expression of the *rhiA* gene, which is highly expressed in the rhizosphere. RhiR regulates the expression of *rhiI* and *rhiABC* operon in response to RhiI-made C6-HSL, C7-HSL and C8-HSL. Mutations in *rhiA* or *rhiR* can cause a significant reduction in nodulation in strains already compromised for nodulation ability, but although the sequence of the *rhiABC* genes has been known for several years, no function has been demonstrated for the gene products, which show no close similarities to proteins of known function. The observations that the *rhi* genes are closely linked to nodulation and nitrogen fixation genes and that the *rhi* genes are found only in bv. *viciae* but not in other biovars of *R. leguminosarum* suggest that they probably play a role in growth and/or survival in association with specific legume hosts.

***traI and traR:*** TraR induces *traI* in response to TraI-made 3-oxo-C8-HSL. These genes are located on the symbiosis plasmid pRL1JI and together with *bisR* (encoding another LuxR-type regulator) are required to induce the plasmid transfer genes. However, in the sequenced strain *R. leguminosarum* bv. *viciae* 3841, no equivalent genes were found on the symbiosis plasmid (which is called pRL10JI in that strain. Homologues of *traI* and *traR* in strain 3841 are found on pRL7JI and pRL8JI, respectively, but their role in plasmid transfer has not been reported.

***Other LuxR-type regulators:*** In addition to the genes described above, there are three other LuxR-type regulators encoded in the genome of *R. leguminosarum* strain 3841. One is ExpR, which is located on the chromosome and is the orthologue of *expR* from *S. meliloti*.

***Unravelling the quorum-sensing cascade in r. Leguminosarum bv. Viciae***

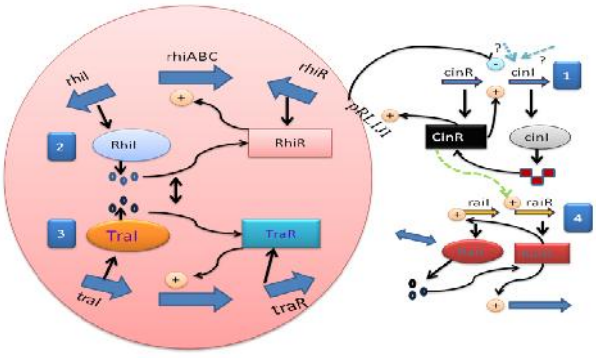



**Fig.3** short acyl chain AHLs; → indicates a demonstrated regulation; . . . . *. .> indicates a putative regulation; <. . . . . > indicates possible* cross-talk between the different loops.

Quorum-sensing cascade in *R. leguminosarum* bv. *Viciae.* are discussed below:

1. CinR induces cinI expression allowing the production of 3OH, C14:1-HSL, which together with CinR activates cinI to form a positive feedback loop.
2. 3OH, C14:1-HSL influences the expression of rhiI, an AHL production gene located on pRL1JI. RhiR, with the AHLs made by RhiI, induces rhiI and rhiABC.
3. Another quorum-sensing loop located on pRL1JI is involved in plasmid transfer; expression of traI, also influenced by 3OH, C14:1-HSL, leads to the production of several short chain AHLs which along with TraR allow the expression of the trb genes.
4. A fourth quorum-sensing loop, also influenced by the master loop cinI R is located outside pRL1JI. RaiI also produces several short acyl chain AHLs; the genes regulated by RaiR have not yet been identified. Functions located on pRL1JI are responsible for the repression of 3OH, C14:1-HSL production. Indeed, growth inhibition mediated by 3OH, C14:1-HSL is observed with strains carrying pRL1JI and hence is due to genes carried by this plasmid.

***Applications***

***Commercial inoculants:*** One of the major challenges to the practical utilization of improved commercial inoculant strains is competitiveness and persistence of the inoculant strain. Competition from less efficient native strains and decreased survival in the soil make inoculant strains appear less practical and has led to a decline in the use of symbiotic nitrogen fixation as a source of plant nitrogen. Specifically bacterium-bacterium communication should play a role in coordinating events in the establishment of the symbiosis.

***Pathogen/pest management:*** Pathogen and pest management comprise most of the current applications of quorum-sensing technology. Inhibition of quorum signalling is the most obvious and, in practice, most ubiquitous application of quorum-sensing knowledge. The limiting factor for many applications is delivery of a quorum functional compound to the organism to be controlled.

***Recombinant gene expression:*** Exciting areas for investigation in quorum sensing is the synthesis of recombinant gene products and in metabolic engineering. Quorum sensing has been used to regulate gene expression and control cellular growth. In the area of biological engineering, quorum-sensing approaches to protein synthesis are developing in both prokaryotic and eukaryotic models. In E. coli, an artificial quorum-signalling system was used to induce synthesis of recombinant green fluorescent protein (GFP).

***Biosensors****:* Engineered QS-based circuits have a wide range of applications such as production of biochemicals, tissue engineering, and mixed-species fermentations. They are also highly useful in designing microbial biosensors to identify bacterial species present in the environment and within living organisms.

***Antimicrobial drug therapy :*** Recently, it has been advised to develop new therapeutics that attacks bacterial virulence rather than killing bacteria. Such drugs are called "antipathogenic" and are believed to lower the development of antibiotic resistance. Specifically, cell-density-dependent gene regulation (quorum-sensing) in bacteria has been proposed as a potential

target. It has been suggested that targeting the QS system, instead of killing bacteria, may provide a solution to antibiotic resistance.

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