International Journal of Current Science Research and Review
ISSN: 2581-8341
Volume 08 Issue 08 August 2025
DOI: 10.47191/ijcsrr/V8-i8-27, Impact Factor: 8.048
IJCSRR @ 2025
www.ijcsrr.org

Serratia marcescens whispering world: Mechanisms and Implications

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SUMMARY: As widely distributed Gram-negative bacilli, *Serratia marcescens* is in soil, vegetation, food and aquatic environments as well as human tissues. *S. marcescens* is well known for its opportunistic pathogenicity, regularly influencing immunocompromised individuals. This pathogen employs cell to cell communication system known as quorum sensing (QS) to coordinate multiple physiological and virulence activities via controlling the gene expression of involved determinants through three major systems referred to as SwrIR, SmaIR, and SpnIR.

In *S. marcescens* the core autoinducers comprise N-acyl-homoserine lactones (AHLs), with N-butanoyl-L-homoserine lactone (BHL) being the main one. These autoinducers combine with LuxR-analogue receptors (e.g. SmaR) that lead to initiate the gene expression modifications; thereby starting various coordinated behaviours.

Thorough awareness of QS strategies is considered imperative for developing techniques to alleviate the pathogenicity of *S. marcescens*, principally in clinical facilities in which it exerts considerable challenges owing to its multidrug resistance as well as its capacity to establish recalcitrant biofilms. Upon that, the current review explores the QS mechanisms of *S. marcescens*, aiming to uncover novel methods to alleviate its harmful consequences.

KEYWORDS: *Serratia marcescens*, quorum sensing, AHL, SwrI/SwrR, SmaI/SmaR, SpnI/SpnR

INTRODUCTION

As widely distributed Gram-negative bacilli, *Serratia marcescens* is characterized by very distinguishing features rendering them into influential agents of a wide range of infections as well as interesting research topic. Originally named for its ability to produce a red pigment resembling blood, *S. marcescens* has since been extensively studied for its diverse traits and its association with various infections (1).

The microbial cells, communities, or even their populations are not isolated residents; instead, they are governed by cell-to-cell communication systems mediated by private conversations, a fundamental part is played by this conversation, termed Quorum sensing (QS), in harmonizing various cellular activities (2)

QS in bacteria can be defined as a system enabling bacterial cells to communicate with each other, which is associated with population density. The bacterial population of high-density is able to produce sufficient signalling molecules and by doing so a wide spectrum of cell functions that cause severe damage to the host will be achieved, among which, are coordinated gene expression, capacity to initiate an infection, as well as antimicrobial resistance (3).

The establishment of bacterial chronic infection partly takes place via QS through virulence determinant expression, enzyme elaboration, and biofilm formation, in addition to sporulation. Markedly, the distribution of resistance determinants in resistant microbiomes constitutes a huge challenge related to public health. QS-related biofilm is a core for antimicrobial resistance gene horizontal transfer (2, 3).

Regarding the purpose of establishing a practical approach aiming at the alleviation of bacterial pathogenesis, it is imperative to shed light upon the QS. This review highlights the latest awareness of the QS mechanisms of *S. marcescens* to explore a novel approach to control QS.

Serratia marcescens

It is widely spread in soil (4), vegetation (5), food and aquatic environments as well as human tissues (6). *Serratia marcescens* is well known for its opportunistic pathogenicity, regularly influencing immunocompromised individuals, for instance, hospitalized patients, elderlies, and those suffering various comorbidities. Infections of *S. marcescens* might be exemplified as urinary tract infections, respiratory infections, wound and burn infections, as well as bacteraemia (7, 8).

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Apart from other pathogens, *S. marcescens* swarms with the aid of peritrichous flagella enabling these cells to reach nutrients and escape the toxic materials, through building colonies of a multicellular nature. These multicellular colonies promptly spread over surfaces. Swarming motility is enabled through biosurfactant elaboration alongside highly coordinated cell motility (9).

Elaborated by *S. marcescens*, the antibacterial and antitumor red pigment Prodigiosin synthesis is achieved through a complicated biochemical pathway, in which many enzymes are participated. Much attention was paid to prodigiosin owing to its prospective therapeutic implementations, embracing antibacterial compounds as well as antitumour agents (10).

Al-Fayyadh *et al.* (11) reported that *S. marcescens* can establish biofilms on many surfaces whether they are living or non-living ones, including prosthetics and catheters. Nonetheless, Rice *et al.* (12) highlighted that biofilm facilitated the firm adherence of bacterial cells to various surfaces rendering them recalcitrant to physical or chemical stresses. Given that bacterial biofilms are shielding cells from the aggressive environment including antibiotics inside the host thereby establishing chronic infections.

Interestingly, *S. marcescens* is well-known for its aptitude to develop multiple resistance mechanisms including efflux pumps, target modification, and inactivation of enzymes. Such resistant variants raise problematic issues in health institutions, which elevates death rates (13).

QUORUM SENSING

Within the complicated nature of the microbiomes, highly intricate systems of communication have emerged for coordinating various functions as well as adapting to environmental alterations. Quorum Sensing **(**QS) is one of these sophisticated systems that enable bacterial cells to sense population density via producing and detecting signalling molecules that are referred to as autoinducers (AI) and respond correspondingly (14). The expansion of the microbiome community is accompanied by an increase in the concentration of AI. When the AI reaches a certain limit, it docks with precise receptors, thereafter, a series of intracellular signals will be initiated leading to particular modifications in the gene expression (15).

The QS-facilitated responses are broadly varied per the bacterial species; moreover, environmental stresses also have an impact on these responses. In that context, the expression of virulence determinants is regulated via QS, thus, the pathogen can coordinate its pathogenicity in the host. Furthermore, biofilm establishment and dispersal are also under the control of QS (12). Markedly, bacterial species via using QS circuits can synchronize many physiological actions, among which sporulation, biosynthesis of antibiotics in addition to the acquisition of nutritional materials. Of interest, they utilize this synchronization for their thrive and persistence in different ecosystems (16).

The bacterial species use signalling molecules as words to communicate with each other; therefore, QS is characterized by its chemical nature. By doing so, some particular pathogenic microorganisms employ exclusive signalling molecules and receptors. This sophisticated machinery of cell-to-cell communication enables the bacterial species to “sense” and correspondingly respond to the density alteration of their population, and stresses in the surrounding environment, in addition to the nearby microbiota (17).

LuxI/LuxR paradigm

The first detected QS circuit is the LuxI/LuxR system that is classically utilized by Gram-negative bacteria (Figure 1), particularly, the marine symbiotic bioluminescent species *Vibrio fischeri* (18). In this QS system and its homologs, the LuxI represented by AI synthase is responsible for the production of the freely diffusible AI (acyl homoserine lactone, AHL) via catalyzing the reaction of an acyl carrier protein (ACP) with S-adenosylmethionine (SAM) (19). Once the AHL reaches elevated concentrations, it binds the cognate cytoplasmic LuxR-like transcription factors. In the absence of this binding, the LuxR is promptly disintegrated, apparently to avoid the bacterium *per se* from “short-circuiting” its QS circuit. Notably, attachment of AI with LuxR will lead to stabilizing the latter, by doing so, it permits folding the newly formed complex and binding to DNA, then ultimately activation of the target genes transcription (20). Normally, the complex of AHL and LuxR-like receptors also activates the synthesis of luxI, creating a loop of forward autoinduction which releases AI that spreads throughout the surrounding medium. Remarkably, LuxI/LuxR homologs were characterized by a myriad of Gram-negative species (21).

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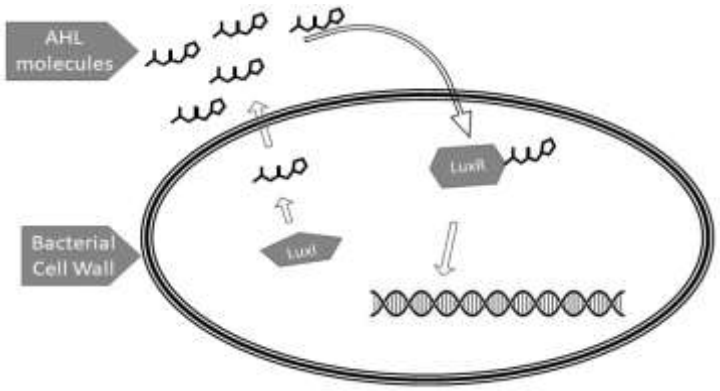

Figure 1: LuxIR model of quorum sensing in Gram-negative Bacteria (22)

Communication System of *Serratia marcescens*

S. marcescens utilizes different QS systems including SwrI/ SwrR and is responsible for the fermentation of butanediol, swarming motility (via serrawettin elaboration and expression of protease and S-layer protein), in addition to the establishment of biofilm (23). Coulthurst *et al.* (24) reported that *S. marcescens* also uses the SmaI/R system for regulating various activities such as production of hemolysins, swarming phenomenon, developing biofilm, biosynthesis of chitinase, as well as elaboration of caseinase. In *S. marcescens*, The SpnI/R system governs the surface migration of flagellum-independent population (i.e. sliding), prodigiosin elaboration, production of nuclease, and biosurfactant biosynthesis (25).

Prodigiosin production

Under certain growth conditions, *S. marcescens* biogroups A1, A2 and A6, some *S. rubidaea*, and some *S. plymuthica* isolates elaborate a pigment referred to as prodigiosin characterized by its distinguished colour that has a wide spectrum from pale pink up to dark red (26). Chemically it is a 2-methyl-3-pentyl-6methoxyprodiginine molecule composed of a unique structure of three pyrrole rings, the first and second rings are attached directly. However, the third ring constitutes pyrryldipyrrylmethene via special binding to a methene bridge (27).

No clear cellular functions of prodigiosin have been identified in the producing strains; nonetheless, the definite participation in the physiology of the cell is still controversial; however, this pigment with other members of its family was signified by a wide spectrum of antimicrobial characteristics (28) in addition to having powerful antitumour as well as immunosuppressive features (29).

Thomson *et al.* (30) demonstrated that the C4-HSL (the more abundant molecule) and C6-HSL of the SmaI/SmaR circuit have the ability to regulate the production of prodigiosin in *Serratia* sp. ATCC 39006. Fineran *et al.* (31) indicated that once C4-HSL/C6-HSL binds the SmaR transcription of the pig cluster will be derepressed at high density of population, however, when the population density is decreased, the transcription is repressed. What's more, Horng *et al.* (25) stated that prodigiosin transcription in *S. marcescens* SS-1 is facilitated by QS systems; Spn (sliding, prodigiosin and nuclease) particularly, SpnI and SpnR. An investigation by

Slater *et al.* (32) revealed the vital controlling role of a transcriptional regulator of *PigP* in *Serratia* sp. ATCC 39006 that performs throughout the binding to DNA. It also seems that environmental conditions mainly phosphate availability could regulate prodigiosin synthesis.

Biofilm formation

Costerton *et al.* (33) defined biofilm as a community of surface-adherent bacterial cells embedded in a matrix of exopolymeric substances. Regarding a medical approach, catheters, prosthetics, or any other implants inhabited with biofilm-forming species are a significant problematic issue represented by persistent infections (34). Besides, the transformation of the free swimming cells into a sessile entity (i.e. biofilm) through a series of phenotypic cascade of steps that eventually lead to significant consequences, for instance, avoiding host immune responses and equip them with elevated levels of resistance against antimicrobial agents (35).

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Apart from the traditional model of biofilms established by *E. coli* and *P. aeruginosa* that involves aggregates of undifferentiated cells grouped in microcolonies, biofilms developed by *S. marcescens* are quite different (36, 37). For instance, the process of biofilm developed by *S. marcescens* MG1 is shown to be a genetically coordinated protocol that embraces structural and cellular differentiation involving sequential steps leading to the production of elongated cellular filaments alongside bacterial aggregates in addition to interlacing chains of cells, thus, forming mature biofilm (38).

A mutant of *S. marcescens* MG1 lacking the *swrI* gene, which cannot synthesize both C4-HSL and C6-HSL, was shown to produce a thin and immature biofilm with no cell aggregates as well as chains of differentiated cells (39). Of interest, complementation with C4-HSL resulted in a biofilm with the wild-type architecture. Moreover, two additional QS-regulated genes that are implicated in the establishment of biofilm were characterized, *bsmA* and *bsmB*. The former encoded an adhesin responsible for regulating the cell aggregate size, nonetheless, the other gene encodes a positive effector obligatory for activating the cellular aggregation (1). *bsmA* and *bsmA* genes were assumed to have a part in controlling the establishment of cellular grouping at a certain time within a suggested genetically controlled protocol of biofilm formation. Additionally, QS plays a crucial role in biofilm dispersal as a vital step in the life cycle of bacterial biofilm (12).

Upon that, QS in *S. marcescens* MG1 has an essential participation in no less than four steps of biofilm formation, starting from adhesion, swarming, biofilm maturation, and ending with dispersal (12, 38). As a secondary metabolite activator, *smI* participates significantly in the formation of biofilm of *S. marcescens* strain 12 calculated by the microtiter plate method. Interestingly, AHL is responsible for controlling the swarming motility in *S. marcescens* strain 12 and *S. marcescens* strain MG1 (24).

Swarming regulation

The divergently arranged genes *swrI* encodes the AHL synthase (LuxI homologue) and *swrR* encodes a putative regulatory LuxR homologue, SwrR as highlighted in Figure 2. Across the cytoplasmic membrane of bacteria, the BHL as a signal molecule is freely diffusible as specified by the up and down shaded arrows. Notably, the binding of BHL with SwrR in flip will activate the *swrA* transcription. Noteworthy, is the peptide synthase, SwrA that responsible for the production of the surfactant serrawettin W2. Nevertheless, the passing of W2 across the cytoplasmic membrane is still obscure as to whether it is passive or takes place with the aid of a transporter (40).

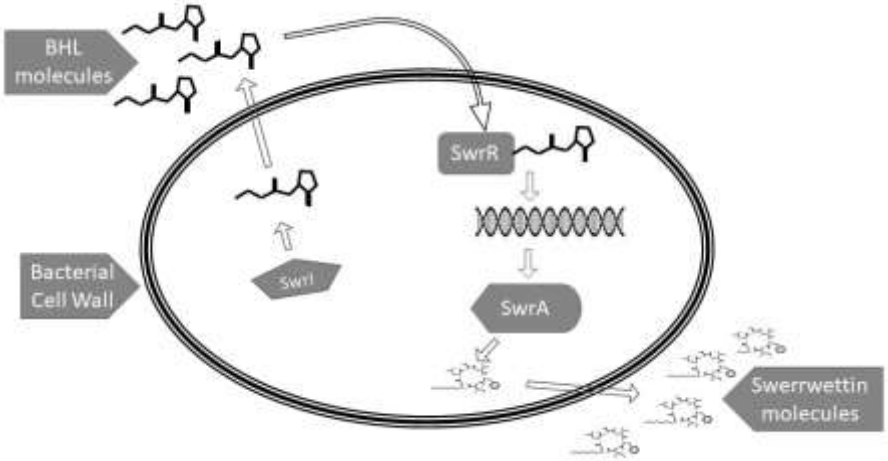

Figure 2: Swarming control via the swrIR system (40)

The QS-related autoinducers in *Serratia marcescens* N-acyl-homoserine lactones

In the late 1960s and early 1970s, N-acyl-homoserine lactones (AHL)-QS was first discovered in *V. fischeri*. AHLs are small signalling molecules that play a crucial role in QS, facilitating communication between bacterial cells. (41). They consist of a lactone ring linked to an N-acyl side chain, with variations in the length and structure of the acyl chain influencing their activity and specificity (42). *S. marcescens* relies greatly on AHLs for regulating and coordinating gene expression of many determinants responsible for various cellular activities (43).

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Boursier *et al.* (44) stated that among these signalling molecules that have an essential part the regulation process of QS in *S. marcescens* is N-butanoyl-Lhomoserine lactone (BHL) which is considered the most abundant type of AHL being composed of C4 acyl residue connected to a lacton ring. Moreover, many virulence determinants encoding prodigiosin production, chitinases, lipases, biofilm formation, swarming as well as hemolysins are controlled by the signalling molecules, BHL . In comparison to BHL, *S. marcescens* elaborates, significantly in lesser amounts, another signalling molecule referred to as N-hexanoyl-Lhomoserine lactone (HHL) responsible for similar regulatory cellular activities, notably, it is a six carbon rather than four carbon molecules (43).

AHL Synthesis

Fuqua *et al.* (45) indicated that the first step in QS of *S. marcescens* commences with the AHL biosynthesis, which is the product of incorportation of SAM with acylated acyl carrier proteins (acyl-ACPs) by an aid of LuxI-type synthase (i.e. SamI). Likewise, Latifi *et al.* (46) stated that N-butanoyl-L-homoserine lactone (BHL) is biosynthesised by SmaI; nevertheless, environmental factors may have a crucial role in producing other AHLs. For instance, N-hexanoyl-L-homoserine (HHL) might be synthesised through various substrates of acyl-ACP (47, 48). Fuqua *et al.* (17) demonstrated that cell concentration as well as ecological factors can control the smaI expression, additionally, this expression might be upregulated through binding of different AHLs with their receptors causing autostimulation and extra expression of smaI .

AHL Diffusion:

Upon AHLs production, it passively transferred through cytoplasmic membrane or it pumped out by the efflux pumps leading these signalling molecules to transfer freely among cells and magnifying the signals of QS (15, 48). Depending on such passive diffusion, cell to cell communication with gene expression coordination within the bacterial population will take place. However, many factors affect this diffusion like AHL concentration across the membrane, extracellular enzymes, and permeability of cytoplasmic membrane (49).

Perception by SmaR

In *S. marcescens*, once AHLs binds to its receptor the LuxR-type transcriptional regulator, SmaR, (50) a conformational alteration will be induced leading to establish a bound with a certain sequence of DNA (18). The newly formed complex (SmaR with AHL) functions as a transcription factor, which play a central part in coordinating the expression of genes implicated in cell physiology (50). Nevertheless, upregulation or downregulation of these determinants is determined by binding to their promoters (18). Among the genes controlled by the SmaR are AHL-synthesis determinants, resulting in magnifying the production of AHL via establishing a positive feedback loop (48).

These changes may include increased production of virulence factors, enhanced biofilm formation, altered motility patterns, and modulation of antibiotic resistance mechanisms (51, 52).

CONCLUSION

Serratia marcescens is an opportunistic bacterium; however, it could also infect human beings, in particular those with weakened immune systems. *S. marcescens* reveals swarming motility, allowing colonization, and forms resilient biofilms, contributing to chronic infections. It produces a pink pigment, prodigiosin, with antibiotic and anticancer residences, regulated through its quorum sensing (QS) systems. Those QS structures, inclusive of SwrI/SwrR, SmaI/SmaR, and SpnI/R, use N-acyl-homoserine lactones to coordinate behaviours such as biofilm formation and virulence aspect manufacturing.

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Cite this Article: Tawfeeq, H.K., Abbas Hosain, Z.A., Omran, A.H. (2025). Serratia marcescens whispering world: Mechanisms and Implications. International Journal of Current Science Research and Review, 8(8), pp. 4196-4203. DOI: https://doi.org/10.47191/ijcsrr/V8-i8-27