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Effect of Quorum sensing and quorum Quenching in plant microbe invasion

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ABSTRACT
Numerous bacteria use the quorum sensing to control different gene expressions in a cell density-dependent way through the production and recognition of tiny molecules known as autoinducer. In various bacterial species, there are many types of quorum-sensing networks. The most well-studied and common signal molecule in bacteria is the acyl homoserine lactone signal molecule, that are produced by gram negative bacteria. Numerous bacteria in the rhizosphere have a QS mechanism. Due to the abundance of nutrients delivered in the form of root exudates, the rhizosphere is a dynamic environment where there is a maximum interaction between microbes and plants. Quorum sensing coordinates the ecological and interdependent key characteristics of bacteria, such as antibiotic, nitrogen fixation, siderophore, biofilm production or enzyme secretion, phytopathogen virulence factors, as well as plant-microbe interactions. Quorum quenching is the process in which quorum sensing is disrupted, it can be achieved by inhibiting the production of auto-inducers, their detection by receptors, or their degradation. Quorum quenching approaches by accompanying microbes and also by plants. Moreover, it has been demonstrated that PGPR exhibit quorum quenching activity. In this review we will provide brief fundamental aspects of the quorum sensing mechanism of plant growth promoting symbiotic and non-symbiotic bacteria. It also focuses on the effect of autoinducer molecules producing bacteria and autoinducer on plant growth, development and defence response. Here we will discuss the signaling abilities of plant metabolites that control the associated microbiota's quorum sensing dependent behaviour through the activation or inhibition of bacterial quorum sensing systems.

Keywords: Quorum sensing(QS). Symbiotic bacteria. Non-symbiotic bacteria. Quorum Quenching(QQ). AHL mimics. Plant Microbe interactions.

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INTRODUCTION

Quorum sensing is the mechanism in which bacteria communicate to each other by its density dependent manner. Quorum sensing is also called as autoinduction. Most of the study system autoinducer molecules are acyl homoserine lactone. When bacterial concentration rises, autoinducer molecules diffuse out and re-enter into the cell, attach to the respective receptor and activated transcriptional genes [1] QS is discovered and described in two marine symbiotic bacteria *Vibrio fischeri* and *Vibrio harveyi*. Luciferase structural operons luxCDABE are responsible for bioluminescence production in *vibrio harveyi* and *fischari*. Accumulation of secreted autoinducer molecules is based on density dependent manner and its regulated bioluminescence on the both species [2], [3] **.** AHL (acyl homoserine lactone) is an autoinducer chemical produced by gram-negative bacteria. It is also known as Autoinducer I type or LuxI/ LuxR based QS system. Peptide-mediated Qs, also known as two component mediated Qs, are autoinducer molecules produced by gram - positive organisms. Both gram positive and gram-negative bacteria have autoinducer II type Qs system. It was discovered in the marine bacterium *V.harveyi* and is also known as inter species QS [4], [5]**.** N-acyl homoserine lactones are frequently investigated autoinducer signals but there are a dozen other compounds, such as diketopiperazines and 4-hydroxy-2-alkylquinolines (HAQs) are present in Gram-negative bacteria and it's also called as autoinducer-3 (AI-3)[6]**.** Gram-positive and Gram-negative bacteria use quorum sensing signaling circuits to control a wide range of physiological processes. Symbiosis, pathogenicity, competence, conjugation, generation of antibiotics, motility, sporulation, Nitrogen fixation and biofilm formation are some of these processes[2]. Quorum quenching (QQ)

is the process of inhibiting QS by interfering with signalling molecules. It refers to the mechanism through which bacterial communication can be disrupted. QQ can be attained through a variety of strategies, including preventing the synthesis of auto-inducers, receptors from detecting them, or their destruction[4]. Quorum sensing signals molecule are broken down by the QQ Rhizospheric bacteria. This reduces the population density required for the expression of virulence genes and lessens the symptoms of the associated illness[7]. Quorum quenching compounds are produced extracellularly by various marine bacteria, fungus, algae, bryozoans, corals, and sponge [8]. Halogenated furanones of the Red alga *Delisea pulchra* was the originator of the first marine quorum quenching compound. *Delisea pulchra* has yielded more than 20 distinct halogenated furanones with antifouling and antibacterial characteristics[9]. Numerous plant species have favourable benefits from the colonisation of plant-growth-promoting rhizobacteria (PGPR), including improved plant growth and lowered susceptibility to illnesses brought on by nematodes, bacteria, viruses, and plant pathogenic fungi. Rhizospheric bacteria have QS system that help in plant microbes interactions[9] . Exudates from pea seedlings contain substances that resemble QS molecules, which support the idea that plants are able to choose their microbial partners [10]. According to research by [11], the roots and seeds of *Oryza sativa* and *Phaseolus vulgaris* release chemicals that specifically interfere with plant-associated bacteria's ability to form bio-films, an essential component of bacteria-eukaryotic host communication. The study of how bacteria communicate with one another and how plants have evolved mechanisms to respond to these signal chemicals is an exciting area of study. In this paper we have reviewed updated literature address to the quorum sensing mechanism of PGPR symbiotic and non-symbiotic bacteria and their plant microbes interactions and their biocontrol activity.

Role of Quorum sensing in PGPR symbiotic and non-symbiotic bacteria

Plant growth promoting bacteria

There are a number of abiotic and biotic elements that affect plant growth. Rhizosphere, a highly significant and dynamic region for root activity and metabolism, is the thin layer of soil immediately around plant roots. PGPR are group of free -living bacteria that located near rhizosphere and contribute to enhance the growth and yield of the crop plants [12]. Plant growth-promoting rhizobacteria (PGPR) are rhizosphere microorganisms that can improve plant growth through a number of different mechanisms, including phosphate solubilization, siderophore production, biological nitrogen fixation, rhizosphere engineering, production of 1-Aminocyclopropane-1-carboxylate deaminase (ACC), interference with quorum sensing (QS) signalling and inhibition of biofilm formation, phytohormones, antifungal action, the synthesis of volatile organic compounds (VOCs), the development of systemic resistance, the encouragement of advantageous plant-microbe symbioses, the disruption of pathogen toxin production, etc [13]. All of these boost the emergence, vitality, and yield of seedling. PGPR can shield plants against the harmful impacts of environmental stress, such as heavy metals, salt, drought, and flooding. Symbiotic relationships between plants and bacteria that promote plant growth. *Rhizobium, Bradyrhizobium,* and *Azospirillium* are a few of the species that live in symbiosis with leguminous plants and some other species does not form symbiotic relationship. His particular strain of bacteria has the capacity to colonise roots and, through a variety of processes, promote the growth of its host plant [14]. Many PGPBs are reported to influence plant hormones like auxins, cytokinin's, or gibberellins to enhance the growth of root systems[15]. PGPRs improve plants' general health by assisting host plants in better nutrient uptake, defending against phytopathogenic microorganisms, and fostering tolerance to a variety of abiotic challenges. [16], [17]. Reported genera of the PGPRs include *Acinetobacter, Aeromonas, Agrobacterium, Allorhizobium, Arthrobacter, Azoarcus, Azorhizobium, Azospirillum, Azotobacter, Bacillus, Bradyrhizobium, Burkholderia, Caulobacter, Chromobacterium, Delftia, Enterobacter, Flavobacterium, Frankia, Gluconacetobacter, Klebsiella, Mesorhizobium, Micrococcus, Paenibacillus, Pantoea, Pseudomonas, Rhizobium, Serratia, Streptomyces,* ns,*Thiobacillus,* and others[18].

Quorum sensing in Symbiotic Bacteria

Studying symbiotic microorganisms requires a multidirectional understanding of these relationships because symbiosis is a biological phenomenon that involves dynamic changes in the genome, metabolism, and signalling network. By using a quorum sensing mechanism, symbiotic bacteria establish relationships with plants. QS mechanisms are involved in numerous symbiosis-related rhizobial function including exopolysaccharide (EPS) production, motility, nitrogen fixation, and nodulation [19] [20]. At least one isolate from each of the following genera of plant-associated bacteria produced AHL: *Agrobacterium, Rhizobium*, *Sinorhizobium, Pantoea*, *Erwinia, Pseudomonas, and Xanthomonas*[21]. Numerous isolates of *Rhizobium fredii, Rhizobium leguminosarum bv. viciae, bv. phaseoli,* and *bv. trifolii*, as well as *Sinorhizobium meliloti, Bradyrhizobium* were among the most common rhizobia evaluated as AHL producers. Different bacterial species can produce the same AHLs or AHLs with comparable structures and properties, indicating that crosstalk between populations occurs. It is also clear that quorum sensing via AHLs is more prevalent among plant-associated bacteria than the general population of soil bacteria [22], [23]. Following are descriptions of the numerous symbiotic bacteria and their quorum sensing mechanism.

Rhizobium leguminosarum

R. leguminosarum possesses three different biovars, including bv. phaseoli, which nodulates Phaseolus beans, bv. trifolii, which nodulates clover, and bv. viciae, which nodulates peas, vetch, and lentils. There are four separate AHL-based QS systems in *Rhizobium leguminosarum* biovar viciae (R.l. viciae), and they are called tra, rai, rhi, and cin [24]. The cinI and cinR genes, which are found on the chromosome, are shared by all the *R. leguminosarum* strains. When CinI produces 3-OH-C14:1-HSL, CinR modulates the expression of cinI, and it also appears to co-regulate nearby genes. The expression of each AHLsynthase gene is decreased by mutations in cinI or cinR [25].

The raiI and raiR genes are found on a large (non-symbiotic) plasmid in *R. leguminosarum* bv. phaseoli strain 8002, but they are missing from the genome of the sequenced strain of *R. leguminosarum* bv. viciae and may also be absent from

some other strains [25]. These genes have a patchy distribution, as one might anticipate, and mutations in them do not significantly alter the phenotype of *R. leguminosarum* under either free-living or symbiotic conditions. RaiR controls the expression of raiI in response to the RaiI-produced AHLs 3-OH-C8-HSL and C8-HSL, but other genes controlled by RaiR have not yet been discovered[26].

One of the earliest quorum-sensing regulators in the bacterial kingdom to be sequenced, the rhiR gene was first discovered because it was located next to the nod gene, which is necessary for legume nodulation and for the production of the rhiA gene, which is highly expressed in the rhizosphere. RhiR controls RhiI and RhiABC operon expression in response to C6-HSL, C7-HSL, and C8-HSL produced by RhiI. 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 similarity to proteins of known function. Mutations in rhiA or rhiR can cause a significant reduction in nodulation in strains already compromised for nodulation ability. The rhi genes are only found in bv. viciae and not in other biovars of R. leguminosarum, which suggests that they likely play a function in growth and/or survival in conjunction with particular legume hosts. The rhi genes are tightly connected to nodulation and nitrogen fixation genes[23].

When TraI produces 3-oxo-C8-HSL, TraR causes traI to be produced. These genes are found on the symbiosis plasmid pRL1JI, and they are necessary for inducing the plasmid transfer genes, together with bisR (which encodes another LuxR-type regulator).

Rhizobium etli

In *rhizobium etli* have three types of Quorum sensing genes cinI/cinR , raiI/raiR and traI/traR. These genes in CNPAF512 appear to be quite similar to those previously reported in *R. leguminosarum*, and CinI is in charge of generating a long-chain AHL known as 3-OH- (slc)- HSL, which is comparable to 3-OH-C14:1-HSL. This AHL exhibits comparable qualities to 3-OH-C14:1-HSL from *R. leguminosarum* in that it can prevent the growth of a tiny bacteriocin-sensitive strain of that organism[27]. raiI/raiR gene of stains CNPAF512 present in chromosome. And produces short chain AHL molecules they are responsible for nitrogen fixation and growth inhibition. traI/traR produce 3-oxo-C8-HSL molecules and they help in plasmid transfer [23].

Through the action of the traI-trb operon, which is contained in the p42a plasmid, QS in R. etli C'FN42 regulates conjugal transfer of the symbiotic plasmid P42d. TraI creates a 3 oxo C8 - HSL signal in this system. There are three encoded LuxR type regulators. traR, cinR, and TraM are all components of this system that are involved in the transfer of p42a. Nevertheless, the symbiotic process appears unaffected because p42a free variants may successfully nodulate beans. There is a second reactive area that comigrates with the 3-oxo- C8-HSL, most likely the 3-OH -C8-HSL, whose synthase may be encoded on a different plasmid from p42a or on the chromosome[28].

Rhizobium etli RT1 produces the most common and biologically active N-acyl homoserine lactone molecules, which control the QS control of swarming motility and biofilm formation.[29].

Sinorhizobium meliloti

Using the reference strain Rm1021, the majority of knowledge regarding QS in *S. meliloti* has been amassed. Three genes, sinI, sinR, and expR, are necessary for QS control in this bacteria. An adequate acyl-acyl carrier protein (acyl-ACP) from fatty acid biosynthesis, which is the precursor of the fatty acyl side chain, and S-adenosyl-L-methionine (SAM), which supplies the homoserine lactone ring moiety, are used to produce AHL via the sinI gene. The quorum-sensing system of *S. meliloti* is made up of the transcriptional regulators SinR and ExpR, as well as the SinR-controlled autoinducer synthase SinI, which is in responsible for generating AHLs. These AHLs regulate numerous downstream genes along with the ExpR regulator. Our research has demonstrated that the ExpR/Sin system plays a critical role in regulating motility and chemotaxis in response to cell population density by inducing the formation of succinoglycan and EPS II [30]. Depending on the culture medium utilized, the sinI gene product produces a variety of long-chain AHLs, including C12-HSL, C14-HSL, 3-oxo-C14-HSL, C16-HSL, C16:1-HSL, 3-oxo-C16-HSL, and C18-HSL [31].

In strain 1021, SinI might be the only AHL synthase present. It has been proposed earlier [31] that a second AHL synthase creates short-chain AHLs, such as C6-HSL, 3-oxo-C6-HSL, and C8-HSL; however, this was not supported by later research.

SinR, a LuxR-like transcription regulator that controls sinI expression but whose activity is unaffected by AHLs, is located next to and upstream of the chromosomal sinI gene, [31][33].In the presence of AHLs, ExpR significantly increases the expression of sinI, creating a positive feedback loop. The classic QS system is known for its positive feedback mechanism [34]. ExpR also inhibits the transcription of sinR at high AHL.

SinR increases sinI expression in response to SinI-made AHLs, increasing AHL synthesis in vitro by 3–10 fold. SinR is located next to sinI on the chromosome [32].

Bradyrhizobium

Rhizobial nodule production in legume roots depends on the nodulation genes nod, nol, and noe. These genes produce a collection of proteins known as the Nod factor, which functions as a signalling molecule for nodulation.

Nod gene expression in the soybean symbiosis *B. japonicum* is a sophisticated mechanism controlled by a cell density-dependent QS system that involves the expression of numerous regulatory pathways, such as nodD1, nodVW, nwsAB, and nolA-nodD2.

In a regulatory feedback loop, the proteins NolA and NodD2 reduce the expression of the Nod gene in response to elevated amounts of Nod factors, specifically chitin tetrameric byproducts or intermediates. NolA gene expression is also induced by the upregulation of tetrameric Nod signals carried through the production of the nodYABC operon in response to soybean isoflavonoids. According to [35] the NodD2 regulator, which suppresses the nodYABC operon, is activated by the NolA regulator. Additionally, Nod gene expression is regulated by NolA and NodD2 in a way depending on cell density. High-density cultures had substantially lower levels of nod gene induction than low-density cultures

did. When the capacity to activate nod genes is diminished, a high cell density expression of this QS-regulated phenotype is seen. NodYABC genes were not inhibited even at high cell densities in a nolA gene mutant, which did not show this dependency on cell density. Two-component mechanisms also control the symbiosis formation in B. japonicum. The two-component system NodVW, which is required for nodulation in cowpea (*Vigna unguiculata),* mung bean (*Vigna radiata*), and siratro (*Macroptilium atropurpureum*), but not in soybean, promotes the expression of nod genes by isoflavonoids [36]**.**

Another two-component system for controlling the nod gene in *B. japonicum* is called NwsAB. In the presence of genistein, the regulatory protein NwsB (encoded by nwsB) is necessary for the complete expression of the nod genes. NolA and NodD2 expression was not stimulated, which allowed a nwsB mutant to generate the quorum signal while being unable to respond to this signal. These results imply that NwsB regulates nod gene activation at low cell density and nod gene repression at high cell density in *B. japonicum*, hence determining the ability of soybean isoflavonoids to promote nod gene expression [35]**.**

Similar to other QS systems, this population density dependency is mediated by the generation of an extracellular signal (CDF; cell density factor) that builds up as a function of culture density [35]**.** *B. diazoefficiens*; [37] showed that CDF is an unique autoinducer molecule distinct from other QS signals. CDF was isolated and purified from *B. japonicum* USDA110. Each aromatic ring in CDF has an amino oxetane group in position p, and the two aromatic rings are connected by an imino group. The hypothesised structure of this chemical, known as bradyoxetin, is 2-[4-[(3-aminooxetan-2-yl)phenyl]-(imino)methyl]phenyloxetan-3-ylamine [38]**.** Bradyoxetin suppresses the nod gene by acting as an inducer of NolA.

Bradyrhizobium strains phylogenetically linked to strains that nodulate peanuts, were novel HSL signalling molecules discovered and characterised as aryl-HSLs and IV-HSLs. *Bradyrhizobium* strains have been reported to include other variants with the chemical structures cinnamoyl-HSL (another aryl-HSL) and IV-HSL (a branched-chain HSL) [39]. *Bradyrhizobium* sp. Another strain that can produce an aryl-HSL is strain ORS278. This bacteria generates cinnamoyl-HSL to encourage the expression of QS-dependent genes [40]**.** The bacterium is a member of a branch of the *Bradyrhizobium* genus that is distinguished by strains with photosynthetic abilities. *Aeschynomene sensitiva* and other legumes can develop nitrogen-fixing nodules on their stems when exposed to ORS278 and similar strains (e.g. BTAi1). ORS278 and BTAi1 don't have the nodABC genes needed to make lipo-chitooligosaccharidic Nod factor signals, in contrast to other rhizobia. *Bradyrhizobium* strain ORS278's quorum sensing is crucial for the colonisation of endophytic roots [41]**.**

Mesorhizobium

The genome of *Mesorhizobium loti* contains two LuxI-type AHL synthase genes, one of which is close to a LuxR-type regulator gene and additional genes that may be involved in conjugal transfer however, the effects of mutations have not yet been documented. *Mesorhizobium huakuii* has been demonstrated to produce AHLs in one strain, and decreased AHL production in this strain was associated with the development of a thinner biofilm [42]**.**

A nitrogen-fixing endosymbiont known as *mesorhizobium loti* associates with the *lotus corniculatus*. For QS systems, two *M.loti* strains have been examined. Three distinct LuxI -type synthases, mrlI2, mrlI2, and mrlI3 yang, were discovered in *M. loti* NZP2213 in the first investigation[43] is in-charge of producing 3-oxo-C6-HSL, C10-HSL, and C12-HSL. The production of C12-HSL was faulty in the mrl1 mutant, whereas the other three AHLs could not be produced by the mrl2 mutant, and no measurable AHL molecules were produced by the mrl3 mutant. Although QS had no effect on growth in NZP2213, it did have an impact on nodulation efficiency, suggesting a key involvement in the early stages of symbiosis[43]**.**

Quorum sensing in non-symbiotic bacteria

Free-living, plant-growth-promoting soil bacteria, often known as PGPRs, can stimulate plant development by colonizing the plant root. These are linked to the rhizosphere, an integral part of the soil ecosystem that facilitates interactions between plants and microbes. It has been demonstrated that bacteria from the species *Azospirillium, Bacillus, Burkholderia, Klebsiella, Pseudomonas,* etc. were identified as a PGPR. These PGPR stimulate the generation of phytohormones, provide biologically fixed nitrogen, and boost phosphorous uptake by solubilizing inorganic phosphates, all of which have a direct impact on plant growth. Through suppressing bacterial, fungal, viral, and nematode diseases, these bacteria have an indirect impact on plant growth[59]**.** There are some details about non symbiotic bacteria and their quorum sensing mechanism.

Klebsiella

Natural populations of *Klebsiella* spp. can be found in soil as free-living diazotrophs or as endophytes in the roots of numerous plant species. About 30% of strains have the ability to fix nitrogen in anaerobic environments, while isolates related to these diazotrophs are also linked to human illnesses[60]**.**

There are two quorum sensing mechanisms known to exist in *K. pneumoniae*. *Klebsiella pneumoniae* uses Autoinducer type II for quorum sensing. It is thought that Type II QS facilitates interspecies communication, permitting the bacteria to respond to both their own AI-2 and the AI-2 produced by other species. LuxS gene is responsible for formation of AI-2 molecules which controls gene expression and processes such biofilm formation [61], [62]**.** LuxS converts S- ribosylhomocysteine (SRH) to 4,5- dihydroxy-2,3-pentanedione (DPD)[61]. The unstable DPD form spontaneously cycles to create a furanosyl borate diester (the AI-2 molecule)[63]**.** According to [64]**,** the biosensor strain V. harveyi BB170 can be used to identify the AI-2 molecule-based QS found in *Klebsiella pneumoniae.*

[65] describe the identification of *K. pneumoniae* strain CSG20, a clinical isolate that is multidrug resistant, using MALDI-TOF mass spectrometry. We used HPLC- GC to further validate quorum sensing activity in this strain and presented proof that K. pneumoniae strain CSG20 generated N-hexanoyl-homoserine lactone (C6-HSL).

Dorsal human tongue profiling research revealed the subsequent AHL-mediated process. N-octanoyl homoserine lactone (C8-HSL) and N-3-dodecanoyl-L-homoserine lactone (C12-HSL) were found to be the AHL molecules generated by *K. pneumoniae* by high resolution mass spectrometry investigations [66]**.**

Pseudomonas

Pseudomonads are widespread Gram-negative bacteria that may adapt to exist in a variety of environmental niches and have the potential to develop into significant and harmful human diseases. Pseudomonads are investigated for their functions as opportunistic human diseases like *P. aeruginosa* infections and plant pathogens like *Pseudomonas syringae*. They are also investigated for their capacity to colonise plant-related niches, such as the rhizosphere (e.g. *P. aeruginosa, Pseudomonas fluorescens, Pseudomonas putida, Pseudomonas aureofaciens,* and *Pseudomonas chlororaphis*), where they can function as plant-beneficial bacteria by combating plant-destructive microorganisms and by producing characteristics that directly affect plant development and disease resistance[67] **.***P. aeruginosa* has undergone AHL-dependent QS experiments, making it one of the most researched bacterial systems. The las and rhl AHL QS systems are both present in *P. aeruginosa*. In the las system, the lasI gene product drives the production of N-(3-oxo-dodecanoyl)-L-homoserine lactone (3-oxo-C12-AHL), which interacts with LasR and activates target promoters. The cognate regulator RhlR interacts with N-(butanoyl)-L-homoserine lactone (C4-AHL), which is produced under the control of rhlI, and activates target gene promoters. *P. aeruginosa* produces a third signalling molecule, 2-heptyl-3-hydroxy-4(1H)-quinolone, called Pseudomonas Quinolone Signal (PQS) The synthesis of numerous virulence factors, such as elastase, alkaline protease, exotoxin A, rhamnolipids, pyocyanin, lectins, superoxide dismutases, and biofilm formation, has been revealed to be tightly regulated by the Las and Rhl systems [68], [69]**.** P. fluorescens strain 395 generated C4-HSL and 3OC8-HSL, while P. fluorescens 07 and P. fluorescens UK4 produced both short-chain and long-chain AHLs [70], [71]**.** Many publications have revealed the structures of the homoserine lactone molecules (HLSs) produced by P. fluorescens.

Bacillus

The proteins ComQXPA are part of a QS system in B. subtilis that has been extensively researched. ComP is the sensor protein kinase and ComX is the autoinducer that make up the ComP-ComA two-component signal transduction system. ComA is the system's cognate DNA-binding response regulator. Processing, modifying, and exporting ComX are necessary steps in order to produce the mature QS signal. ComX's extra cytoplasmic attachment to ComP's receiver domain activates ComA in the cytoplasm by phosphorylating it. Through control of degQ transcription, the phosphorylated form of ComA positively regulates the production of surfactin and indirectly triggers the production of other public goods. Exoproteases and other extracellular enzymes are synthesised as a result of DegQ modulating DegU phosphorylation[72]**.**

Bacillus subtills has a particular kind of LuxS gene that produces autoindicer-2 molecules, which are the constituent parts of the QS mechanism and are in-charge of producing biofilm [73], [74]**.**

Azospirillium

As a free-living diazotroph, *Azospirillum* can stimulate the development of grasses and cereal plants, increasing crop yield by up to 30%. This effect is mostly related to the production of phytohormones, particularly indole-3-acetic acid (IAA). Out of the 40 strains studied, four strains from the *lipoferum* species that were isolated from rice have recently been reported to produce AHL. Two strains of *A. lipoferum* had their AHL molecules structurally identified. *A. lipoferum* TVV3 produces N-3-oxo-octanoyl-homoserine-lactone (3oxo,C8-HSL), C8-HSL (N-octanoyl-homoserine-lactone), 3oxo,C10-HSL (N-3-oxo-decanoyl-homerine lactone) 3OH,C10-HSL (N-3-hydroxy-decanoyl-homoserine-lactone) and C10-HSL (N-decanoyl-homoserine-lactone), whereas *A. lipoferum* B518 produces 3oxo,C6-HSL (N-3-oxo-hexanoyl-homoserinelactone), C6-HSL (N-hexanoyl homoserine-lactone), 3oxo,C8- HSL, 3OH,C8-HSL and C8-HSL. The involvement of AHL-regulated functions in *Azospirillume* plant interactions is still debatable because the genetic factors required for AHL production (luxI and luxR homologs) could only be found in *A. lipoferum* TVV3 and mutants lacking in AHL production could not be created through allelic exchange[75]**.**

Burkholderia

All *Burkholderia* species exhibit quorum sensing using N-acyl homoserine lactone signals, which is thought to be crucial for lifestyle changes like colonisation and niche invasion. The quorum sensing mechanism of *burkholderia* sp. is of the LuxS/R type. Burkholderia sp. produce various forms of AHL molecules, including N-hexanoyl-L-homoserine lactone C6-HSL, C8-HSL, OHC8-HSL, OC14-HSL. Some other AHL molecules produce by different sp. Of Burkholderia gene – burkholderia cepacian complex, Burkholderia

pseudomallei Group, Plant-Beneficial and Environmental (PBE) Group. Burkholderia cepacia complex (BCC) is made up of 17 different species, including *B. cepacia, B. multivorans, B. cenocepacia, B. vietnamiensis, B. ambifaria, B. stabilis, B. dolosa, B. anthina, and B. pyrrocina* [76]. The BCC group's luxI/R homologs cepI and cepR make up the AHL QS. The C8-HSL and C6-HSL, two AHL signals, are produced by CepI in varying degrees. CepR attaches to the plentiful cognate C8-HSL and then reacts to it.

The subgroups of Burkholderia mallei *and B. pseudomallei* make up the *Burkholderia pseudomallei* group. Both are distinguished by additional luxR homologs and multiple AHL QS systems. B. mallei's entire QS systems are known as BmaI/R, and their luxR homologues, bmaR1 and bmaR3, respectively, respond to signals generated by nearby luxI homolog genes, bmaI1 and bmaI3, in order [77]. In *B. pseudomallei*, BmaI1/R1 and BpsI1/R1 have sequence similarities and both produce and react to C8-HSL. BmaI3 produces multiple AHL molecules and includes abundant levels of N-3-hydroxy-octanoyl-HSL. BmaI3 also produces small amounts of N-3-hydroxy-decanoyl-HSL, N-3-hydroxy-hexanoyl-HSL and 3OHC8-HSL. The most prevalent product, 3OHC8-HSL, causes BmaR3 to react [77].

Three luxI/R pair homologs—bpsI1/R1, bpsI2/R2, and bpsI3/R3—as well as two orphan or single luxR regulator homologs—bpsR4 and bpsR5—have been found in the *B. pseudomallei* genome. Most of the QS genes are located on chromosome 2, with the exception of bpsR5, which is located on chromosome 1 [78]. C8-HSL is the main AHL produced by BpsI1, whereas BpsI2 and BpsI3 are mostly linked to N-3-hydroxy-octanoyl homoserine lactone and N-3-hydroxy-decanoyl homoserine lactone, respectively [76], [79].

Burkholderia sp., a plant-beneficial microorganism, has two Qs genes: xenR2/xenI2 and braR/rsaL/braI. Some Burkholderia xenovorans, graminis, and phytofirmans subclasses of the PBE group members have an extra AHL system that is similar to LuxI/R pairs in other Burkholderia species. Numerous AHLs, such as 3-oxo-C6-HSL, 3-oxo-C8-HSL, 3-oxo-C10-HSL, 3-oxo-C12-HSL, and 3-oxo-C14-HSL, are produced by BraI. 3oxo-C14-HSL is the AHL that BraR responds to the best, indicating that it is most likely the cognate AHL for BraI/R systems. The XenI2/R2 extra AHL system produces 3-hydroxy-C8-HSL[80]. To control its numerous biological functions and pathogenicity, *Burkholderia cenocepacia* has two different quorum-sensing (QS) systems: the cis-2-dodecenoic acid (BDSF) system and the N-acyl homoserine lactone (AHL) system. The two systems indicated above have overlapping impacts on a number of biological processes, including motility, biofilm formation, and the synthesis of virulence factors. RqpSR, a two-component system, was recently discovered to regulate the transcriptional expression levels of signal synthase-encoding genes in B. cenocepacia, hence controlling the generation of BDSF and AHL signals[81].

Role of Quorum Quenching in Biocontrol Activity-

Quorum Quenching

Quorum quenching is the process that inhibit the bacterial cell to cell communication. The aim of quorum quenching strategies is not to kill or inhibit the growth of microorganism rather they affect expression of specific function. It is most common in niches where bacterial populations compete for scarce resources that one bacterial species may have an advantage over another in its capacity to disrupt quorum sensing. Similar to how the host's capacity to interfere with bacterial cell-cell communication may be crucial in preventing the colonisation of harmful bacteria that use quorum sensing to coordinate virulence. In order to prevent bacterial cells from communicating with one another, quorum quenching has developed as a mechanism[82]. This is an important quality to develop for long-term biocontrol or therapeutic methods in the current environment of increasing antibiotic resistance[83]. Quorum quenching compounds are produced extracellularly by various marine bacteria, fungus, algae, bryozoans, corals, and sponge [8]. Halogenated furanones of the Red alga *Delisea pulchra* was the originator of the first marine quorum quenching compound. *Delisea pulchra* has yielded more than 20 distinct halogenated furanones with antifouling and antibacterial characteristics[9]. Cyclic dipeptide 2,5-piperazinedione, which functions as a quorum quencher, inhibits quorum sensing dependent characteristics, such as elastase activity, protease activity, and the synthesis of pyocyanin [84]. According to studies by [85] several of the quorum quenching bacteria were isolated from healthy coral species. Anti-QS chemicals found in corals may hold the key to understanding the rivalry amongst coral-associated microorganisms. To minimise undesired marine biofouling, quorum quenching substances are released from the dominating communities.

There are many quorum quenching strategies describe below.

A. **Modification of Acyl chain:** Only bacteria were found to modify the acyl chain. In a strain of *Rhodocuccus erythropolis,* the first AHL oxido-reductase activity was discovered. An AHLase that oxidises fatty acids and N-fatty acyl amino acids is P450 monooxygenase, which is derived from Bacillus megaterium. Here, the signal's structure changes rather than the AHL molecules being destroyed, and this change may have an impact on how the QS-related processes are regulated[83], [86].

B. **Amide bond hydrolysis -** The enzymes necessary for the total and irreversible breakdown of AHLs are known as AHL acylases. They are hydrolysed, releasing the relevant fatty acid and homoserine lactone. Both prokaryotes and eukaryotes were described as having this enzymatic activity. Variovorax paradoxus was the first to exhibit this type of enzymatic activity, as shown by [83], [87].

C. **Lactone hydrolysis -** In this instance, AHL lactonases cause the homoserine lactone ring of the AHLs to hydrolyse, which results in the production of acyl homoserine. The medium can be made more acidic to stop this reaction because it resembles lactonolysis that is pH-mediated. The first evidence of AHL-lactonase activity was found in *Bacillus* sp.[83], [88].

D. **Paraoxonase enzymes-** In human epithelial cells, the paraoxonase enzyme was used to inactivate AHL. Later, it was discovered that the sera of 6 mammalian species—human, bovine, sheep, horse, mouse, and rabbit—contain significant amounts of these AHL inactivation abilities. These AHL inactivation enzymes depend on the Ca2+ ion and have properties similar to lactonase in terms of their characteristics. These paraoxonase enzymes provide hydrolytic functions that are crucial for human health (PONs). The paraoxonase enzymes PON1, PON2, and PON3 are among them. These enzymes are essential for the detoxification of organophosphates and the metabolism of drugs [8].

Natural quorum quenching compounds

The capability to affect QS has been tested for a variety of drugs. For millions of years, plants and fungi have coexisted with QS bacteria, and some of them are predicted to produce quorum quenching substances. Plants may have evolved to create quorum quenching compounds (antiquorum sensing compounds) that can be used to defeat quorum sensing diseases that invade plants since they do not now possess an advanced immune system like humans and other mammals do [89]. A Penicillium species was discovered to produce secondary metabolites with quorum-quenching properties. Patulin and penicillic acid (PA), two of these substances that have been discovered, specifically target the quorum sensing regulators Rh1R and LasR.

It has been discovered that certain plants may create compounds that can interfere with bacterial quorum sensing. These include *Pisum sativum* (pea), *Daucus carota subsp. sativus* (carrot), *Glycine max* (soybean), *Capsicum chinense* (chilli), *Nymphaea* (water lily), *Solanum lycopersicum* (tomato), and *Allium sativum* (garlic) [8]. The first known flavonoid, flaven-3-ol catechin, was discovered in the bark of Combretum albiflorum, and it inhibits Rh1R to reduce the synthesis of virulence factors in *Pseudomonas aeruginosa* PAO1 [90], [91].

Another class of phenolic compounds known as hydrolysable tannins have demonstrated quorum sensing inhibition against *Chromobacterium violaceum* and *Pseudomonas aeruginosa* in diverse plant species [91], [92]. Farnesol, a common sesquiterpene, has been discovered to be used by *Candida albicans*, an opportunistic pathogen, as a quorum-sensing signal that suppresses Pseudomonas quinolone signal (PQS) circuit of *Pseudomonas aeruginosa* by promoting ineffective contact between PqsR and the pqsA promoter [91], [93] According to studies by [93], farnesol may likely play a part in interkingdom communications. Cinnamaldehyde has been discovered to be efficient at inhibiting the QS mechanism in *Vibrio harveyi* at low doses [91].

In the marine environment, corals, sponges, algae, bryozoans, bacteria, fungi, and algae are the most frequent sources of quorum quenching substances. Diverse species of marine cyanobacteria have been reported to contain AHL-dependent quorum sensing inhibitors. Tumonoic acids (E, F, G, and H) are isolated from *Blennothrix cantharidomum* and suppress the bioluminescence of *Vibrio harveyi* BB120 without affecting bacterial growth. It has been discovered that tumonoic acid F is more powerful than the other tumonoic acids [91], [94]. Honaucins A–C, which were isolated from *Leptolyngbya crossbyana*, are discovered to exhibit dual action, which means that they function as both anti-inflammatory and anti-quorum sensing chemicals [89]. In the presence of exogenous AHLs, the Gram-positive bacterium *Halobacillus salinus* can suppress the manufacture of violacein in *Chromobacterium violaceum* CV026 by producing N-(2- Phenylethyl)-isobutyramide and 3-methyl-N-(2-Phenylethyl)-butyramide [91]. Both Gram-positive *Bacillus cereus* and Gram-negative *Marinobacter* sp. SK-3 produce diketopiperazines (DKPs) which inhibit AHL dependent Quorum Sensing [91], [95]. *Chromobacterium violaceum* CV026 is inhibited by piericidin, an identified compound from marine actinobacteria [91], [96].

AHL mimic compounds (Interaction of Plant and AHL molecules)

Plants develop AHL mimic chemicals in response to interactions with rhizosphere bacteria that produce AHL molecules [10]. Although it is chemically distinct from AHLs and is a derivative of riboflavin, lumichrome was the first eukaryotic compound to be recognised as a substance that might activate bacterial QS systems [97]. The AHL-binding domain of the LasR reporter protein, which is a LuxR-type AHL receptor, is most likely the site of direct interaction between lumichrome and riboflavin [98]. These substances are known as AHL mimics. Other plant metabolites that are potential AHL mimics were

subsequently discovered, most of which were phenolic in character. In *Pseudomonas aeruginosa*, rosmarinic acid, a phenylpropanoid derivative, promoted RhlR transcription regulator function [99], [100]**.** Some bacteria can recognise the unique QS signal formed by the lignin precursor, p-coumaric acid, which is released by plant roots [101]**.** Numerous plant species include the flavonoids catechin and naringenin, which have the ability to mimic the QS-activities [90]**.**

It's interesting to note that the QS signals of rhizobacteria promote the synthesis of AHL mimics in plants. The Medicago truncatula's flavonoid production was enhanced by bacterial AHLs [102]**.** The *P. aeruginosa* PAO1 strain invaded the plant, causing the roots to secrete rosmarinic acid [100]. These findings compellingly demonstrate that plants can detect bacterial signals and produce AHL mimics in response. [103] demonstrated that Bradyrhizobium species interact with *Arachis hypogaea* L. seed and root exudates to produce AHL mimic molecules. Seven-day-old chickpea seedlings produced in vitro and treated with plant growth-promoting microorganisms (PGPRs) were utilised to screen for AHL mimicking compounds as well as secondary metabolites like phenolics and flavonoids and phytochemicals like phytohormones[104]

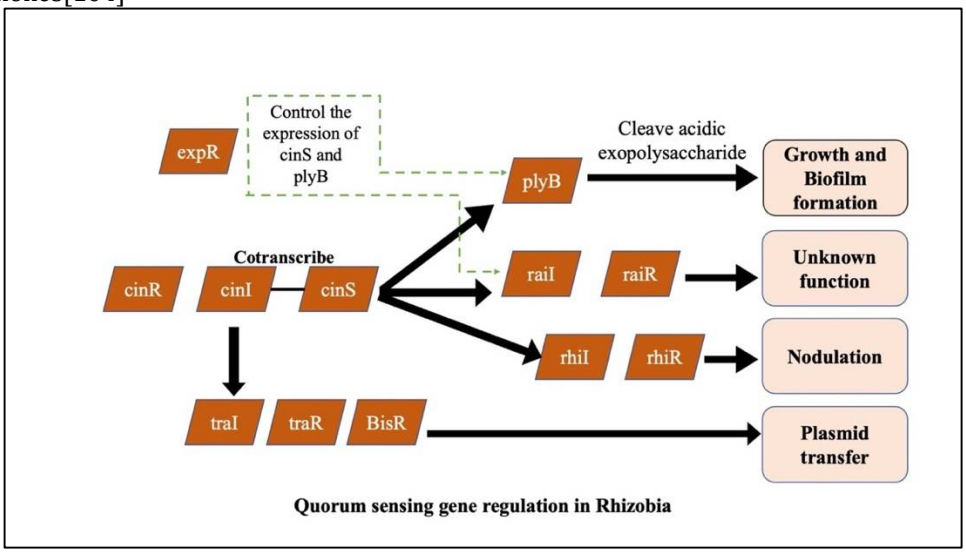

Figure 1 Quorum sensing gene regulation in Rhizobia- In rhizobia, the cinI/cinR QS system stimulates the expression of other quorum sensing systems since it is located at the top of regulatory networks. cinI induce the expression of traI along with BisR regulate the plasmid transfer. cinS Cotranscribe with cinI and control plyB, raiI, RhiI gene expression. Here plyB regulate biofilm formation, raiI gene have unknown function and rhiI function involved in the nodulation process. expR regulate the expression of plyB and cinS

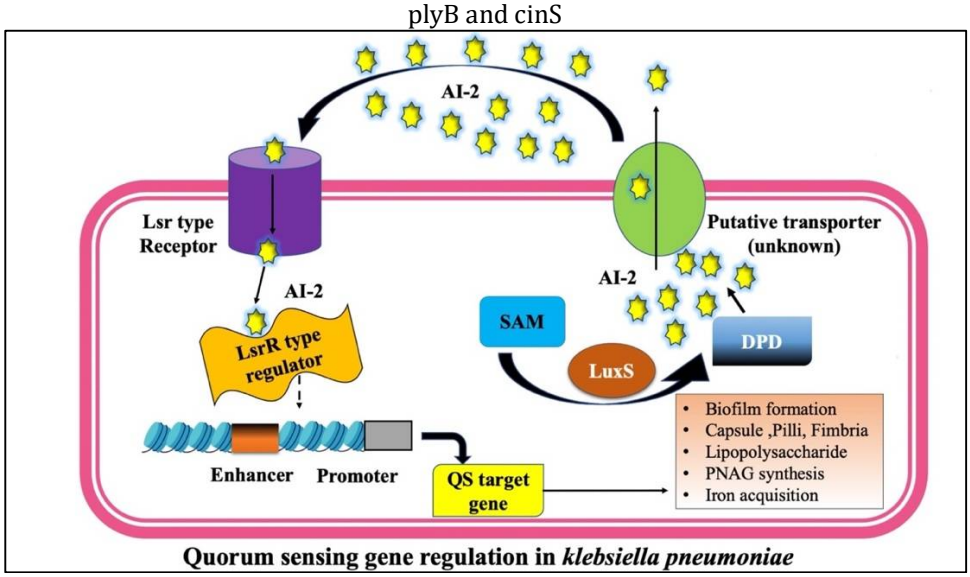

Figure 2 Quorum sensing gene regulation in non -symbiotic bacteria – AI-2 dependent regulated quorum sensing in klebsiella pneumoniae. AI-2 is expressed by a luxS homolog, as well as N-octanoyl homoserine lactone and N-3-dodecanoyl-L-homoserine lactone. LuxS convert S-adenosyl methionine to 4,5 dihydroxy 2,3

pentanedione (DPD) and they produce AI-2 molecules. LuxS gene associated with the expression of lipid polysaccharide synthesis genes and their expression of capsule, fimbria, PNAG synthesis and Iron acquisition as well as biofilm formation.

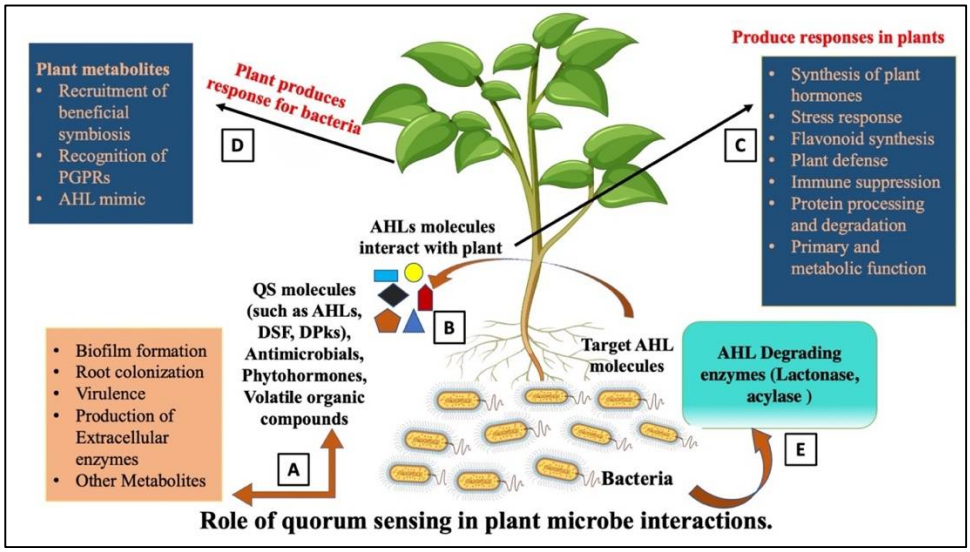

Figure 3 Role of quorum sensing in plant microbe interactions – [A] Bacteria interact with the plant by biofilm formation and root colonization. **[B]** Bacteria produce AHL molecules by QS mechanism**. [C]** AHL molecules interact with the plants and plant produce Reponses. **[D]** Plant produce repones for bacteria that is beneficial for the bacteria.**[E]** Bacteria produce AHL degrading enzymes (Lactonase, acylase, oxidoreductase).

Table 1 Quorum sensing system in member of Rhizobiaceae family.

S.No.	Organism /strains	Legume host	Gene and location	Signalling molecules	Phenotype regulated	Reference
	Rhizobium leguminosarum bv.viciae	Vicia sativa	cinR/cinI (chromosome)	3-OH-C14:1-HSL	Growth inhibition	[25]
			traR/traI (pRL1JI)	3-OXO-C8-HSL,C8-HSL	Plasmid transfer	[44]
		Pea	rhiR/rhiI (pRl1JI)	C6-HSL,C7-HSL,C8-HSL	Nodulation efficiency	[23], [45], [46]
			ExpR, CinS		Regulation of CinR/CinI-RaiR/RaiI system	[47]
	bv.phaseoli		raiR/raiI (non-symbiotic plasmid)	3-OH-C8-HSL,C8-HSL	unknown	[27], [48]
	Sinorhizobium meliloti strain Rm1021	Medicago sativa	sinR/sinI (chromosome)	3-oxo-C14-HSL, C16:1-HSL,C-18-HSL,C12-HSL	EPSII production, swarming	[21], [30], [31], [49]
		alfalfa	expr (chromosome)	C16:1-HSL	EPSII production, swarming	[32], [49], [50]
			Mel (putative)	C8-HSL,other short-chain AHLs	Unknown	[31]
	Sinorhizobium Strain Rm41	Medicago trunactula	traR/traI (pRm41a)	3-oxo-C8-HSL	Plasmid transfer	[31]
	Sinorhizobium fredii HH103	Glycine max and Glycyrrhiza uralensis	TraI-TraR and SinI-SinR(-ExpR)	C8-HSL, 3-oxo-C8-HSL, C12-HSL, C14-HSL,	plasmid transfer, production of surface	[51]

				and 3-oxo-C14-HSL -short- and long-chain AHLs	polysaccharides, motility, growth rate and nodulation.	
	Rhizobium sp. Strain NGR234	Vigna unguiculata	traR/traI (pNGR234a) unknown genes (chromosome)	3-oxo-C8-HSL other AHLs	Plasmid transfer Growth inhibition	[52]
	Bradyrhizobium Japonicum USDA110	Glycine max	Unknown	Bradyoxetin	Nod gene control	[35], [38]
	*japonicum*USDA110 and *B.elkanii*	Glycine max	BjaR/BjaI	Isovaleryl -HSL	Unknown	[39]
	B. japonicum	Glycine max	Unknown	Acyl- HSLs	Unknown	[53]
	B.sp. native strains.	Arachis hypogaea	Unknown	3-O-C10-HSL 3-O-C12-HSL 3-O-C14-HSL	Biofilm formation, auto aggregation, swimming motility	[54]
	B. sp. ORS278 B. sp. BTai1	Aechynomene genus	BraR/BraI	Cinnamoyl-HSL	Colonization of endophytic root	[40], [41]
	Mesorhizobium M.tianshanense	Glycyrrhiza uralensis, various legume plant species	MrtR/MrtI	C8-HSL 3-O-C8-HSL 3-O-C12-HSL	Growth rate, nodulation	[55], [56]
	Mesorhizobium loti	Lotus corniculate, various legume plant species	TraR/traI	3-O-C6-HSL	Plasmid transfer	[57]
	Rhizobium etli CNPAF512	Phaselous valgaris	CinR/CinI	3-OH-(slc)-HSL	Nitrogen fixation, symbiosome development, growth inhibition, swarming motility	[27]
			RaiR/RaiI	Short chain HSL	Nitrogen fixation, growth inhibition	[27]
	CFN42		TraR/TraI	3-O-C8-HSL 3-OH-C8-HSL	Plasmid transfer	[28]
	Rhizovium etli RT1	L. culinaris	Unknown	3-oxo-C8-HSL and 3-OH-C14-HSL	Bacterial motility and biofilm formation	[29]
	Agrobacterium tumefaciens		TraR/TraI	3-O-C8-HSL	Plasmid transfer	[58]
			TraR2/TraI2	3-O-C8-HSL	Unknown	

CONCLUSION AND FUTURE PROSPECTIVE

Recent studies have revealed that quorum sensing is a widespread worldwide regulating mechanism of gene expression in a density-dependent way among many bacteria, including both harmful and beneficial species. Plant associated microorganism, PGPR symbiotic and non- symbiotic have QS mechanism. By this mechanism these bacteria coordinate to each other and regulate their specific phenomenon. Some of these are crucial for the interaction with the host plant or other bacteria. These bacteria produce Autoinducer signalling molecules. There are numerous QS systems however they are primarily investigated and reliant on LuxI/LuxR in gram negative. The signal molecules support not only in signaling within bacterial population in the rhizosphere but also contribute in plant-microbe interactions.

These signal molecules facilitate intercellular communication among intra species, interspecies and between bacteria and higher organisms. Some bacteria produce AHL degrading enzymes that inhibit the QS mechanism, this phenomenon is called Quorum quenching. AHLs that affect microbial consortia composition and crucial plant functions are produced by plant-associated bacteria. Plants are able to detect and react to bacterial AHL signals. Apart from adapting to changeable conditions, plants release their own signals that can mimic AHLs. According to recent findings, bacteria create substances that serve as plant signals receptors. The treatment of plants with AHLs causes a plant response that increases tolerance to infections and stressors.

There are further questions for which further in-depth research is still required to fully understand the mechanisms behind these relationships. In addition, more research is required to determine how QS-

mediated signalling and other signalling systems in the rhizosphere contribute to the development and maintenance of a dynamic root microbiome. A greater understanding of all these factors is anticipated to open up new opportunities to modify the root microbiome through the employment of the right consortia of advantageous microorganisms for increased crop productivity and soil health.

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