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# Quorum-Sensing Inhibitors from Probiotics as a Strategy to Combat Bacterial Cell-to-Cell Communication Involved in Food Spoilage and Food Safety

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**Abstract:** Experience-based knowledge has shown that bacteria can communicate with each other through a cell-density-dependent mechanism called quorum sensing (QS). QS controls specific bacterial phenotypes, such as sporulation, virulence and pathogenesis, the production of degrading enzymes, bioluminescence, swarming motility, and biofilm formation. The expression of these phenotypes in food spoiling and pathogenic bacteria, which may occur in food, can have dramatic consequences on food production, the economy, and health. Due to the many reports showing that the use of conventional methods (i.e., antibiotics and sanitizers) to inhibit bacterial growth leads to the emergence of antibiotic resistance, it is necessary to research and exploit new strategies. Several studies have already demonstrated positive results in this direction by inhibiting autoinducers (low-molecular-weight signaling compounds controlling QS) and by other means, leading to QS inhibition via a mechanism called quorum quenching (QQ). Thus far, several QS inhibitors (QSIs) have been isolated from various sources, such as plants, some animals from aqueous ecosystems, fungi, and bacteria. The present study aims to discuss the involvement of QS in food spoilage and to review the potential role of probiotics as QSIs.

**Keywords:** food spoilage; quorum sensing (QS); quorum quenching (QQ); QS inhibitors; probiotics

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## 1. Introduction

A few decades after the discovery of bacteria, the idea that bacteria were individualized organisms, and therefore did not communicate with each other, was accepted and established. However, after early research by Kenneth H. Nealson et al. [1] on the luminescence of the Gram-negative bacterium *Vibrio fischeri* (newly named *Aliivibrio fischeri*) [2], it became clear that bacteria communicate with each other [1]. Indeed, this research shows that bioluminescence in *A. fischeri* is induced and closely linked to bacterial density [1]. Later, it was found that this luminescence in *A. fischeri* is caused by the LuxI/LuxR transcriptional activator and autoinducer system mediating the cell-density-dependent control of Lux gene expression [3]. This communicational regulation, which has since taken the name of quorum sensing, is generally defined as a mechanism of microbial communication owing to a genetic regulation that involves the exchange and sensing of low-molecular-weight signaling compounds called autoinducers (AIs) [4,5]. Over the last few years, there have been a significant number of studies on the role of QS systems in the formation of various cellular patterns and their behavioral response [6,7]. Thus, to date, several other bacteria have demonstrated their ability to communicate through QS, and some inter-species communications have even been brought to light [8]. QS can have serious consequences, as it is involved in many important

biological processes that can have a detrimental impact on the economy and health, such as sporulation, virulence and pathogenesis, and biofilm formation [9,10]. The consequences on human health are not discussed here, but economically speaking, phenomena such as biofilm formation can cause enormous losses in the agriculture and food industry [11,12]. It is well known that biofilms are largely responsible for the contamination of processed products within the food industry [12]. These microbial consortia embedded in self-produced exopolymer matrices [13] adhere to food processing, packaging, and equipment surfaces, and can negatively affect food safety [8,14]. Recent studies have demonstrated that QS molecules play a major role in the biofilm formation of Gram-positive and Gram-negative bacteria [8]. Although this correlation was not found when studying in vitro biofilms of strains isolated from a raw vegetable processing line, other foodborne bacterial pathogens, such as *Salmonella* spp., *Campylobacter* spp., *Listeria monocytogenes, Escherichia coli, Staphylococcus aureus*, and *Bacillus cereus*, can attach to various surfaces within the food industry and develop biofilms, leading to concerning hygienic disorders and a severe public health risk [14].

Studies conducted in recent years have suggested that QS inhibition could be an attractive alternative strategy for current bacterial control practices employed in industrial settings [8,14,15]. Unlike conventional antibacterials and sanitizers, instead of killing bacteria, a strategy using QS inhibitors consists of blocking intercellular communication and significantly limiting the expression of phenotypes, such as the formation of biofilms, while reducing the likelihood of resistance development [15,16]. Several products with important biological functions (e.g., phytochemicals, nanoparticles, halogenated natural furanones, and synthesized derivatives) have already demonstrated their ability to delay the microbial deterioration of foods and defeat important bacterial strains involved in spoilage [8,17]. However, although several studies have shown that certain strains of probiotics can interfere with the QS system [18–20], reports or evidence of their use as QS inhibitors (QSIs) in food preservation are scarce.

According to the Food and Agriculture Organization (FAO) and the World Health Organization (WHO), probiotics are living microorganisms that provide health benefits to their hosts in appropriate doses [21]. Probiotics have applications in a variety of fields, including food processing, animal breeding, and human health [21]. The fact that probiotics are "generally recognized as safe" means that these food additives and their by-products can be used in different processes, including food preservation and the maintenance of industrial food surfaces, since their addition will not have side effects on food safety [22].

This review focuses on microbial communication, the role of QS in food spoilage, and the potential role of probiotics as QSIs in food preservation.

## 2. Microbial Communication

Microbial communication was first demonstrated in bacteria by Kenneth H. Nealson et al. [1], and the term quorum sensing (QS) was first introduced by Fuqua and Winans [23]. Skandamis and Nychas [17] described QS as the mechanism used by bacteria to understand changes in their environment and, consequently, to apply specific strategies for adapting to environmental stress in space and time [17]. QS expression depends on the concentration of low-molecular-weight signaling compounds called autoinducers (AIs), and the amount of these AIs increases with the increase in bacterial density. In a simplified way, as bacteria reproduce, there are progressively more individual cells producing autoinducers, and the extracellular concentration of the autoinducers increases, eventually reaching a "critical mass" [24]. This threshold makes the outflow of intracellular AIs difficult or impossible, resulting in an increase in their intracellular concentration [24]. Once the intracellular concentration reaches a certain level, AIs bind to their receptors, triggering signaling cascades that alter transcription factor activity and, therefore, gene expression [24]. It is this gene expression that, depending on the microorganism, can lead to sporulation, bioluminescence, the secretion of virulence factors, conjugation, competence, and biofilm formation [25–27]. It was recently reported that QS mechanisms present similarities among different bacteria (Gram-positive or Gram-negative) but that the exact AI involved in each

mechanism may differ from one organism to another [8]. However, it was reported that some QS systems, such as DPD (dihydroxy pentanedione)/AI-2, can be found in both Gram-positive and Gram-negative bacteria (Figure 1). DPD/AI-2 has been detected in more than 50% of QS-competent bacteria whose genomes have been sequenced and is known as the most ubiquitous signaling system employed by both Gram-positive and Gram-negative bacteria [6]. AI-2 is reported to be involved in several bacterial phenotypes, such as bioluminescence in *Vibrio harveyi* [28] and biofilm formation in *Bacillus subtilis* [28], *Lactobacillus rhamnosus* [29], *Streptococcus intermedius* [30], and *Campylobacter jejuni* [31]. In *C. jejuni*, AI-2 also plays an important role in stress response, motility, the expression of virulence factors, and colonization [32]. Since AI-2 is present and can be recognized/interpreted by different bacterial species, it is often involved in interspecies communication and, consequently, several authors have attributed the nickname of "universal autoinducer" to AI-2 [8,32–35]. However, some differences exist between specific autoinducers in Gram-positive and Gram-negative bacteria. In general, the QS system most encountered in Gram-negative bacteria is the acylated homoserine lactone (HSL), or LuxI/LuxR-type QS (AI-1), which essentially uses N-acyl homoserine lactones (AHLs: AHL-mediated QS) (Figure 1) [8]. AHLs and derivatives passively diffuse through the bacterial membrane and accumulate both intra- and extra-cellularly in proportion to cell density [8]. To our knowledge, to date, no Gram-positive bacteria have been reported to produce AHLs. In Gram-positive bacteria, the QS system uses oligopeptides called autoinducer peptides (AIPs: AIP-mediated QS), and these molecules are transported out of the cell using ATP-binding cassette (ABC) transporters. The molecules necessary for effective communication in Gram-positive bacteria are usually AIPs used as signaling molecules and a two-component type of histidine kinase (HK) used as a signal-sensing and transduction module (Figure 1) [8]. The QS system mechanism is not developed in depth here since it has been extensively analyzed elsewhere for both Gram-positive [36–38] and Gram-negative bacteria [39,40]. In addition to bacterial communication, fungal communication has also been highlighted [3,41,42], though it has scarcely been investigated. Indeed, the QS system, similar to that of bacteria, has been reported in several fungi, such as *Saccharomyces cerevisiae* [43–45], *Histoplasma capsulatum* [3], *Cryptococcus neoformanss* [41,46,47], *Ceratocystis ulmi* [45], *Ustilago maydis* [3,48], Aspergillus species (*A. fumigates* and *A. niger*) [49,50], and Candida species (*C. albicans, C. krusei, C. utilis, C. zeylanoides, C. stellata, C. intermedia, C. solani, C. tenuis*) [3,51]. Padder et al. [3] reported that the discovery of the QS molecule (QSM) farnesol in *C. albicans* constituted a major turning point in the knowledge of cell-to-cell communication in eukaryotes. Since then, other molecules, such as tyrosol [52], tryptophol [53], 1-phenylethanol [54], oxylipins [49], pheromones [55], and acetaldehydes [56], have been recognized as actively involved in fungal QS. The mechanism of QS in fungi is almost similar to that of bacteria and regulates various key functions, such as pathogenesis, morphogenesis, and filamentation [3].

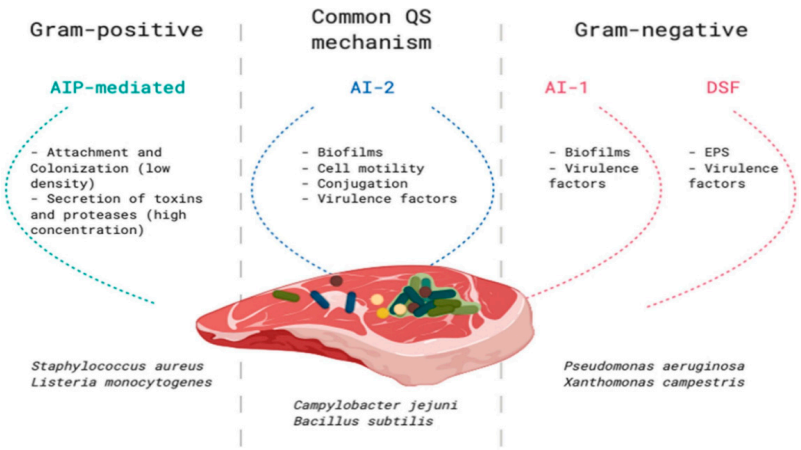


**Figure 1.** Schematic representation of the main QS mechanisms (from [8] with permission from Elsevier; license number: 5433491396764).

## 3. Quorum Sensing in Food Spoilage

Food spoilage can be defined as the deterioration of food manifested by the degradation of organoleptic and nutritional properties, which makes the food unacceptable to the consumer [57]. The causes of food spoilage can be physical (drying, changes in texture), chemical (oxidation, color changes), and microbiological. Meanwhile, it was recently reported that microbial-induced spoilage is by far the most common cause of spoilage [8]. Microorganisms involved in food spoilage can cause changes that manifest as visible growth (biofilm), textural changes (degradation of polymers), off-odors, and off-flavors [8]. In recent years, the involvement of cell-to-cell communication in food spoilage has caught the attention of several researchers, and QS molecules have been detected in several foodstuffs, such as vegetables, poultry, meat, fish, and milk [58]. Researchers reported that several phenotypes, such as enzymatic activities (pectinolytic, lipolytic, proteolytic, and chitinolytic), sporulation, and biofilm formation, are linked to food spoilage [8]. Microorganisms expressing food-spoilage-related phenotypes can be classified into three groups: (1) those that are food-specific (specific spoilage organisms: SSOs), (2) those that become dominant through selection during food storage (ephemeral spoilage organism: ESOs), and (3) those coming from the external environment (contaminant) [8,58]. Regardless of the type of microorganism, the microbial spoilage mechanism strongly depends on the ecosystem and, consequently, on the type of food.

For example, in milk, Bai and Rai [59] reported that pseudomonads and other psychrotrophic Gram-negative bacteria are involved in spoilage through the production of extracellular proteinases, lipases, lecithinases, and glycosidases. Gram-positive psychrotrophic aerobic *Bacillus* spp. were also reported to produce phospholipases that are responsible for spoilage in some dairy products [60]. In a study by Pinto et al. that aimed to detect AHL production in Gram-negative psychrotrophic bacteria isolated from raw milk, it was found that 84.9% of the bacteria were AHL producers, suggesting that quorum sensing may play an important role in the spoilage of this product [61]. The production of extracellular lipolytic and proteolytic enzymes, which is known to be regulated by AHL-based QS in *Serratia proteamaculans* strain B5a, confirmed the involvement of the QS of this strain in milk spoilage. Indeed, the inoculation of pasteurized milk with wild-type *S. proteamaculans* in the study by Christensen et al. [62] led to a degradation of the milk, whereas the inoculation of a mutant strain (with an inactivated *sprI gene*) under the same conditions did not result in degradation. However, the involvement of signaling molecules in milk spoilage was confirmed when spoilage was observed after the addition of 3-oxo-C6-HSL to milk inoculated with the sprI mutant [62].

In addition, in fish and other aquatic products, studies have observed that microorganisms are the most common causes of spoilage [63]. Storage conditions play a major role in changing the microbiological profile in fish and, therefore, in its spoilage [63]. For example, it has been reported that the psychrotolerant Gram-negative *Shewanella* spp. and *Pseudomonas* spp. cause chilled fish spoilage [64], whereas in the absence of effective preservation conditions, the *Vibrionaceae* family is known to cause food degradation [65]. Although certain phenotypic factors are found to be associated with the production of proteases, siderophores, and toxins in some fish-pathogenic bacteria that produce AHLs (e.g., *Yersinia ruckeri, Aeromonas salmonicida, A. anguillarum, Vibrio salmonicida,* and *V. harveyi*), very few studies have demonstrated the involvement of their AHLs in spoilage. However, some researchers have concluded that the AHLs produced by other bacteria may be involved in fish spoilage, such as refrigerated shrimp spoiled by *Shewanella baltica* [66]. Later, Zhu et al. [67] found that the AHLs responsible for spoilage by *S. baltica* were produced by *Acinetobacter* strains. In the same vein, the production of AHLs (mainly 3-hydroxy-C8-HSL) was reported by Flodgaard et al. [68] in *Photobacterium phosphoreum* and *Aeromonas* spp. strains isolated as the dominant cultivable spoilage flora of packed cod fillets, thus suggesting the possible role of an AHL-based system in the regulation of the chitinase activity, which enhances the degradation of crustaceans [58].

In addition, QS may also be involved in spoilage in fruits and vegetables [8,58]. Spoilage microorganisms can enter fruits and vegetables via the farm environment and post-harvest handling and processing [69]. This spoilage is manifested by visual defects, such as enzymatic browning, off-odors, off-flavors, and/or texture breakdown [58]. Pectinolytic (such as pectin lyases, pectate lyase, polygalacturonase, and pectin methyl esterases), proteolytic, lipolytic, and chitinolytic enzymes produced by certain microorganisms are directly involved in the deterioration of fruits and vegetables [58]. *Erwinia* and *Pseudomonas* strains, which are pectinolytic and proteolytic, are known to produce AHLs (mainly 3-oxo-C6-HSL and C6-HSL) [70], and are very often involved in fruit spoilage, suggesting an involvement of AHL-based QS systems in the modulation of vegetables [58].

Biofilm formation, which is already known to be governed by QS [8], constitutes a major problem for the safety of several foodstuffs and for meats in particular [14]. The attachment of potential spoilage and pathogenic bacteria to food contact surfaces and subsequent biofilm formation represent serious challenges to the meat industry, since they may lead to cross-contamination of the products, resulting in a lowered shelf life and the transmission of diseases [14]. To date, the involvement of several bacteria (including foodborne pathogens, such as Salmonella enterica, *L. monocytogenes*, and *E. coli*, together with common meat spoilage bacteria, such as *Pseudomonas* spp., *Brochothrix thermosphacta*, and *Lactobacillus* spp.) in the formation of biofilms and food spoilage has been well documented, and detailed information can be found in the review by [14].

## 4. Quorum Quenching and QS Inhibitors from Probiotics

QS inhibition is due to quorum quenching (QQ) enzymes or, more generally, to other chemicals known as QS inhibitors (QSIs). Whether due to enzymes or other chemicals, the disruption of the QS system commonly takes the name of QQ [22]. QQ has been suggested as a strategy for disrupting a pathogen's ability to sense its cell density and to modulate the production of virulence factors [22]. Some data suggest that QQ is increasingly recognized as a new strategy used to control specific bacterial phenotypes, such as sporulation, virulence and pathogenesis, bioluminescence, swarming motility, and biofilm formation [15]. As shown in Figure 2 (taken from the review by [8] with the permission of Elsevier), there are several putative ways to inhibit QS (Figure 2): (a) the interruption of AHL signal synthesis by blocking the LuxI-type synthase; (b) the degradation of AHL signal dissemination by enzymes (AHL-acylase and AHL-lactonase), which will impair AHL accumulation; and (c) interference with signal receptors or the blockage of the AHL/LuxR complex [8]. Natural and synthetic QSIs have been intensively studied and are produced by a wide range of organisms, such as plants, some animals from aqueous ecosystems, fungi, and bacteria [71].

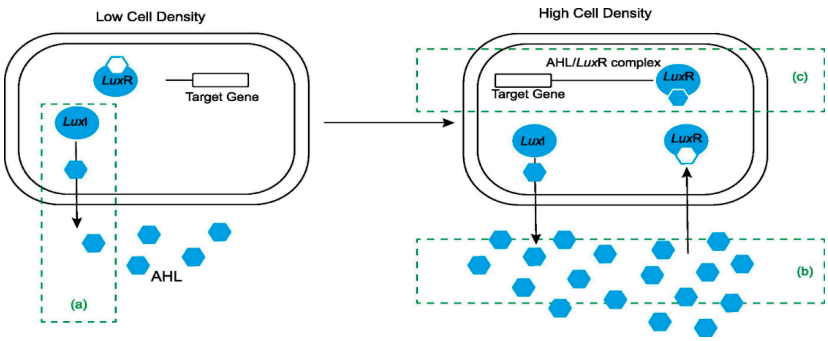


**Figure 2.** Inhibition of quorum sensing in Gram-negative bacteria: (**a**) inhibition of AHL synthesis; (**b**) degradation of AI using enzymes; (**c**) interference with signal receptors (From [8] with permission from Elsevier; license number: 5433491396764).

To our knowledge, the first QSI discovered was an enzyme called AiiA [72]. This enzyme, which was isolated from *Bacillus sp.* 240B1, is able to inactivate the AI (acylho-

moserine lactone (AH2)) of *Erwinia carotovora* (*Pectobacterium carotovorum*), significantly decrease extracellular pectolytic enzyme activities, and attenuate the pathogenicity of this strain in potato, eggplant, Chinese cabbage, carrot, celery, cauliflower, and tobacco [72]. Later, other microorganisms, including probiotic bacteria, have been reported for their QQ activity [22]. Probiotics are shown to be effective for a variety of diseases, and their various bio-functional effects and potential for industrial application have been characterized and proven in vitro [73]. Most QS-inhibiting probiotics belong to the genera Lactobacillus, Bifidobacterium, and Bacillus. Table 1 presents some probiotics that are shown to have QQ activity and that could potentially have industrial applications; in particular, limiting food spoilage by interfering with QS in food-spoiling bacteria.

Bacteria of the lactobacillus genus are among the most widely used as probiotics [74]. Lactobacilli and other probiotics belonging to the genera *Lactococcus, Enterococcus, Pediococcus, Leuconostoc, Streptococcus, Carnobacterium, Fructobacillus, Oenococcus*, and *Weissella* are included in the group of lactic acid bacteria (LAB), which means that they can produce lactic acid and other substances (bacteriocins, hydrogen peroxide, diacyls, and others) that may inhibit the growth of other bacteria [75]. LAB and bifidobacteria, or other probiotics for food preservation, have been used since ancient times due to their beneficial properties [75,76]; however, evidence based on experience reveals that their immunomodulating and antagonistic properties make them applicable in both the clinical field and animal breeding [77]. For example, regarding the clinical area, *Lactobacillus acidophilus* was reported to reduce the duration of diarrhea in children with acute gastroenteritis when administered at a dosage of more than $10^9$ CFU [78]. Another strain, *L. fermentum*, can attenuate the inflammatory process and improve the production of some of the mediators involved in colitis (PGE2, IL-4, IL-6, IL-10, IL-17, TNF- $\alpha$, IFN-$\gamma$, NO) [79]. Several other immunomodulatory effects of *L. fermentum* in vitro, in cell and animal models, and in human trials were extensively reviewed by Zhao et al. [80]. Gomi et al. [81] conducted a preliminary open trial and a double-blind, placebo-controlled, crossover trial to examine how fermented milk containing the probiotic *Bifidobacterium bifidum* YIT 10347 affects gastric and lower abdominal symptoms in adults taking no medication. The authors concluded that *B. bifidum* YIT 10347 could provide health benefits by alleviating gastric symptoms in these subjects [81]. Several other clinical benefits of probiotics are well documented in the review by Sánchez et al. [82]. In addition, regarding animal breeding, our recent review entitled "The use of probiotics in animal feeding for safe production and as potential alternatives to antibiotics" extensively documented evidence for the effective use of probiotics in animals [77].

Probiotics appear to have multiple properties and, although evidence is scarce, their involvement in the regulation of quorum sensing (QS) may bring new solutions in several areas, including food preservation. From our point of view, probiotics inhibiting the growth of other bacteria (including putrefying bacteria) in a medium is not necessarily caused by the inhibition of QS (QSI), but rather by antagonist activity linked to the acidification of the medium and the production of other bacteriocins [75,83]. However, there is evidence that some probiotics can potentially affect QS mediated by acylated homoserine lactones (AHLs, HSLs) and autoinducer 2 (furanosyl borate diester) [75]. As shown in Table 1, several species of lactobacillus (*L. plantarum, L. fermentum, L. acidophilus, L. casei, L. brevis, L. reuteri*, and *L. curvatus*), Bifidobacterium (*B. longum* and *B. licheniformis*), Bacillus (*B. cereus, B. subtilis*, and *B. pumilus*) and *Streptococcus* (*S. salivarius* and *S. oralis*) have already been reported at least once as quorum-quenching (QQ) agents. Although the results reported in Table 1 on the QQ activity of these probiotics are not related to food products, extrapolations in food preservation can be made because most of the pathogens affected by QQ are also known as foodborne pathogens (Table 1). For example, the fact that *L. plantarum* M.2 and *L. curvatus* B.67 demonstrated the ability to inhibit swimming motility, biofilm formation, and QS molecules related to biofilms in *Listeria monocytogenes* [84], a foodborne pathogen, could indicate that QSI molecules can be used to solve problems related to this bacterium in the food industry. As a reminder, *L. monocytogenes* is capable of adhering to food contact surfaces and forming matured biofilms, which are not easy to remove during the cleaning process and may therefore

persist during food processing [85]. The physical means (for example, pulsed ultraviolet, ozone, and atmospheric cold plasma) employed to reduce the risks of contamination are very often effective but might affect food quality by changing sensory characteristics, such as appearance, color, flavor, and texture [22]. In the same way, the persistence of chemical agents (chlorinated disinfectants and oxidant fungicides) used during cleaning with chemical methods to minimize the growth of *L. monocytogenes* can have consequences on metabolism and the consumer's health [75]. Therefore, in this context, it is important to seek alternative cleaning routes, subject to additional studies. The results obtained by Hossain et al. on the QQ activity of *L. plantarum* M.2 and *L. curvatus* B.67 against QS in *L. monocytogenes* can be used to suggest and develop new cleaning methods using biological means that are safe for the consumer [84]. A similar suggestion was made by Wu et al., who effectively documented the properties of probiotics (other than QSI potential) that can be employed in the search for alternative cleansing methods [22]. In general, with regard to the potential use of QSIs in the cleaning of industrial food surfaces, it can be concluded that the search for alternative cleaning solutions using QSI molecules from probiotics will need to pass through the extrapolation of existing data by considering the pathogen inhibited by QS.

**Table 1.** Some probiotic strains with QQ activity and the mechanism involved.

| Probiotics | | Bacteria Inhibited | QSI Mechanism | References |
|---|---|---|---|---|
| **Genus** | **Species** | | | |
| Bacillus | *B. subtilis* | *L. monocytogenes*<br>*E. coli*<br>*Gardnerella vaginalis* | Inhibits AI-2 activity and biofilm formation | [86] |
| | *B. cereus* RC1 | *Lelliottia amnigena*<br>*seudomonas aeruginosa*<br>MTCC2297 | Inhibits pyocyanin production in *P. aeruginosa* and modulates the pathogenicity in *L. amnigena* | [87] |
| | *B. subtilis* R-18 | *Serratia marcescens* | The bacterial extract inhibits biofilm formation, protease, lipase, and hemolysin production | [88] |
| | *B. subtilis* BR4 | *P. aeruginosa* | Inhibits biofilm formation | [89] |
| | *B. pumilus* | *P. aeruginosa PAO1* (las, rhl)<br>*S. marcescens* (shl). | Reduces the accumulation of N-acyl homoserine lactone (AHL) and shows significant inhibition of LasA protease, LasB elastase, caseinase, pyocyanin, pyoverdin, and biofilm formation. | [90] |
| Bifidobacterium | *B. licheniformis* DAHB1, | *Vibrio parahaemolyticus* | Inhibits biofilm formation in vitro and reduces shrimp intestinal colonization and mortality | [91] |
| | *B. licheniformis* T-1 | *Aeromonas hydrophila* | Quorum-quenching gene *ytnP* encodes an acyl-homoserine lactone metallo-β-lactamase | [92] |
| | *B. longum* ATCC15707 | *Escherichia coli* 0157:H7 | Inhibits AI-2 and reduces biofilm formation | [18] |
| Lactobacillus | *L. acidophilus* 30SC | *E. coli* O157:H7 | Inhibits AI-2 | [93] |
| | *L. plantarum* M.2,<br>*L. curvatus* B.67 | *L. monocytogenes* | Inhibits swimming motility, biofilm formation, and expression levels of target genes related to biofilm formation | [85] |
| | *L. plantarum* SBR04MA | Microbiota of activated sludge | Inhibits N-Hexanoyl-L-homoserine lactone (6-HSL) | [94] |
| | *L. plantarum,* | *S. aureus* | Reduces expression of some genes involved in biofilm formation | [95] |
| | *L. acidophilus GP1B* | *Clostridium difficile* | Reduces production of AI-2 molecules | [20] |
| | *L. acidophilus* La-5 | *Escherichia coli* 0157:H7 | Interferes with QS molecules and reduces adherence and colonization | [19] |
| | *L. acidophilus* NCFM | - | Not in pathogenic bacteria, but increases adherence of probiotic to intestinal cells by increasing AI-2 in LuxS system | [96] |
| | *L. brevis* 3M004 | *P. aeruginosa* | Inhibits biofilm formation | [97] |
| | *L. casei* | *Streptococcus mutans* | Inhibits QS genes vicKR and comCD | [98] |
| | *L. casei* ATCC 393,<br>*L. reuteri* ATCC23272,<br>*L. plantarum* ATCC14917<br>*L. salivarius* ATCC11741 | *Streptococcus mutans* | Inhibits acyl-homoserine lactone activity and blocks their synthesis | [98] |
| | *L. fermentum Lim2* | *Clostridium difficile* | Reduces the AI-2 in QS gene *luxS* | [99] |
| | *L. plantarum* PA 100 | *P. aeruginosa* | Inhibits acyl-homoserine lactone activity and blocks their synthesis | [100] |

**Table 1.** *Cont.*

| Probiotics | | Bacteria Inhibited | QSI Mechanism | References |
|---|---|---|---|---|
| **Genus** | **Species** | | | |
| *Streptococcus* | *S. salivarius* | *S. mutans* | Inhibits biofilm formation in vitro when cultured with *S. mutans* | [101] |
| | *S. salivarius* K12 | *C. albicans* | Inhibits *C. albicans* aggregation, biofilm formation, and dimorphism. | [102] |
| | *S. salivarius* 24SMB and *S. oralis* 89a | *S. aureus*, *S. epidermidis*, *S. pyogenes*, *S. pneumoniae*, *M. catarrhalis* and *P. acnes* | Inhibits biofilm formation in pathogens of the upper respiratory tract | [103] |

## 5. Concluding Remarks and Perspectives

Food spoilage and foodborne diseases associated with quorum sensing in microorganisms cause huge economic losses and health issues in food production and food-processing industries. Although the use of antibiotics is the traditional method used to inhibit bacteria, it has also been reported to enhance antibiotic resistance. For this reason, safer, ecologically friendly, and cheaper methods have been employed, and QQ using probiotics is one of these methods. Extensive research has been conducted in this direction, and the results demonstrate the effectiveness of probiotics as QQ agents. Unfortunately, these bio-functional activities were mostly reported and proven in vitro, and reports showing industrial applications are scarce. Therefore, the most important recommendation that can be given here is to promote more industrial applications to exploit the well-known QQ aptitudes of probiotics to reduce food spoilage.

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