

# Quorum sensing - a promising tool for degradation of industrial waste containing persistent organic pollutants

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## Highlights

- QS Mediates formation of biofilm through AHL.
- Biofilm helps degrade POPs via solubilization and biotransformation.
- Environmental niche, abundance, and population of QS bacteria are reviewed.
- QS-mediated process can be used to treat pulp paper mill waste and PAHs.
- QS plays a role in phytoremediation and the production of VBNC cells.

## ABSTRACT

Restoring an environment contaminated with persistent organic pollutants (POPs) is highly challenging. Biodegradation by biofilm-forming bacteria through quorum sensing (QS) is a promising treatment process to remove these pollutants and promote eco-restoration. QS plays an important role in biofilm formation, solubilization, and biotransformation of pollutants. QS is a density-based communication between microbial cells via signalling molecules, which coordinates specific characters and helps bacteria to acclimatize against stress conditions. Genetic diversification of a biofilm offers excellent opportunities for horizontal gene transfer, improves resistance against stress, and provides a suitable environment for the metabolism of POPs. To develop this technology in industrial scale, it is important to understand the fundamentals and ubiquitous nature of QS bacteria and appreciate the role of QS in the degradation of POPs. Currently, there are knowledge gaps regarding the environmental niche, abundance, and population of QS bacteria in wastewater treatment systems. This review aims to present up-to-date and state-of-the-art information on the roles of QS and QS-mediated strategies in industrial waste treatment including biological treatments (such as activated sludge), highlighting their potentials using

examples from the pulp and papermill industry, hydrocarbon remediation and phytoremediation. The information will help to provide a throughout understanding of the potential of QS to degrade POPs and advance the use of this technology. Current knowledge of QS strategies is limited to laboratory studies, full-scale applications remain challenging and more research is need to explore QS gene expression and test in full-scale reactors for wastewater treatment.

**Keywords:** Biodegradation; Hydrocarbons; Persistent Organic Pollutants; Phytoremediation; Quorum sensing

## 1. Introduction

The first report on the formation of a network by bacteria and their nearby cells in a population was published in 1965, where the “hormone-like activators” was observed to play a significant part in the propagation of bacteria (Tomasz, 1965). These activators have now been identified as autoinducers that trigger quorum sensing (QS). QS is a phenomenon in which the same or different bacterial species communicate with each other using chemical signals or autoinducers, which are essential for gene expression to control their behavior (Shivaprasad et al., 2021; Tripathi et al., 2021a). Two categories of signalling molecules are usually present during the QS. The first category works in a concentration-dependent manner for bacterial cell-to-cell communication, while the second was secreted by a bacterium at different stages of its life cycle; for example, the production of indole by *Escherichia coli* during its growth (Li et al., 2021a). QS is regulated by single-stranded RNAs (sRNAs) that control the expression of a specific gene and provides an important feedback loop (Papenfort and Bassler, 2016). QS controls the behaviors of bacteria enabling them to adapt and survive in stressful environments. It regulates an array of genes, such as biofilm formation, secretion of catabolic enzymes, sporulation, siderophore formation,

pigmentation, N<sub>2</sub> fixation, intracellular dynamics, motility, chemotaxis, clumping, biosurfactant production, exopolysaccharide production, fruiting body development, bioluminescence, cellular evolution, secondary metabolites production, production of viable but nonculturable (VBNC) cells and virulence, etc. (Algburi et al., 2021; Huang et al., 2016; Whiteley et al., 2017; Tripathi et al., 2021 b,c).

Persistent organic pollutants (POPs) are highly recalcitrant and non-biodegradable chemicals due to their complex structures. They persist in the ecosystem and can cause adverse effects through the exposure and bioaccumulation in human and animal tissues as well as biomagnification in the food chains and food webs (Yadav and Chandra, 2018). POPs can cause significant health problems, including multiple types of cancers, birth defects, immune and reproductive system disruption, endocrine disruption, high vulnerability to disease, and decreased intelligence (Li et al., 2021b; Tripathi et al., 2021 d,e). Therefore, the treatment and removal of these pollutants are essential in safeguarding human health and the environment. Various physical, chemical, and biological treatments of POPs have been reported (e.g., Gaur et al., 2018; Trojanowicz et al., 2020). The activated sludge process is commonly used in wastewater treatment, where QS causes the bacteria to aggregate, leading to pollutants removal (Soma et al., 2021). Biofilm-forming bacteria produce an autoinducer, acyl homoserine lactone (AHL), that leads to QS and the subsequent biofilm formation. The resulting biofilm improves the performance of wastewater treatment (Hu et al., 2021; Ma et al., 2018; Maddela et al., 2019). AHL has also been reported to play a vital role in phytoremediation, rhizo-filtration, microbial aggregation and stabilization, granule formation, and exoenzyme secretion (Ma et al., 2016; Sarkar et al., 2020; Tan et al., 2014). Though indigenous free-living bacteria have the capability to metabolize POPs and biotransform heavy metal contaminants, their performance could be affected by their low abundance, limited

bioavailability of the contaminants, or restricted supply of nutrients in the environment (Yu et al., 2021; Chandra et al., 2018 a,b). In contrast, attached and sessile microorganisms in the biofilm communities can flourish due to the structure and protection offered by the self-produced and complex polymeric matrix. Moreover, genetic diversification in biofilms (both aerobic and anaerobic bacteria) enables microbes to complement each other metabolically to better survive in adverse conditions (Duddy et al., 2021). This durability and metabolic range make them particularly useful in bioremediation.

Knowledge of the kinetics of organic pollutants degradation and the mechanisms of toxic metals immobilization in biofilm are likely to maximize the bioremediation potential of the biofilm community. To date, the majority of reviews published on wastewater treatment focuses on either the isolation of microbes and/or the development of wastewater treatment, there is a dearth of information on QS-based wastewater treatment (Feng et al., 2013; Sarkar et al., 2020; Sun et al., 2018). This review aims to provide a comprehensive and state-of-the art information on QS, the potential applications of QS for the treatment of POPs in complex industrial wastewater containing different types of pollutants. In addition, the roles of QS during the production of VBNC cells, which is also an adaptive feature of bacteria under stress conditions. The information will help to provide a throughout understanding of the potential of QS to degrade POPs and advance the use of this technology.

## **2. Overview of Quorum Sensing (QS)**

QS is a form of cross-conversation between bacteria that signal bacteria to synchronize and express their physiological behaviours in a density-dependent manner in response to environmental changes. This exchange is governed by a small-signal molecule, known as

autoinducers (AIs). Autoinducers are synthesized intracellularly and shared with the external environment either actively or passively (Sholpan et al., 2021). Generally, there are three major types of signalling molecules secreted by bacteria during QS. The first is found in Gram-negative bacteria, the second in Gram-positive bacteria, and the third, a non-species-specific hybrid QS, exist between Gram-negative and Gram-positive as “universal language” (Haque et al., 2021). The detail of QS signals and regulatory systems of microorganisms during degradation of industrial waste are shown in Table 1.

Most Gram-negative bacteria have the *luxCDABE* operon with LuxI/LuxR systems for QS (Ameen et al., 2020). When the level of autoinducer is low or absent, the autoinducer-binding domain cover the DNA-binding activity of the carboxy-terminal domain of LuxR. It is released when concentrations of autoinducers reached the threshold, leading to activation (expression) of the target gene of a specific function (Aravinthan et al., 2015). The two-component signal transduction systems (TCSTs) are the most common forms of signal transduction mechanisms in bacteria (Govarathan et al., 2015). Many TCSTs play a significant role in stress adaptation and virulence by initiating signalling cascades in which different sets of genes can be switched on or off (Hudaiberdiev et al., 2015). In general, Gram-positive bacteria use autoinduced peptides (AIP) as autoinducers instead of AHL, with the exception of *Exiguobacterium* isolated from the ocean that is capable of producing C3-oxo-octanoyl homoserine lactone (OOHL) (Govarathan et al., 2018). Gram-negative and Gram-positive bacteria also have a common QS system mediated by autoinducer-2 (AI-2), this type of QS is known as hybrid QS (Govarathan et al., 2016). AI-2 is a novel furanosyl borate diester. One of the most unique characters of AI-2 is the presence of a boron atom. AI-2 is the modified product of 4,5-dihydroxy-2,3 pentanedione (DPD), which is produced by activated methyl cycle (AMC) (Zhang et al. 2011).

**Table 1**

Quorum sensing signals and regulatory systems of microorganisms during degradation of industrial waste.

QS signal and structure	Autoinducers	Microorganisms	Molecular synthase	Regulatory protein	Roles	References
Autoinducers (AI-1) with short chain Molecules, A lactone ring and an acylated chain containing 4 to 18 carbons	C4-HSL	<i>Nitrosomonas europaea</i> , <i>Hyphomicrobium</i> spp., <i>Hydrogenophaga</i> spp., <i>Halobium</i> spp., <i>Pseudomonas aeruginosa</i> , <i>P. putida</i> , <i>Aeromonas hydrophila</i> , <i>Serratia marcescens</i> , <i>Erwinia stewartii</i> G, <i>Sphingobium fuliginis</i> , <i>Sphingomonas</i> sp., <i>Acinetobacter</i> sp.	Lux-M, RH II, AhyI, Asa I, SWrI,	LuxR type Protein RhlR	1. Ammonium-oxidation 2. Denitrifiers 3. Biofilm formation 4. Enzyme production 5. Swarming, 6. Degradation in PAHs, nitrobenzene, toluene, phenol, Hexadecane 7. EPS synthesis,	(Schuster et al., 2013; Yong and Zhong 2013a&b; Perez et al., 2015; Papenfort and Bassler 2016)
	C6-HSL	<i>A. salmonicida</i> , <i>Chromobacterium violaceum</i> , <i>Agrobacterium tumefaciens</i> , <i>Erwinia carotovora</i> , <i>P. aureofaciens</i> , <i>Nitrosomonas europaea</i> , <i>Serratia liquefaciens</i> , Nitrite-oxidizing bacteria <i>Nitrobacter winogradskyi</i> (N. R.), <i>Acinetobacter junii</i> BB1A (NR), <i>Acinetobacter calcoaceticus</i> P23, <i>Pseudomonas putida</i> (N.R.), <i>Bacterella</i> , Yeast biofilm <i>Pseudomonas aeruginosa</i>	AhyI, CV I, YpsI, Yps I, LuxI, HhdS	LuxR type protein	1. Biofilm formation 2. Enzyme production 3. Motility 4. Aggregation 5. Settlement activity 6. Ammonium oxidation, 7. PAHs degradation 8. Regulation of possible nitrogen oxide flux and nitrification 9. Heavy metal tolerance 10. Bioremediation of phenol, 1,2,4-trichlorobenzene mineralization 11. diesel oil degradation	(Yamaga et al., 2010; Mellbye et al., 2016; Shen et al., 2016; Sheng et al., 2017)
	PqsABCDH, PqnAB and pqsH		Las I/RhlI in addition 3,4-dihydroxy-2-heptylquinoline (PQS)	Las R/Rhl R PqsR	1. Biofilm and extracellular enzymes formation 2. Phenol, phenanthrene and nicotine degradation,	(Yong and Zhong 2013 a&b; Toyofuku et al., 2014; Wang et al. 2014a & b Papenfort and Bassler, 2016)
LuxI and RpaI	3-oxo-C8-HSL, C14-HSL, 3OH-C4-HSL, Isovaleryl-HSL, 3-oxo-C12-HSL, P-coumaroyl-HSL, Cinnamoyl-HSL	<i>Pseudoalteromonas</i> sp. 520P (N.R.), <i>Burkholderia cepacia</i> , <i>Pseudomonas aeruginosa</i>	3-hydroxy-butyl HSL, furanosyl borate diester, CAI-1	Lux N, BjaR, LasR, QscR, RpaI, BsaR	1. Biofilm formation 2. PCBs degradation	(Papenfort and Bassler, 2016; Yadav and Chandra, 2019)
Autoinducers (AI-1) with long chain molecules	C8-HSL	<i>Agrobacterium tumefaciens</i> , <i>Pseudoalteromonas</i> sp. NJ6-3-1 (N.R.), <i>Nitrosomonas europaea</i> (N.R.), <i>Roseobacter</i> spp., <i>Marinobacter</i> sp.,	Yps I	-	1. Swimming and Flocculant production	(Guo et al., 2011)
	C12-HSL	<i>Vibrio alginolyticus</i>	Las I	LuxR	1. Ammonium-oxidation, Virulence formation	(Gao et al., 2019; Yadav and Chandra, 2019)
	3-oxo-C6-HSL, C6-HSL	<i>Xanthomonas campestris</i> , <i>E. coli</i> ,	LuxS	Lux P/Q type protein Lux O type protein, mRNA dependent regulation, such as 5SRNAs, SdiA	1. Biofilm formation, 2. wastewater treatment, acid tolerance	
AI-2 (S-THMF-borate) Furanosyl borate diester molecules	LuxS, presence of boron	<i>Vibrio harveyi</i>	-	LuxP or LuxQ	1. Quorum sensing	Papenfort and Bassler (2016)
AI-2 (R-THMF)	LuxS, absence of boron	<i>E. coli</i> , <i>Salmonella typhimurium</i>	-	LsrB	2. Biofilm formation	Papenfort and Bassler (2016)
AI-3 Aromatic compound		<i>Streptococcus gordonii</i>	-	-	1. Biofilm formation	-
Autoinducing peptides (AIP-I) Oligopeptides	Butyrolactonase, Thiolactone [Diketopiperazines (DPKS), cyclo(L-Ala-LVal) and cyclo(L-Pro-L-Tyr)]	<i>Pseudomonas</i> sp. <i>Streptomyces griseus</i> <i>Staphylococcus aureus</i> , <i>B. subtilis</i> (N.R.)	LuxR	-	1. Activates AHL biosensors 2. Pyrene and benzo[a] pyrene degradation	Yadav and Chandra (2019)
Others	Beadyosetin Hydroxy palmitic acid methyl	<i>Rhizobium</i> sp., <i>Bradyrhizobium japonicum</i> , <i>Pseudomonas</i>	Nod gene PheS-pheR		1. Polysaccharide biosynthesis, 2. Nitrogen-fixing	(Bogino et al., 2015; Yadav and Chandra, 2019)

**Table 1 (continued)**

QS signal and structure	Autoinducers	Microorganisms	Molecular synthase	Regulatory protein	Roles	References
	ester [2-(4-[[4-(3-aminoacetate-2-yl)phenyl] (amino)methyl]phenyl) acetate-3-yl amine.	<i>aeruginosa</i> <i>Ralstonia solanacearum</i> <i>Alphaproteo bacteria sp.</i>				
	2-(4-[[4-(3-aminoacetate-2-yl)phenyl] (amino)methyl]phenyl) acetate-3-yl amine	Algae symbiotic bacterium	<i>PhcS-phcR</i>		1. Competence, 2. Morphogenesis	
DSF (cis-11-Methyl-2-dodecanoic acid and butyrolactone)	RpfF	<i>S. maltophilia</i> , <i>Xanthomonas campestris</i>		RpfC	1. Hexachlorocyclohexane bioremediation, 2. High molecular weight PAHs, 3. p-nitrophenol degradation, 4. Biofilm, 5. EPS and extracellular enzymes secretion	(Pompilio et al., 2011; Papenfort and Bassler, 2016; Yadav and Chandra, 2019)
AmbBCDE	Rpf 2-(2-hydroxyphenyl)-thiazole-4-carbaldehyde IQS	<i>Stenotrophomonas maltophilia</i> <i>Pseudomonas aeruginosa</i>		?	1. Cell-cell communication	Abouzahra (2013) Papenfort and Bassler (2016)
DarABC	Dialkylresorcinols	<i>Photorhabdus symbiotica</i>		PauR	Cell-cell communication	(Papenfort and Bassler, 2016; Yadav and Chandra, 2019)
PpyS	photopyrones	<i>Photorhabdus luminescens</i>		PluR	Cell-cell communication	(Papenfort and Bassler, 2016; Yadav and Chandra, 2019)

N.R.-regulatory systems are not reported.

Spatial distribution of microorganisms and mass transformation in an environment are the some of the key factors that affected QS (Gao et al., 2016; Wang et al., 2018). Several new chemical signals, such as diffusible signal variables (DSFs), *Pseudomonas* quinolone signals i.e., 3,4-dihydroxy-2-heptylquinolone (PQSs),  $\pi$ -butyrolactones, indole, butyrolactones, 3-hydroxy palmitic acid methyl ester, and cyclic dipeptides have been reported to extend the behavioral domain of QS signal molecules (Govarthanan et al., 2013). Indole can also act as a QS molecule in *E. coli* and *Salmonella*, which activates the expression of many genes (Sharma et al., 2020; Sharma et al., 2021 a,b). Indole plays an important role in the adaptation of these bacteria in nutrient stress conditions, and in such conditions amino acids become catabolized as an energy source. Genome analysis shows the existence of multiple QS structures in other microorganisms (Personnic et al., 2021), but many have not yet been described either structurally or functionally.



### 3. QS and biofilm

The biofilm matrix comprises of 97% water, which is bound to capsules of microbial cells (Broniewski et al., 2021). Bacterial biofilms have many surface-active groups, which are useful in the immobilization and depletion of pollutants, making them an ideal candidate for the degradation of POPs. Many QS-mediated biofilm microorganisms have been isolated from the POPs contaminated sites, which can be further modified and used for bioremediation. For example, several *Novosphingobium* species isolated from aquatic sources were to degrade of aniline, phenol, 4-chlorobenzene, nitrobenzene, phenanthrene, pyrene, dibenzofuran and carbofuran, pulp and papermill waste. (Gan et al., 2015). Gan et al. (2016) also showed the first functional validation of AHL synthases from the *Sphingomonadaceae* family. *Pseudomonas aeruginosa* has four well-known QS pathways: LasI/LasR and RhII/RhIR are LuxI/LuxR type systems, responsible for elastase and proteases production as virulence factors and biofilms formation; the third PqsR-controlled system is for quinolone production, and the fourth 2-(2-hydroxyphenyl)-thiazole-4-carbaldehyde (IQS) system operates under phosphate stress conditions for phosphate solubilization (Shah et al., 2021). Biofilm formation and virulence are also controlled by 2-heptyl-3-hydroxy-4-quinolone (PQS) generated by the *pqsABCDH* genes (Bruger et al., 2021). Many studies have shown that biofilm is a hot spot of horizontal gene transfer of biodegradation (Abe et al., 2020; Suzuki et al., 2019).

Biofilm formation comprises five stages: reversible adsorption, irreversible attachment, maturation I, maturation II and dispersion (Wang et al., 2021). McLean et al. (1997) first reported on the participation of AHLs during biofilm formations. The biofilm architecture is significantly influenced by QS. The nutrient and oxygen concentrations decrease from biofilm surface to depth, supporting different group of aerobic bacteria to anaerobic bacteria from surface to the core of the

biofilm (Soto-Aceves et al., 2021). The gradient profiles of pH, hydrogen peroxide, nitrate, nitrite, ammonium, methane, chlorine, and carbon dioxide have also been investigated (Sela et al., 2021). These parameters have shown that different chemical niches support the existence of various microbial species within biofilms at different depths.

Environmental microorganisms exist in biofilms have high tolerance against physical, chemical, and biological stresses. Several biofilm-forming microorganisms (bacteria, cyanobacteria, and fungi) are known to have potential in phytoremediation, bioremediation of industrial waste, herbicides, pesticides, fungicides, etc (Jin et al., 2021). QS activity can improve the bacterial growth in biofilms and exopolymeric substances (EPS) composition resulting in effective bioremediation of pollutants by several bacterial species of *Pseudomonas*, *Aeromonas*, *Burkholderia*, *Xanthomonas*, and *Bacillus* genera (Sela et al., 2021). Biosorption, bioaccumulation, and biomineralization of POPs involves several procedures, such as secretion of immobilized enzymes, cofactors, or whole cell as catalysts (Flemming et al., 2016). Bioremediation through biofilm could be promoted by increased gene transfer among biofilm organisms to mixed populations present in biofilms (Soto-Aceves et al., 2021). It can be further improved by genetic engineering of strains to increase the bioavailability of pollutants, and optimization of the physicochemical conditions for biofilm formation (Dogsa et al., 2021).

#### **4. QS and the degradation of industrial wastewater**

The importance of biofilm for enhancing detoxification is now being realized and appreciated. Numerous QS bacteria have been isolated from wastewater treatment systems that provide excellent opportunities to further explore QS-assisted wastewater treatment (Balan et al., 2021; Shah et al., 2021). While, till date, information is still scarce in the following issues: (i) QS between

the microbes in complex industrial wastewater treatment; (ii) gene responsible for QS during the treatment of POPs in industrial waste; (iii) the role of other autoinducers, and autoinducing peptides (AIPs) in wastewater treatment; (iv) environmental impacts on QS; and (v) detailed knowledge of QS during VBNC cells formation during the POPs removal. The following sections aim to address some of these knowledge gaps. Sections 4.1 examines the use of biofilm and the role of QS in biological treatment of wastewater and section 4.2 considers the potential of QS-mediated waste treatment and provides examples in the pulp and papermill industry. In section 3.3, the examples of QS involvement in polycyclic aromatic hydrocarbons (PAHs) removal are highlighted, and section 3.4 provides examples on the role of QS in phytoremediation. Finally, the involvement of QS in VBNC cell formation during POPs removal is discussed.

#### 4.1. QS and the biological wastewater treatment

Many of the environmental pollutants are discharged from industries, for example, pulp and papermill industries, distilleries, tanneries, pharmaceutical industries, fertilizers manufacturers, and pesticides and herbicides manufacturers. Many POPs are hydrophobic tend to accumulate in the food chain, when discharged into the environment they could damage the whole food web and cause endocrine-disrupting effect on aquatic organisms (Chandra et al., 2018b; Yadav and Chandra, 2018). The degradation of POPs remains a challenge because of their stable nature, chemical inertness, hydrophobicity, and toxicity. Conventional approaches, such as physical and chemical process (e.g., coagulation, reverse osmosis, ion exchange, adsorption by activated carbons and natural materials) have been reported for detoxification and degradation of these pollutant (Personnic et al., 2021). However, these methods are expensive and may generate unwanted secondary products (Broniewski et al., 2021). In contrast, biological treatment process for POPs degradation is a more efficient and lower in cost treatment process (Herrero and Stuckey,

2015). Upflow sludge blanket (USB), trickle-bed biofilm bioreactor (TBR), biofilm fluidized bed (BFB), rotating Biological Contactors (RBC), expanded granular sludge blanket (EGSB), and biofilm airlift suspension (BAS) are biofilm bioreactors that have been used for industrial wastewater treatments (Shah et al., 2021). In TBR, wastewater can trickle down on the biofilm surface growing in fixed media. In the case of BFR, polluted water is pumped upward through a column of biofilm-coated beads. In RBC, discs are submerged in the effluent and slowly rotating under natural conditions led to biofilm formation. RBCs have been used for the treatment of water contaminated with heavy metals, volatile compounds, and polyaromatic hydrocarbons (Bruger et al., 2021). Electrochemical membrane bioreactors have been used to treat pharmaceutical wastewater containing chemicals like amoxicillin, carbamazepine and diclofenac, QS also play important role in their removal to protect public health (Borea et al., 2018).

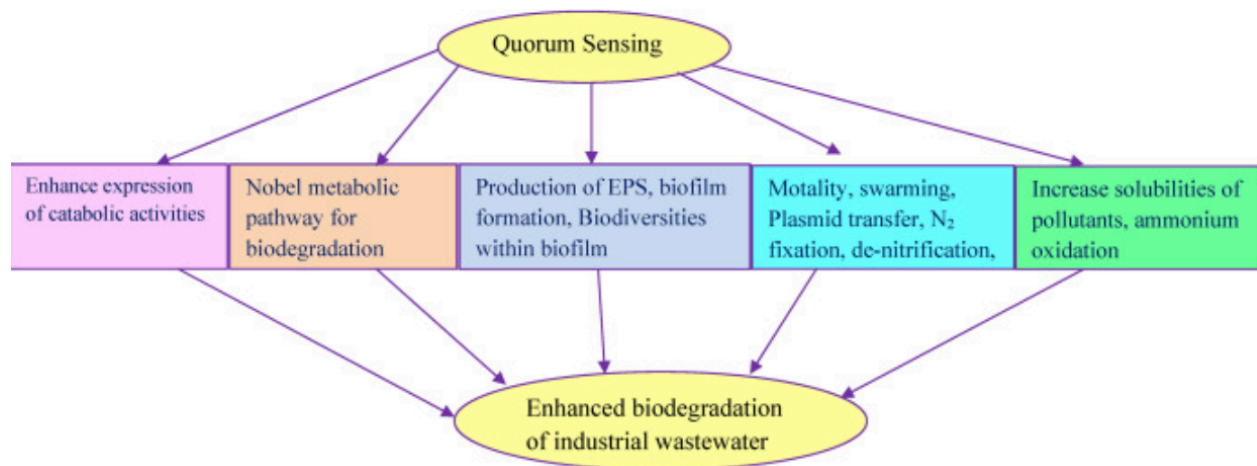
The activated sludge process is an established biological treatment process for treating industrial wastewater. Aerobic granular sludge (AGS) has excellent settling ability and treatment efficiency compared with the traditional activated sludge presumably due to QS and cell signalling among microorganisms in AGS (Wang et al., 2017). Long-chain AHLs are found in the granular sludge, while short and medium acyl chain AHLs spread in the aqueous media (Chen et al., 2019). Song et al. (2014) observed that AHL concentrations are usually higher around the sludge floc surface than in the bulk solution due to the endogenous existence of quorum quenching (QQ) in activated sludge. Activated sludge flocks are aggregates of inorganic, organic particles integrated into a matrix of extracellular polymeric substances with microbial diversities. QS plays a role in the particle size and protein content of bioflocs (Jin et al., 2021). It can also be inferred that the nutritional content of bioflocs in microenvironment is affected by the QS mechanism. It is possible that the microbial structure and diversity of the community is influenced by QS mechanisms, which

affects the amino acid composition of the exoproteins generated by each bacterium. However, it is not clear how QS affects the amino acid composition of microbial extracellular protein or bioflocs. Fatimah et al. (2019) demonstrated that the addition of QS signal molecules enhanced the volume, particle size, protein content, biofloc ammonia, and bioflocs consumption in African juvenile catfish. Wu et al. (2015) demonstrated that the microbial flocculant production was regulated by N-3-Oxo-octanoyl-homoserine lactone (an AI-2) mediated QS mechanisms in *Agrobacterium tumefaciens*. AI-2 is reported to have a crucial role in activated granule formation and maturation process (Zhang et al., 2011; Zhao et al., 2018). Other autoinducers have also been reported in granular flocs and sludge (Balan et al., 2021). Gao et al. (2019) showed that the addition of AHLs to activated sludge increased the rate of ammonia oxidation by ammonia-oxidizing archaea (AOA) and ammonia-oxidizing bacteria (AOB). Xu et al. (2012) reported the efficiency of biofilm to remove  $\text{NH}_4^+\text{-N}$  and chemical oxygen demand (COD) increased from 84.41 to 94.21% and 69.66 to 76.60%, respectively from polluted water. AOB such as *Nitrosomonas*, and *Nitrospira* co-existed in the biofilm, and *Corynebacterium aurimucosum*, *Janthinobacterium* sp., *Pseudomonas* sp., *Sphaerotilus* sp., were found dominant in the oligotrophic nich (Xu et al, 2012). In non-contaminated area, microbes use electron donors as foods that are usually restricted. However, microbes may be stimulated to compete for available acceptors to restore the equilibrium of the system at a polluted site releasing organic electron donors (Sholpan et al., 2021). In the case of anaerobic degradation, other electron receptors are used instead of oxygen, such as iron, manganese, sulfate, nitrate, etc. Sulfur reducing bacteria converts sulfates into sulfides that making it easier to stabilize and remove sulfates from wastewater (Saxena et al., 2019).

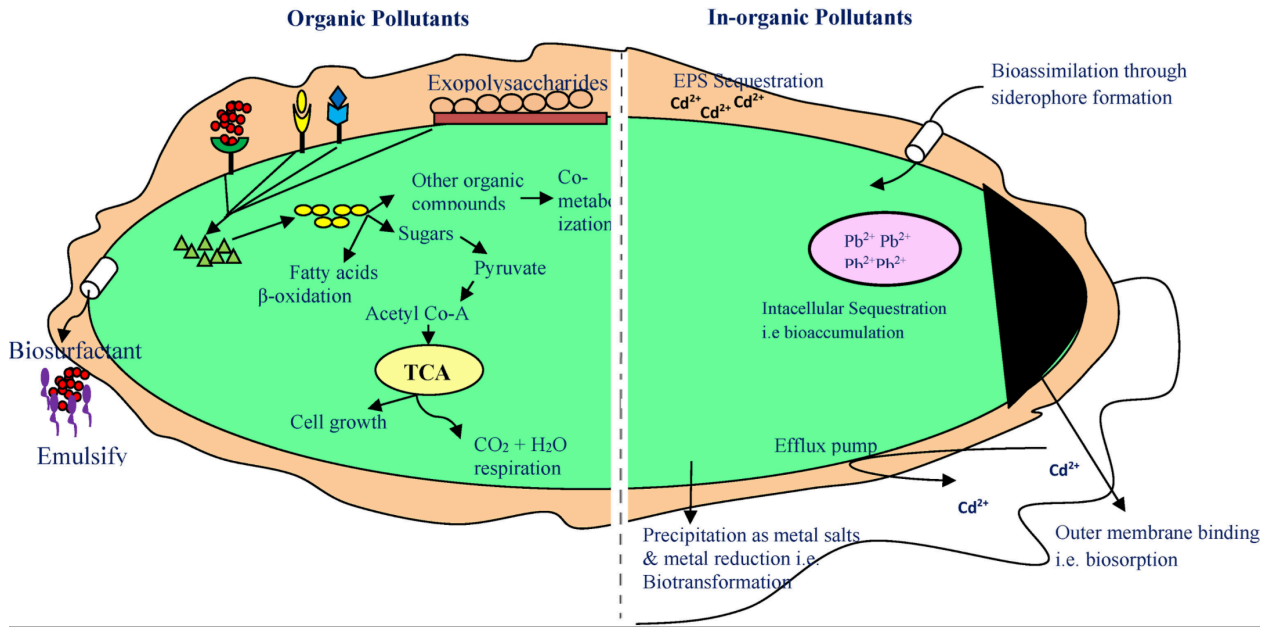
The involvement of QS systems in various bacterial strains during bioremediation of different pollutants are shown in Table 1. Microorganisms that secrete polymers and form biofilms on the

surface of organic compounds can provide a positive niche in stressful settings and helpful in POPs degradation (Li et al., 2021b). Mechanisms of organic and inorganic industrial pollutants removal by biofilm-forming bacteria are portrayed in Figs. 1 and 2. Bioaugmentation by adding exogenous strains is a useful way to improve the biodegradation and detoxification of organic pollutants in sewage treatment, which is also a component of QS. The involvement of AHLs and AI-2 mediated QS systems was demonstrated by bioaugmented processes, particularly in the phase of strain colonization during nicotine removal (Wang et al., 2014a; Chen et al., 2018). In bioaugmentation process, functional genes, strains, or microbial consortia are incorporated into bioaugmented systems to enhance the survival rates and metabolic activities of existing communities. Removal of nicotine by *Pseudomonas* sp. HF-1 has been reported to relate to a QS-regulated biofilm formation in bioaugmented system (Balan et al., 2021). C<sub>6</sub>-HSL, 3-oxo-C<sub>6</sub>-HSL, and 3-oxo-C<sub>8</sub>-HSL were secreted by strain HF-1 as autoinducers that promoted EPS production biofilm formation and swarming, leading to successful colonization and bioaugmentation (Wang et al., 2014a). In another study, nicotine degrading strain *Acinetobacter* sp. TW was used in bioaugmentation process and observed that short-chain AHLs control the biofilm formation, while long-chain AHLs increase resistance to nicotine toxicity. These results showed that different AHLs may perform various functions in bioaugmentation. Survival of microbes under stress conditions might be due to EPS, polysaccharides, proteins, nucleic acids, humic acids, surfactants, divalent ions, and lipids. EPS act as a cementing material and form the main attached matrix for transiently immobilizing biofilm cells, bridging cells, and other particulates (Chen et al., 2016; Shi et al., 2017). As metabolic products and EPS accumulate on bacterial cells, it changes the physicochemical properties of bacterial cells like charge, hydrophobicity, etc. (Ding et al., 2015). The manipulation of AHL material by optimizing the pH of the environment efficiently promoted

EPS secretion, biofilm formation and thus increased effectiveness in bioaugmentation for degradation of POPs (Wang et al., 2014b). The presence of denitrifying bacteria, *Hyphomicrobium spp.*, *Hydrogenophaga spp.* and *Rhizobium spp.* in an aerobic suspended carrier biofilm reactor suggested that not only oxygen and microgradients within the biofilm are present, but aerobic denitrifiers are also present for nitrification and denitrification in the aerobic biofilm (Wu et al., 2021). Sun et al. (2018) reported the biofilm mediated anammox-based nitrogen removal from wastewater. The removal of nitrogen and COD could be enhanced by the addition of AHL in biofilm reactors. Cell aggregation is an important function that regulates biofilm development in several species and is often regulated by QS. Feng et al. (2013) showed QS governing cell aggregation during aerobic granule formation and activated sludge treatment process. *Aeromonas sp.* and *Pseudomonas sp.* are the dominant AHL producers, which are ubiquitously present in activated sludge treatment systems for the treatment of domestic and industrial wastewater. It is noted that wastewater treatments are influenced by many factors, like hydrodynamic condition, dissolved oxygen, temperature, hydraulic retention time, carrier material, etc. The remediation of polluted water, which usually a low level of nutrients, needs to enhance biofilm formation and optimize the microbial community.



**Fig. 1.** Mechanism of biodegradation of industrial wastewater by bacteria showing quorum sensing.



**Fig. 2.** Mechanisms of organic and inorganic pollutants removal by biofilm forming bacteria.

Bacterial QQ has been proven as an innovative approach for biofouling control in membrane bioreactors (MBRs) for advanced wastewater treatment. Several excellent reviews on the QS/QQ studies related to the elucidation and control of biofouling in MBRs have been published recently (Huang et al., 2019; Lee et al., 2018; Liu et al., 2020). The effect of QQ on anoxic/oxic MBRs on microbial communities of biofilm was investigated by Jo et al. (2016) and showed that QQ favours the diversity of microbial communities. Using QQ, the role of QS during aerobic granules formation for wastewater treatment was stabilized (Balan et al., 2021). Tan et al. (2014) reported when the floccular biomass was fully converted into granular sludge, QQ activity of the community was 30% decreased, whereas the concentration of C4-C8 AHLs by 10-100-folds by the initiation of granule formation. This showed the involvement of QS in the treatment of complex wastewater. In-depth knowledge about these processes will be useful for the researcher to develop a suitable technology for the treatment of complex industrial wastewater.



Microbial Fuel Cell (MFC) as a wastewater biological treatment biotechnology has received increasing attention, as simultaneously treat wastewater and generate energy. Generally, the MFC consists of two electrodes in the chamber. The microbe present in the anode chamber breaks down organic waste via enzyme activity, releasing electrons that are transmitted via membranes to the cathode chamber and measuring the electric voltage. It could be possible to increase energy production by QS via the anode biofilm enrichment (Sivasankar et al., 2019). For example, bacterial QS molecules enhanced the lipid content, photosynthetic efficiency of *Chlorella sorokiniana* during power generation in the MFC (Das et al., 2015). QS manipulation has become increasingly important in environmental bioremediation at the population and molecular level. Moreover, manipulation in the QS system also improved the degradation of wastewater by engineering the QS system (Zhang et al., 2016; Zhau et al., 2020).

**Table 1.** Quorum sensing signals and regulatory systems of microorganisms during degradation of industrial waste.

#### 4.2. Case study - QS in degradation of POPs in pulp and paper mill industrial treatment

The pulp and papermill industry is one of the major source of industrial pollutions. Indiscriminate discharge of waste contaminates the surrounding environment due to the presence of several pollutants, including POPs render the receiving water unfit for domestic and irrigation purposes (Yadav and Chandra, 2018). POPs are organic compounds that have a high lipid solubility leading to bioaccumulation of fatty tissues and are resistant to environmental degradation through chemical, biological and photolytic processes (Sholpan et al., 2021). Pulp and papermill wastewater contains a high level of biological oxygen demand (BOD), COD, nitrogen, sulfur, chloride, heavy metals, etc. During industrial wastewater treatment systems, a significant amount of nitrogen content can be reduced by biofilm-forming microbes (Ameen et al., 2020). The presence of nitrifying microorganisms in biofilm is the major reason for successful nitrogen removal during wastewater treatment. Autotrophic nitrifier development and metabolization are control through the QS signal. An AOB *Nitrosomonas europaea* strain produces three acyl AHL signals: C6-HSL, C8-HSL, and C10-HSL for biofilm formation, which play a major role in balancing the nitrogen in the environment (Miller et al., 2020). Zhao et al. (2021) demonstrated that AHLs increased the anoxic AOB activity of autotrophic nitrification/denitrification biofilms under oxygen-limited conditions without influencing the aerobic ammonium-oxidizing bacteria (AerAOB). QS controls heterotrophic nitrification-aerobic denitrification through changes in nitrogen processing enzyme activity (Zhu et al., 2020). The genomes of many nitrifiers and denitrifiers showed putative genes associated with AHL production and QS. Nitrogen oxide fluxes and other significant nitrifying bacterial phenotypes have been shown to involve AHL and bacterial cell-cell signals (Mellbye et al., 2017). The knowledge of QS regulation in denitrification can help

to understand the conversion of nitrate and nitrite towards new solutions to improving bioreactor efficiency.

#### **4.3. QS and polycyclic aromatic hydrocarbons (PAHs) degradation**

PAHs are composed of carbon/hydrogen, fused benzene rings in linear, angular, or cluster arrangements (simple to complex structural set-up). PAH compounds are hydrophobic, organic, and low water-soluble molecules that are resistant to biological, chemical, and photolytic breakdown (Saxena et al., 2019). These pollutants have diverse physico-chemical and toxicological characteristics according to their molecular weight, many are mutagenic, recalcitrant and carcinogenic (Camele et al., 2019). These hydrophobic pollutants are usually not readily available for microbial degradation. However, this limitation could be overcome by biofilms as they could increase the solubility and biotransformation of PAHs (Nakagawa et al., 2020). The application of isolates showing QS-mediated biofilm formation could be a promising strategy to improve the PAHs degradation. Zhang et al. (2021) reported xenobiotic and PAH degradation as a co-metabolism in biofilms in the engineered Biozo process. Increase in *lasI* and *rhlI* expressions have significantly improved PAH degradation by *P. aeruginosa* N6P6. Enhanced expression of the QS gene improves the formation of biofilms and the manufacturing of EPS resulted in degradation of PAH (Mangwani et al. 2015). An increase in the production of AHLs also initiated the biofilm formation in *Bordetella*, which led to enhanced biodegradation of 1,2,4-trichlorobenzene (Sheng et al., 2017). Polychlorinated biphenyl (PCB) and PAH remediation were shown by *Burkholderia cepacia*, a biofilm-forming and AHL-producing strain (Zhong et al., 2021). Dasgupta et al. (2013) observed that the biofilm formation in *Pseudomonas* species enhanced the degradability of crude oil. The efficiency of the planktonic cell and biofilm-assisted degradation of naphthalene with *Pseudomonas stutzeri* T102 is also well documented (Shimada et al., 2012). In the bioremediation

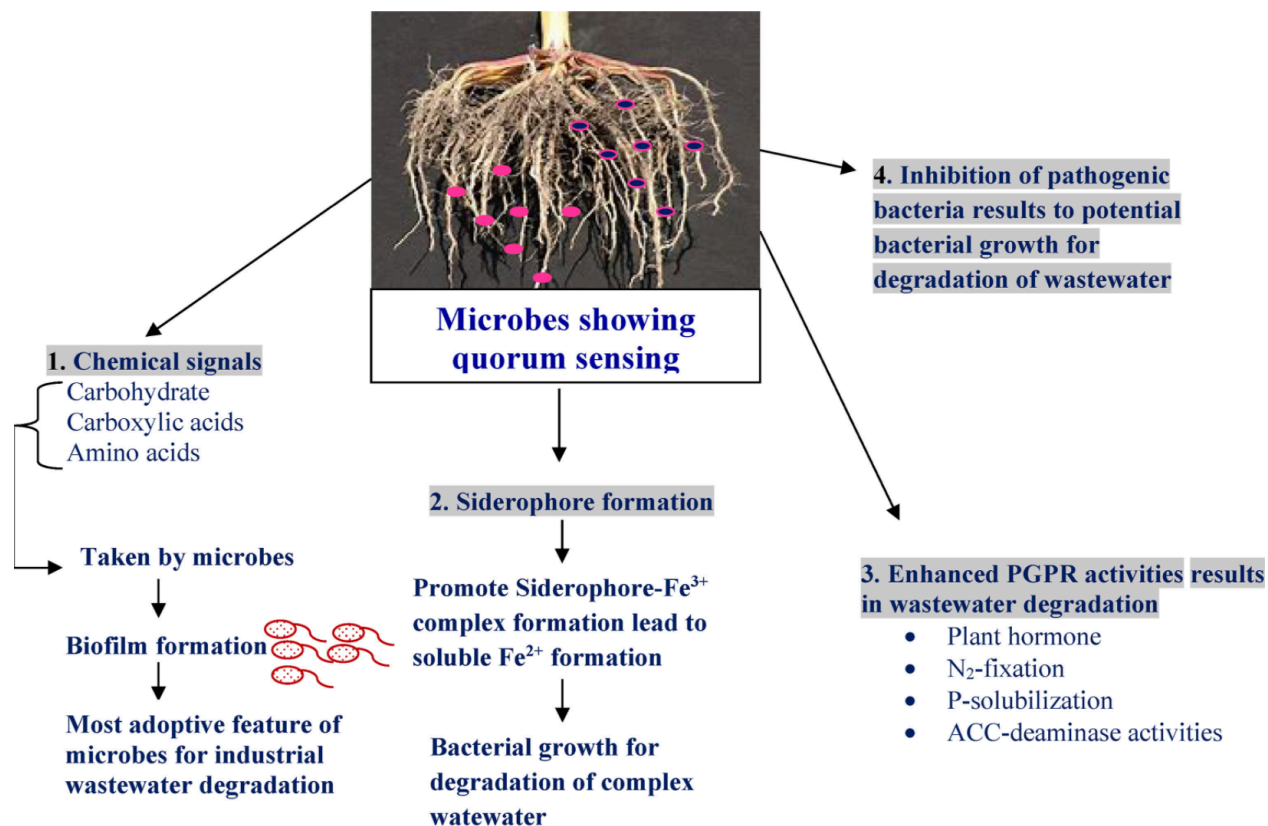
of PAHs i.e., phenanthrene and pyrene, the function of QS genes coding for AHL synthase enzyme (lasI and rhII) have also been established (Kumari et al., 2016). *P. aeruginosa* showed a gene responsible for PAHs degradation, however, no gene acts alone as various stresses often initiate different metabolic pathways, QS, biofilm formation, antibiotic tolerance, etc (Zhang et al., 2021). A network of genes PA3629, PA0817 and PA2516 are involved in PAH degradation. An unknown function gene PA1673 and a phenazine biosynthesis protein PA4211 were associated with a PAH degrading gene PA3389 (Yan and Wu, 2017). The capability of biofilm-associated *P. mendocina* EGD-AQ5 was first time compared with planktonic cells to utilize toxic intermediate catechol during benzoate degradation (Ghosh et al., 2017). The catechol accumulation of certain strains could be caused by the formation of biofilms. Sarah et al. (2013) investigated the strategies taken by microbes to exploit the essential durability of biofilms and the microbiome's varied nutrient cycling for bioremediation. QS system in *Acinetobacter sp.* strain DR1 also made an important contribution in hexadecane degradation and biofilm formation (Yu et al., 2021). Algburi et al., (2021) assessed the removal of hydrocarbons by biofilm-forming bacteria developed on supporting material of vertical flow biofilter in anaerobic condition. The combination of granular activated carbon amendment with biofilm engineering enhanced the PCB bioremediation (Edwards and Kjellerup 2013). In another study, Li et al. (2018) cloned and transformed the nitrile hydratase and amidase genes into the biofilm-forming bacteria *B. subtilis* N4, which play important roles in organonitriles degradation. Sphingomonadales are Gram-negative bacteria of the Alphaproteobacteria family that is mostly reported for their ability to form biofilm and PAHs degradation. A functional LuxI/LuxR-type AHL-mediated QS system has been identified in *Croceicoccus naphthovorans* PQ-2 (Yu et al., 2020). The PQ-2 strain QS system positively regulates LuxI/LuxR-Type QS System for PAH degradation through enhanced hydrophobicity of

the bacterial cell surface and direct and/or indirect induction of PAH degrading genes, *ahdA1e*, *xyIE*, and *xyIG*. The large plasmid in *C. naphthovorans* PQ-2 is responsible for phenanthrene degradation. This megaplasmid contains a cluster of 32 open reading frames for the PAH-degrading gene (Duddy et al., 2021). There are several transposase genes in the flanked regions of the gene cluster, which means that this cluster can be transferred horizontally from other bacteria.

#### **4.4. QS in phytoremediation**

In situ phytoremediation is an effective, sustainable, and cost-effective remediation process for industrial wastewater. The plant and microorganisms that exist in the rhizosphere, the soil region directly influenced by root secretions, are used in plant remediation to promote biodegradation of pollutants. Effective phytoremediation depends on the survival and growth of the plants in the contaminated sites as well as on the rhizosphere's capacity to support an active microbial population of the ground (Shivaprasad et al., 2021). The rhizosphere is a microecological zone of 2 mm thickness around a root, which can create an ecological niche in the soil, where the nutrient rich condition is present. Mechanism of metal and other organic pollutants degradation during phytoremediation includes (i) proton, inorganics, amino acids, and acids contained in root exudate secretion enhancing the mobility of metals and nutrients through acidification; (ii) intracellular interaction of pollutants with various compounds, such as organic acids, phytochelatins and amino acids; (iii) electron transfer with enzymes; and (iv) stimulation of rhizospheric microbial communities (Soma et al., 2021). Microbial biofilms can improve phytoremediation by accelerating plant biomass, phytoextraction, phytostabilization; facilitating soil-to-root bioaccumulation and root-to-shoot translocation (Saekiet al., 2020). A specific bacterial diversity has been observed during phytoremediation of pollutants due to QS (Wu et al., 2020). Comprehensive interactions between microbes and plants through signalling molecules plays a

significant role for the growth of both partners where plants released chemicals work as signals that are recognized by the microbes, which give another signal that trigger changes in plant physiology leading to phytoremediation of pollutants (Zhong et al., 2021). The symbiosis between bacteria and plant play an important role in phytoremediation governed by AHL mediated QS. Successful symbiotic relation involves several steps like exchange chemical signals i.e. QS and differential expression of various genes (Miller et al., 2020). Siderophore formation under iron-deficient condition is also known to be controlled by the QS system (Balan et al., 2021). Siderophores are primarily scavengers of iron, but also scavenge other essential elements i.e., Co, Mo, Mn, and Ni present in the environment making them available to microbial cells. Interaction between plants and microbes for siderophore production during phytoremediation is shown in Fig. 3. Another area of biofilms is the studies of biofilms on leaves of plants are known as the phyllosphere. The phyllospheric biofilms consist of bacterial diversity in an exopolymer. However, the natures of the microbial diversities and their role in the phyllosphere are not fully established.



**Fig. 3** Diagrammatic presentation of role of quorum sensing during phytoremediation: (1) during plant growth, roots release exudates, mainly carbohydrates, carboxylic acids and amino acids, which serve as signalling molecule for microbes and helpful in bacterial growth and degradation of industrial waste. (2) Under iron limited conditions, bacterial cell releases siderophores which are also helpful in bacterial growth and degradation activity. (3) Enhanced PGPR activities result in wastewater degradation. (4) Inhibition of pathogenic bacteria and promote growth of potential bacteria.

#### 4.5. QS in viable but non-culturable bacteria

Viable but nonculturable bacteria (VBNC) normally fail to grow and develop into colonies on the routine bacteriological media but are still alive. VBNC are the living cells that cannot grow in common media, in which they are usually grown, and differ in many ways from dead cells. Dead cells do not express genes and metabolically inactive. VBNC is metabolically active, respire, and constantly transcript to produce mRNA (Boo et al., 2021). The strategy of VBNC cells against the



stress environment is by minimizing energy requirements by reduction of cell size, increased area, and volume ratio and protect the fluidity of the cell membrane (Balan et al., 2021). Because of these changes, VBNC cells are more resistant to the organic and inorganic load. VBNC bacterial can be of great significance in environmental bioremediation. VBNC are again culturable upon resuscitation even they have low levels of metabolic activity. Resuscitation is the process in which VBNC bacteria could be made cultivable under favorable conditions. The recovery-factor (Rpf), plays a critical role in reversed VBNC into the normal condition in environmental bacteria. Su et al. (2018a) showed VBNC bacteria was able to degrade PAHs. Many studies have shown that VBNC is governed by the QS system. Vriezen et al. (2012) demonstrated that desiccated *Sinorhizobium meliloti* cells can enter a VBNC state regulated by QS. In fact, central areas deep within biofilms tend to be hypoxic, resource-limited, and acidic central due to deposits of metabolic waste inside biofilms. The presence of VBNC and persistent cells is therefore promoted in biofilms. These stresses induce the VBNC state in biofilm independently (Flemming et al., 2016). VBNC state microorganism species, induction and resuscitation factors, methods of detection and formation and resurrection mechanisms has been systematically and comprehensively summarised (Dong et al., 2020). Resuscitation of VBNC bacteria improves the bacterial community's cellulose degradation capacity present in compost (Su et al., 2018b). Since VBNC bacteria are regenerated, it may be worked as seed after the reclamation of water leading to increase health issues. Much more work needs to reveal the indigenous microorganisms in the VBNC state from the perspective of environmental functions (Su et al., 2018) to better understand the mechanism of biodegradation of recalcitrant organic pollutants removal from the environment.

## 5. Future outlook

As POPs are more frequently accumulated in the environment, the search for alternatives to minimize toxic effects is continuing. Microbes provides simple, economic, and environmentally friendly strategies to reduce pollution. Biofilm-mediated bioremediation is considered an effective and sustainable method for the restoration of environments. The optimal environment for cell-cell interaction, intercellular genetic material exchange, communication signals, and metabolite diffusion is provided by biofilm. Thus, QS-mediated bioremediation is an improved bioremediation technique for contaminated sites and industrial wastewater treatment. However, as a result of various external stressors, the efficiency and performance of biofilm-producing microorganisms was lower when applied in contaminated field sites compared to laboratories studies (Wang et al., 2021). Mutation, transformation, conjugation, transmission, and horizontal gene transfer could improve the degradation and detoxification of hazardous substrates (Abe et al. 2020), engineered biofilm could be developed to improve the bioremediation processes with enhanced kinetics. Apart from biofilm growth, QS regulates the genesis, synthesis, and manufacturing of biosurfactants and EPS, which are also important for organic and inorganic pollutant removal. Approximately, 100 species of *Proteobacteria* isolated from the plants, rumen, microbial mats, wastewater treatment plant have been reported to secrete AHLs (Ma et al., 2018). For advanced bioremediation practices, it is possible to use the development of bacterial consortia of different species having QS systems together with other defined specificities.

Huang et al. (2016) published a detailed review, which showed AHL-based QS and QQ hold promise to determine the performance of biological wastewater treatments. The roles of QS and QQ in industrial wastewater containing POPs treatment deserve more attention. Microbial community structures in biofilm used for the treatment of wastewater have been described (Yousra

et al., 2017), but most of the research based on QS mediated wastewater treatment was conducted at laboratory scales (Ghosh et al., 2017; Sheng et al., 2017; Wang et al., 2021). This is inadequate to understand the real roles of QS in large-scale processes. AHL distribution during the biofilm development process in response to variable environmental factors has been studied by Wang et al. (2019) in an integrated fixed-film activated sludge system in a full-scale municipal wastewater treatment plant, but more research work is needed to understand the effect of environmental factors, i.e. temperature, pH, oxygen level, salinity, xenobiotic stress, concentration of toxic pollutants on QS, EPS secretion, and biofilm formation.

## **6. Concluding remarks**

QS is known to modulate intra- and inter-species cell communication, which supports the formation of biofilm and regulating other physiological characteristics, such as EPS production, biofilm, siderophore formation, genetic transformation, aggregation, colonization, granulation, the removal of nutrients, increase solubilization of pollutants, biological/inorganic pollutant degradations, and the control of biofouling. This review examines the role of QS in this relatively new and rapidly developing technology to biodegrade complex wastewater such as pulp and papermills and PAHs. QS also regulates in rhizospheric activities in phytoremediation and the VBNC state in stressed bacteria. More research is needed to understand the role of environmental factors on QS and the use of engineered biofilm to overcome maximise the potential of QS strategies to treat real wastewater in a full-scale wastewater treatment plant.

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### **Credit**

ST-conceptualization, data curation, investigation, writing; DP, MB & AS – review and revision; SY& RC – funding acquisition, supervision and writing -original draft.

### **Compliance with ethical standards.**

**Conflict of Interest:** - The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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