Bacterial Quorum Sensing and Food: A Review

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ABSTRACT

The discovery that bacteria are able to communicate with each other has changed our perceptions of many single organisms that inhabit our world. Bacteria cells communicate among themselves using low-molecular-weight compounds called autoinduceres, through what is known as quorum sensing (QS), a cell density-dependent signaling system. The principle components of the QS circuit are; two regulatory genes *LuxI* and *LuxR* and the target operon which are usually composed of different genes. Quorum sensing enables bacteria to coordinate their behaviour which involved in some bacterial activities. Overall bacteria may use QS for their growth, survival and virulence in food environments. So, targeting QS may be an effective approach against bacterial proliferation and virulence.

Food spoilage is a complex process, excessive amounts of foods are lost due to the microbial spoilage. Several proteolytic, lipolytic, chitinolytic and pectinolytic activities associated with the deterioration of foods are regulated by QS. Several types of autoinducers (AI), have been detected in different spoiled food products. So, disrupt the QS circuit plays a major role in controlling microbial gene expression related to human infection and food spoilage. The QS inhibitors can be developed that are targeted toward inhibiting the synthesis of the autoinducer molecules or block these signaling systems. Thus, it can lead to prevention of food spoilage, biofilm formation and food born pathogens.

Key words: quorum sensing, bacteria, autoinducers, expression gene, operon, signaling system, proliferation, virulence, food spoilage.

INTRODUCTION

There are billions and billions of incredibly diverse microorganisms within and around us. To function effectively within there diverse environments, bacterial communities have developed very sophisticated means of sensing their local environments and adapting to changing conditions. In recent years it has become apparent that bacteria coordinate their interaction and association with higher organisms by intercellular communication systems. This process is known as quorum sensing (QS), bacteria communicate with one another using chemical signaling molecules called autoinducers. When an autoinducer reaches a critical threshold, the bacteria detect and respond to this signal by altering their gene expression (Andersen *et al*., 2001, Miller & Bassler, 2001, Chen *et al*., 2002, Taga & Bassler, 2003, Reading & Sperandio, 2006).

In some cases a single bacterial species can have more than one QS system and therefore use more than one signal molecule. The bacterium may respond to each molecule in a different way. In this sense the signal molecules can be thought of as words within a language, each having a different meaning. Simply, QS is a mechanism for regulating gene expression in response to changes in cell density of a bacterial population (Bassler, 2002, Aguilar *et al*., 2003).

The purpose of QS is to coordinate certain behaviour or action between bacteria. It can occur within a single bacterial species as well as between disparate species, and can regulate a host of different processes, essentially serving as a simple communication network. Bacteria use QS communication circuits to regulate a diverse array of physiological activities. These processes include symbiosis, virulence, competence, conjugation, antibiotic production, motility, sporulation, and biofilm formation (Miller & Bassler, 2001, Hentzer *et al*., 2003, March & Bentley, 2004).

Quorum sensing allows bacteria to monitor the environment for other bacteria and to alter behaviour on a population-wide scale in response to changes in the number and/or species present in a community. Thus, QS confuses the distinction between *prokaryotes* and *eukaryotes* because it enables bacteria to act as multicellular organisms. So, it is providing a new dimension to our understanding of how complex micro-organisms really are (Chen *et al*., 2002, Waters & Bassler, 2005).

Recently, new information about the different QS systems, the type of autoinducer (AI) molecules, the genes influenced by QS and their role in food spoilage and safety has been studied (Ren *et al*., 2005, Waters & Bassler, 2005, Pillai & Jesudhasan, 2006, Salim *et al*., 2008).

The present review provides a general overview of bacterial quorum sensing and its relevance to food.

History of quorum sensing

Before discussing the discovery of QS we must first go back in history at the begging of observation of bioluminescent. Bioluminescent is the light produced by a chemical reaction that occurs in an organisms. It was first observed as glowing water in the year 500 B.C. which was described as light emitted by the sea when it was struck with an oar (Miller & Bassler, 2001).

Bioluminescence is a primarily marine phenomenon occurs at all depths in the ocean, but is most commonly observed at the surface. Bioluminescence is the only source of light in the deep ocean where sunlight does not penetrate. Amazingly, about ninety percent of the organisms that live in the ocean have the capability to produce light. Four main uses for an organism to bioluminesce have been hypothesized. It can be used to evade predators, attack prey, communicate within their species, or advertise (Whitehead *et al*., 2001). Quorum sensing was first observed and described in the bioluminescent marine bacteria *Vibrio fischeri* and *Vibrio harveyi* which colonize the light organ of the Hawaiion squid *Euprymna scolopes*. There, they grow to high cell density, produce the AI acylhomoserine lactone, and induce the expression of genes required for bioluminescence. The squid (Fig. 1) is able to use the light to avoid predation, while the bacteria are able to proliferate to high numbers within the light organ (Nealson & Hastings, 1979, Lerat & Moran 2004, Pillai & Jesudhasan, 2006, Anonymous, 2009).

At least, two chemicals are required for bioluminescent, the one which produces the light is generically called a "luciferin" and the one that drives or catalyzes the reaction is called a "luciferase". The basic reaction follows the sequence illustrated in Fig. (2).

The luciferase catalyzes the oxidation of luciferin, resulting in light and an inactive "oxyluciferin". In most cases, fresh luciferin must be brought into the system, either through the diet or by internal synthesis. Some times, the luciferin and catalyzing protein (the equivalent of a luciferase), as well as a co-factor such as oxygen, are bound together to form a single unit called a "photoprotein". This molecule can be triggered to produce light when a particular type of ion is added to the system, frequently calcium (Anonymous, 2009).

Fig. 1: The deep-sea fish *Aristostomais* has more than one light organ
Source : Anonymous (2009)

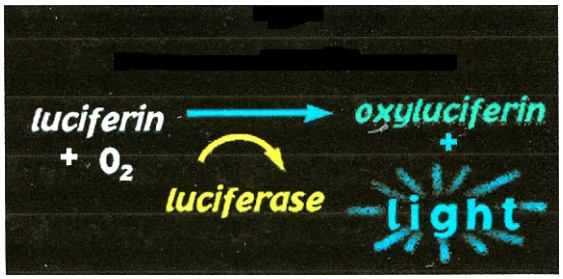

Fig. 2: The Basic reaction of the bioluminescence
Source : Anonymous (2009)

Quorum sensing model

The *Lux* R/I system was the first one to be described in *V. fischeri*. The luciferase operon in *V. fischeri* is regulated by two proteins, *LuxI*, which is responsible for the production of the acylhomoserine lactone (AHL) autoinducer, and *LuxR*, which is activated by this autoinducer to increase transcription of the luciferase operon (Fig. 3). The *LuxR*-type proteins are transcription factors, which upon binding to the AHL signal, regulate transcription of their target genes. It has been shown that AHL binding to these proteins stabilizes them; otherwise, in the absence of signal, they are targeted to degradation (Fuqua *et al*., 1994, Zhang, *et al*., 2002, Reading & Sperandio, 2006).

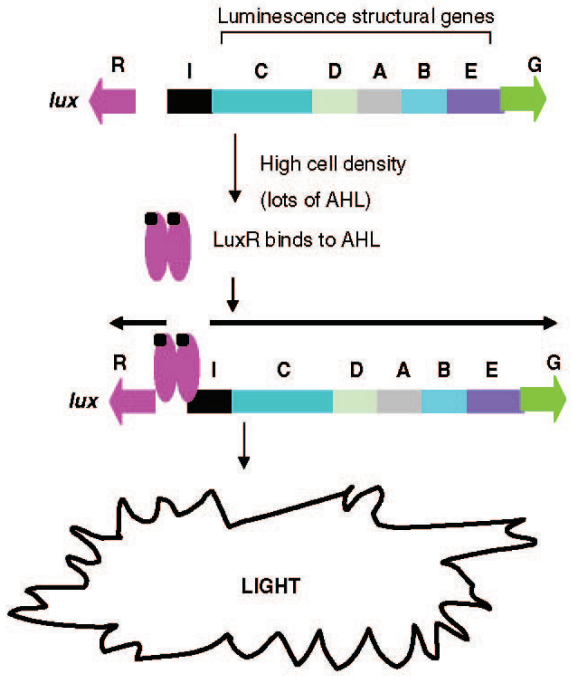

Fig. 3: Model of bioluminescence activation in *Vibrio fischeri* by the *LuxR*/*I* quorum-sensing system. In high cell density, the acyl-homoserine lactone (AHL) autoinducer binds to *LuxR*. *LuxR* complexed with AHL then activates transcription of itself and the luciferase operon

Source: Reading & Sperandio (2006)

Eberl *et al*. (1999) and Gram *et al*. (2002) declared that, the AHL-based quorum sensing systems of the *lux*-homologous family require a minimum of four components for proper functions:

1- A diffusible AHL type signal molecule, synthesised by an enzyme (referred to as the *LuxI* homolog);

2- An AHL-binding receptor (referred to as the *LuxR* homolog) which DNA binding activity is altered in response to binding of its cognate signal molecule,

3- A DNA sequence (typically referred to as the *lux*-box) located in the promoter region of a target gene, acting as target sequence for the regulatory *LuxR* homolog allowing it to act as transcriptional regulator.

4- A set of target genes resulting in a particular phenotype, which is either up-regulated or repressed as a function of the *LuxR*-AHL binding.

Bacterial autoinducer molecules

Quorum sensing bacteria produce and release chemical signal molecules called autoinducers that increase in concentration as a function of cell density. At least some of these molecules can serve as "signals" (Bassler, 1999, Surette, *et al*., 1999, Wang, *et al*., 2001). Cell–to–cell communication via autoinducers occurs both within and between bacterial species. Reading & Sperandio (2006) reported that the nature of autoinducer varies among species and among systems in the same species. The autoinducers may be classified into three subclasses: The first are those used by Gram-negative bacteria, the second concerning the Gram-positive bacteria and the third those which may be used by both.

Four broad categories of signaling molecules have been reported: 1- The fatty acid derivatives of N-acylhomoserine lactones (AHLs) used by Gram-negative bacteria for intraspecies communication (termed AI-1); 2- A furanosyl boronated diester molecule (AI-2) and a non-boronated diester molecule (vAI–2) used by Gram-positive and Gram-negative bacteria for intra- and interspecies communication. 3- An AI of currently unknown structure (AI–3), which is involved in cross-talk between *Escherichia coli* O157–H7 and the host epinephrine cell–signaling system. 4- Peptides and short–chain amino acids used by Gram-positive bacteria such as *Bacillus subtilis* (Miller & Bassler 2001, Wang *et al*., 2001, Sperandio *et al*., 2003, Abraham, 2006, Pillai & Jesudhasan, 2006), Fig. (4).

Recently, a new class of homoserine lactone quorum-sensing signals was investigated by Schaefer *et al*. (2008). They reported that the photosynthetic bacterium *Rhodopsendomnas palustris* uses an acyl-HSL synthetase to produce *p*-coumaroyl-HSL by using environmental *p*-coumaric acid rather than fatty acids from cellular pools. The bacterium has a signal receptor with homology to fatty acyl-HSL receptors that responds to *p*-coumaroyl-HSL to regulate global gene expression.

The main functions of bacterial quorum sensing

The deep understanding of the *LuxR*/I mechanism and stages of QS explained clearly the lifestyle(s) of bacteria. Through this mechanism, bacteria finds its way, like any other living organism, to conserve its live, to survive, and to function effectively within their diverse environments. Microbial populations or microbial life stages in-

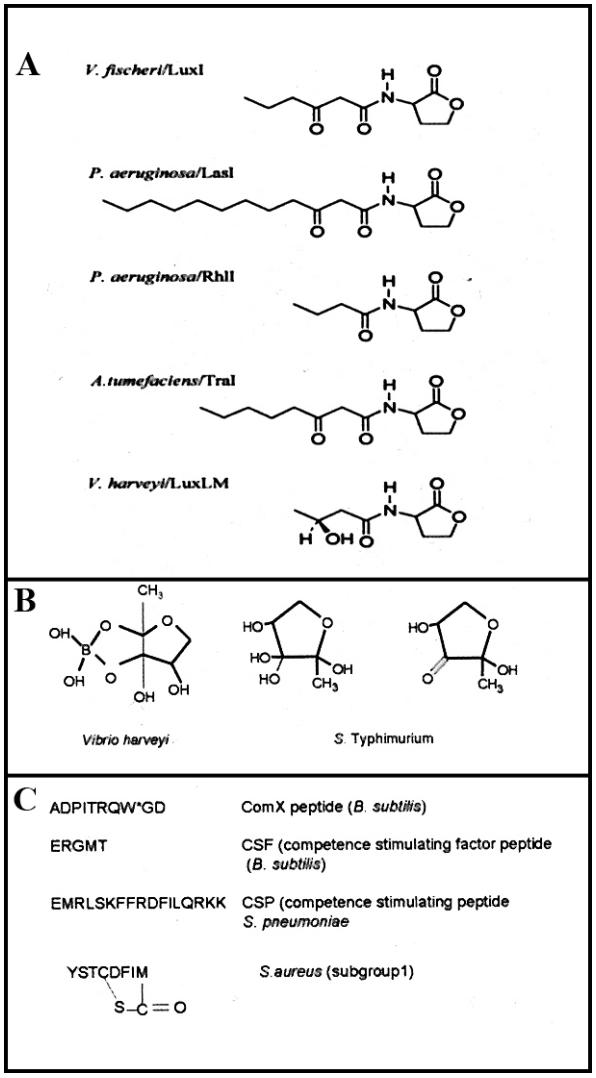

Fig. 4: Schematic representation of molecules that function as autoinducers in bacterial quorum sensing: (A) acyl-homoserine lactones (AHLs), (B) boronated and non-boronated forms of AI–2, and (C) the amino acid sequence of oligopeptides

Source: Pillai & Jesudhasan (2006)

fluence almost every aspect of human, animal and other living organisms. This indicates that there are many contact points between bacteria and the environment and/or different living organisms, including man (Davies *et al*., 1998, Miller & Bassler, 2001, Khamel *et al*., 2008).

Bacteria, through its normal life, affect their environment by different and diverse compounds secreted out of bacterial communities. These compounds have several purposes including:

1- It may be some end products compounds of the normal metabolism of the cells.

2- It may secrete compound use to compete other bacteria or living organism, it is a defense compounds.

3- It may be an enzyme(s) secreted out of the cells. These enzymes are mainly hydrolases which hydrolyse some biomolecules to its main monomers then used as nutrients for the bacterial cell.

All of these effects, and others, are the normal physiological activity of bacteria, which may be harmful or useful to the surrounding media or organisms. For example, biofilm formation, which is one of the main common bacterial lifestyles, is harmful for man since it causes many of infection diseases, but it is useful if used in biofilters. Compounds which secreted out of the bacterial cell may be toxic, botulism formed by *Clostridium botulinum*, or may be beneficial as bacteriocines formed by different bacteria including lactic acid bacteria (LAB). The extracellular hydrolyzing enzymes cause food spoilage and they are also, useful when are used for biofilterizer formation or for waste treatment. Bacteria itself don't intended to be useful or harmful. This is the result of the interactions of bacteria with its neighboring, for example, if the normal lifestyle of bacteria is parallel to that of its surrounding it will be useful, but it will described as harmful if the two types of life are opposite to each other (Davies *et al*., 1998).

All these bacterial effects started by the proliferation of bacteria, which is the first stage in quorum-sensing. So, QS is very important for man and many other living organisms besides it is importance for some biological process (Kanamaru *et al*., 2000, Sperandio *et al*., 2001). Control of quorum sensing may lead to more decrease in the harmful effects of some bacterial communication. It is also beneficial for more utilization of useful bacterial behaviour (Khamel *et al*., 2008).

Detection of quorum sensing autoinducers and/or autoinducer producing bacterial strains

One of the most widely used methods for measuring bacterial autoinduction is based on the bioluminescent response of *V. harveyi*. In this method, a cell-free conditional medium from a culture of interest is incubated with a culture of *V. harveyi* and the bioluminescent response is recorded (Bassler *et al*., 1993)

The AHLs can be extracted from complex samples like foods by homogenising in ethyl acetate. Subsequently, the presence of AHLs can be evaluated using one or several bacterial AHL-monitoring strains. Several types of AHLs which are produced in foods can be visualized by separation of extracted AHLs on thin layer chromatographic plates and subsequent development by AHL-monitor strains (Shaw *et al*., 1997, Ravn *et al*., 2001).

Also, AHL production in foods can be visualized directly using reporter system. If an AHL-producing strain and an AHL-negative strain carrying an AHL monitor system (e.g. the *LuxR*-gene and *LuxI*-promoter) fused to a reporter gene such as green fluorescent protein (GFP), which works well for monitoring gene expression at the single-cell level in biofilms (Andersen *et al*., 2001). The AHL-producing bacteria can also be isolated directly by replica-plating from a non-selective aerobic agar media containing AHL-monitor strains (Gram *et al*., 2002).

Frommberger *et al*. (2004) described a liquid chromatography-based concentration and separation method with mass spectrometer determination for various AHLs in bacterial culture. Also, a colourimetric method for determining salicylic acid carboxyl methyltransferase has been reported (Hendricks *et al*., 2004).

The PCR techniques have greatly simplified quorum data gathering and differentiation between pathogenic and non-pathogenic strains of bacteria. The PCR amplified quorum sensing regions from *Enterococcus*, *Clostridium* and *Lactobacillus* species (Hernandez & Olmos, 2004, March & Bentley, 2004).

Presence of the autoinducer in foods

The autoinducer-2 (AI-2) molecule produced by bacteria as a part of quorum sensing is considered to be a universal inducer signal in bacteria because it reportedly influences gene expression in a variety of both Gram-negative and Gram-positive bacteria (Lu *et al*., 2004). Recent studies have shown that some fruits such as tomatoes, strawberries and pineapples produce 2,5-dimethyl-4-hydroxy-3(2H)-furanone (DMHF), which have AI-2 activity when assayed using the reporter strain *V. harveyi* BB170 (Schauder *et al*., 2001, Winzer *et al*., 2002). Maximum AI-2 activity was seen on the frozen fish sample (203-fold as compared to the negative control) followed by tomato, cantaloupe, carrots, tofu, and milk samples (Lu *et al*. 2004, Pinto *et al*., 2007).

Many studies have shown that another autoinducer molecule (AI-1) mimic can be found in the extracts of some plants such as pea, tomato and rice (Teplitski *et al*., 2000, Bauer & Robinson, 2002). Also, AHLs were extracted and detected from produced vacuum packed meat and fish products. The AHL-producing bacteria of these samples were isolated and identified as *Enterobacterianceae* (*Hafina alvei*) (Ravn *et al*., 2001, Bruhn, *et al*., 2004).

Taylor *et al*. (2004) reported for the first time the production of AHLs by bacteria associated with marine sponges. Also, they suggested that AHLs are being produced *in situ* within sponges. So, QS signals could play a part in interactions between sponge and dense bacterial communities living within them.

Besides, it was found that bacterial infection of plants depends on the exchange of QS signals between nearby bacterial cells. It is now evident that plants, in turn, "listen" to these bacterial signals and respond in sophisticated ways to the information. Plants also secrete compounds that mimic the bacterial signals and thereby confuse QS regulation in bacteria (Bauer & Mathesius, 2004).

Potential application of QS in food spoilage and food industry

I. Quorum sensing and Food spoilage

Food spoilage is a complex process and excessive amounts of foods are lost due to the microbial spoilage even with modern day preservation techniques. Spoilage is characterized by any change in a food product that renders it unacceptable to the consumer from a sensory point of view. This may be physical damage, chemical changes (oxidation, colour changes) or appearance of off-flavours and off-odours resulting from microbial growth in the product. It may be as visible growth (slime, colonies), as textural changes (degradation of polymers). The three main classes of microbial interactive behaviour of potential importance in microbial food spoilage, namely, antagonism, metabiosis cell-to-cell communication which has been termed quorum sensing. The quorum sensing results from the fact, that the autoinducers are diffusible over the cell membrane and that the regulatory gene requires a threshold concentration of the (AIs) in order to be activated (Gram *et al*., 2002).

Proteolytic and pectinolytic activities in some Gram-negative bacteria are regulated by QS. The extracellular enzymes pectate lyase, pectin lyase, polygalacturonase, cellulase and proteases are regulated by N-3-oxohexanoyl-L-homoserine lactone (3-oxo-C6-HSL) dependent QS in some plant pathogens. So, QS could be an important feature of vegetable spoilage, since this process typically involves pectinolytic degradation. Understanding of the microbial processes leading to spoilage would facilitate development of preservation techniques and reduce loss of food (Rasch *et al*., 2005).

It has been reported that bacterial spoilage in various food may be associated with QS. Major pathogenic bacteria such as *E. coli* O157: H7, *Salmonella* and *Campylobacter* species have been found to produce AI-2 molecules in foods (Rasch *et al*., 2005, Salim *et al*., 2008).

(a) Involvement of bacterial quorum-sensing in spoilage of bean sprouts

Rasch *et al*. (2005) investigated the involvement of bacterial QS signals in spoilage of bean sprouts. They chose bean sprouts as a model for vegetables, since it can be produced under controlled conditions in the laboratory. Commercially available bean sprouts usually have very high bacterial count reaching 108 CFU/g during two days of sprouting. Bacterial spoilage of bean sprouts is characterized by soft rot, in which maceration of plant tissue by bacterial enzymes results in collapse of the cell wall structure. The most important bacteria causing soft rot of vegetables and fruits are the Gram-negative *Erwinia carotovora* and pectinolytic strains of *Pseudomonas fluorescens*. Their results indicated that the bacterial communication signals, acylated homoserine lactones (AHLs) were extracted from samples of commercial bean sprouts undergoing soft-rot spoilage. A total of 32 AHL-producing bacterial isolates were obtained from different batches of commercial bean sprouts. All isolated strains were Gram-negative bacteria (*Enterobactriaceae* and *Pseudomonas* spp.). The strains were both proteolytic and pectinolytic and capable of causing soft-rot spoilage in bean sprouts. The results revealed the presence of N-3-oxohexanoyl-L-homoserine lactone in spoiled bean sprouts and its ability to restore the spoilage process of the AHL-negative mutant.

There was a complete lack of soft-rot spoilage in sprouts which contained high levels of non-AHL- producing bacteria. Also, spoilage of bean sprouts inoculated with the AHL-negative mutant was delayed as compared to its AHL-producing parent. Figure (5) shows the appearance of bean sprouts, soaked in water which has been inoculated with different bacterial strains to determine their spoilage potentials.

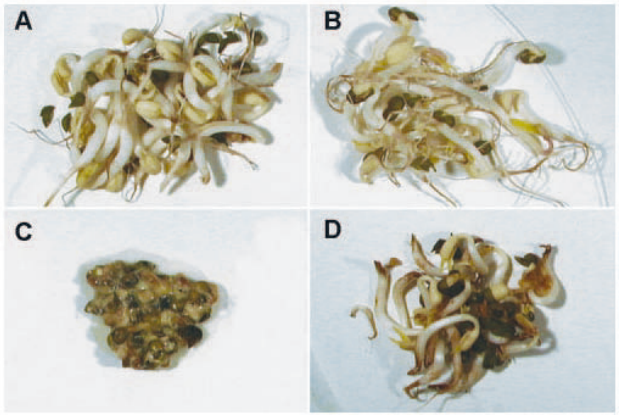

Fig. 5: Appearance of bean sprouts. (A) control (uninoculated); (B) bean sprouts inoculated with the nonspoiling strain C1JM, (C) bean sprouts inoculated with the spoiling strain *Pectobacterium* sp. Strain A2JM, and (D) bean sprouts inoculated with the AHL- negative mutant

Source: Rasch *et al.* (2005)

(b) Quenching of bacterial quorum-sensing

The AHL-lactonase, a new enzyme from Bacillus sp., inactivates AHL activity by hydrolyzing the lactone bond of AHLs. This enzyme is encoded in the aiiA gene of Bacillus sp. 240BI. Plants are able to expressing AHL-lactonase, quenched the pathogen quorum-sensing signalling molecules (AHLs) and showed significantly enhanced resistance to *E. carotovora* infection (Dong *et al*., 2000).

The enzyme activity was tested on N-(3-oxohexanoyl)–L–homoserine lactone (OHHL), which regulates expression of virulence genes in a plant pathogen *Eriwinia carotovora pv. carotovora*. The results demonstrated that the enzyme hydrolysed the ester bond of the hemoserine lactone ring of AHL. This observation was further confirmed by testing three other AHLs with differences in acyl-chain length and substitution at the C_3 position.

To test the effect of AHL-lactonase on bacterial infection using a primary transgenic tobacco and

potato plants along with controls, (untransformed, plants), the *aii*A gene introduced into genome of tobacco and potato by means of *Agrobacterium*-mediated transformation. The gene reached to the intercellular space of plant tissues where *E. carotovora* initiates infection.

The AHL-lactonase activities were observed in all plants transformed with the *aii*A gene. The results indicated that the resistance of the *aii*A transgenic plants is related to the population density of the inoculated pathogen. Control plants displayed typical maceration symptoms several hours after inoculation. The higher the population density of the inoculums, the larger is the maceration area on the tobacco leaves. Fourty hours after inoculation, the leaves of control tobacco were totally macerated (Fig. 6).

The effect of AHL-loctonase on symptom development appears even clearer in the *aii*A transgenic potato. Watery lesions were observed in the control several hours after inoculation. Symptoms worsened progressively until the whole slice was completely macerated. In contrast, inoculation

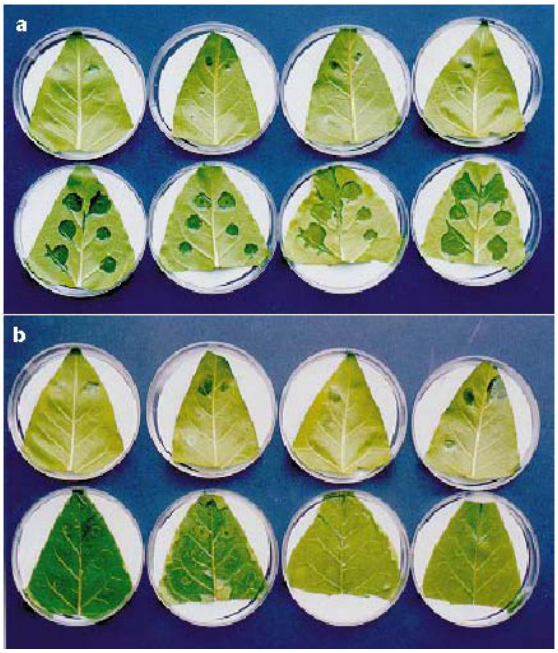

Fig. 6: Plant inoculation with *Erwinia carotovora* SCG1. (a) Top row are tobacco leaves from *aii*A transgeneic plants; bottom row are those from controls, untransformed, plants. The photograph was taken 20 hr after inoculation. (b) Same as (a) except the photograph was taken 40hr after inoculation

Source: modified from Dong *et al.*, 2001)

at high population density initially produced watery lesions in the tubers of *aii*A potato but soon the lesions became dry and symptom development stopped (Figure 7).

Fig. 7: The potato tuber slices in the left columns are controls, untransformed, plants, while all others are from *aii*A transgenic plants. The inoculum cell numbers for rows from top to bottom were 25,000; 50,000, 75,000 and 100,000 CFU, respectively. The photograph was taken 48hr after inoculation

Source: modified from Dong *et al.*, 2001)

II- Quorum sensing and food industry

Bacteria in nature often exist as sessile communities called biofilms. These communities develop structures that are morphologically and physiologically differentiated from free-living bacteria. So, to form biofilms, bacteria have to start a complex genetic program to switch from planktonic to sessile lifestyle. A biofilm is a complex aggregation of microorganisms growing on solid substrate. Biofilms are characterized by structural heterogeneity, genetic diversity, complex community interactions, and an extracellular matrix of polymeric substances (Costerton *et al*., 1999, Moons *et al*., 2006).

A biofilm can be formed by a single bacterial species, but more often biofilms consist of many species of bacteria, as well as fungi, algae, protozoa, debris and corrosion products. Formation of a biofilm begins with the attachment of free-floating microorganisms to the surface. These first colonists adhere to the surface initially through week reversible Van der Waals forces. If the colonists are not immediately separated from the surface, they can anchor themselves more permanently using cell adhesion molecules such as pili. The first colonists

facilitate the arrival of other cells by providing more diverse adhesion sites and beginning to build the matrix that holds the biofilm together and begin to excrete a slimy material (Davies *et al*., 1998, Hentzer *et al*., 2003, Van Houdt *et al*., 2004)

Biofilms are usually found on substrates submerged in-or exposed to some aqueous solutions. Bacteria living in a biofilm can have significantly different properties from free- floating bacteria, as the dense and protect environment of the film allows them to cooperate and interact in various ways. One benefit of this environment is increasing resistance to detergents and antibiotics, as the dense extracellular matrix and the outer layer of cells protect the interior of the community. This matrix protects the cell within it and facilitates communication among them through chemical and physiological signals. Some biofilms have been found to contain water channels that help distribute nutrients and signaling molecules. This matrix is strong enough that in some cases, biofilms can become fossilized (Mah & O'Toole 2001).

The bacterial cells on the surface of the biofilm are different from the cells within the biofilm matrix. The embedded cells behaviour can change as the thickness of the biofilm changes. The surface cells, no matter how old the biofilm is, are likely to mimic surfaces cells of young biofilms which are metabolically active and large. These surface cells divide and increase the thickness of the biofilm. Little oxygen is available to the embedded cells, therefore, they are smaller and grow slower. The bacteria exist in a somewhat dormant state, becoming active when cells in the outer layers are killed (Mah & O'Toole 2001, Van Houdt *et al*., 2006).

For the food industry in particular, the formation of biofilms on food and food- processing surfaces, and potable water distribution systems, increased risk for product contamination with spoilage or pathogenic microflora (Carpentier & Cerf 1993, Donlan, 2002).

In industrial environments, biofilm can develop on the interiors of pipes and lead to clogs and corrosion. Biofilms on floors and counters can make sanitation difficult in food preparation areas. Although biofilms usually cause harmful effects, they can some times be beneficial. For example, biofilms can be used for water treatment, in that they can break down undesirable compounds, thereby purifying the water (Costerton *et al*., 1999, Singh *et al*., 2002).

Some of the environmental signals that have currently been identified to regulate the structure of a mature biofilm are nutrient availability and quorum sensing, and are not species specific. Nutrient availability regulates the depth of the biofilm in such a way that the maximal number of cells in a biofilm appears to occur at suboptimal nutrient concentrations. At either extreme, nutrient-rich or very nutrient-poor conditions, greater number of cells are in the planktonic phase where they have greater acess to the local nutrients or can be distributed to a new environment. Similarly, quorum-sensing control of the formation of channels and pillar-like structure may ensure efficient nutrient delivery to cells in a biofilm (Stanley & Lazazzera, 2004).

Biofilms are important survival mechanism for bacterial cells. According to *in vitro* studies, they can avoid attack by host defense. Also, biofilms are much more resistance than planktonic cells to antimicrobial agents. For example, chlorinated of a biofilm is usually unsuccessful because the biocide only kills the bacteria in the outer layers of the bioflim. The bacteria within the biofilm remain healthy, and the biofilm can regrow. Repeated use of antimicrobial agents on biofilms can cause bacteria within the bioflim to develop and increase resistance to biocides (Costerton *et al*., 1999).

One mechanism of biofilm resistance to antimicrobial agents is the failure of an agent to penetrate the full depth of the biofilm. Polymeric substances like those that make up the matrix of a biofilm are known to retard the diffusion of antibiotics and solutes in general diffuse at slower rates within biofilms than they do in water. A second hypothesis to explain reduced biofilm susceptibility to antibiotics posits that at least some of the cells in a biofilm experience nutrient limitation and therefore exist in a slow-growing or starved state. Slow-growing or nongrowing cells are not very susceptible to many antimicrobial agents. A third mechanism of reduced biofilm susceptibility, which is more speculative than the preceding hypothesis, is that at least some of the cells in the biofilm adapt a distinct and protected biofilm phenotype. This phenotype is not a response to nutrient limitation, it is biologically programmed response to growth on a surfaces (Costerton *et al*., 1999, Mah & O'Toole, 2001, Olson *et al*., 2002).

Van Houdt *et al*. (2004) investigated the biofilm-forming capacity and the production of quorum sensing signals in Gram-negative bacteria

isolated from a food production environment, and the possible correlation between both phenotypes. Sixty-eight Gram-negative bacteria were isolated from the equipment and working surfaces in a raw vegetable processing line, and tested for biofilm-forming capacity using an *in vitro* microplate assay. Various assays based on reporter bacteria were used to detect quorum signals produced by the isolates. They reported that all isolates showed significantly ($P<0.05$) higher biofilm-forming capacity than *Eshcerichia coli* laboratory strain DH5α, which was induced as a negative control. Also, there was a large variation in the relative biofilm forming capacity among the isolates from the vegetable processing line.

The expression of many phenotypic traits in microorganisms is governed by tight gene regulation and influenced by growth phase, nutrients, external stresses and a multitude of other factors. Quorum sensing is the mechanism of gene regulation in bacteria is response to changes in cell density of a bacterial population (Fuque *et al*., 1994, Jayaraman & Wood, 2008).

Quorum sensing inhibitors

Bacterial cells can communicate with each other through autoinducer molecules which function as signaling molecules. Thus, it is logical to control the proliferation and survival of bacterial communities, through developing strategies to inhibit their quorum-sensing by interrupt or modulate these communication signals using one or more of the following sites of attack: inhibiting the synthesis of the AI molecules, inhibiting the dissemination, inactivate or blocking the AI signalling, or inhibiting or blocking the sensing of the AI signals (Pillai & Jesudhasan, 2006).

An intense work has been done on stability and degradation of AI as well as search for compounds that specifically could block AIs communications. It was found that such quorum sensing inhibitors (QSI) are typically analogues of the AHLs (Eberhard *et al*., 1986) or compounds that degrade AHLs (Dong *et al*. 2000). One group of QSI is the halogenated furanones produced by red alga *Delisea pulchra* and synthetic furanones. Other studies have shown that a number of foods contain furanone compounds (Slaughter, 1999). These compounds are reported to be strong inhibitors for both AI-1 and AI-2 quorum sensing system. Natural furanones have shown to interfere with the receptor proteins and release the AHL- signal (Givskov *et al*. 1996, Manefield *et al*., 2002, Ren *et al*., 2004). The antimicrobial triclosan suppressed AHL biosynthesis through inhibiting the reaction catalysed by enoyl-acyl carrier protein reductase (Hoang & Schweizer 1999, Leadbetter & Greenberg, 2000).

Certain foods have the ability to partially or completely inhibit AI-2 activity. Turkey patties showed the highest inhibition (99.8% compared with the positive control), followed by chicken breast (97.5%), homemade cheeses (93.7%), beef steak (90.6%), and beef patties (84.4%)(Lu *et al*., 2004).

The AI-2 activity was almost totally inhibited by sodium propionate, whereas sodium benzoate caused 93.3% inhibition, compared with 75% inhibition by sodium acetate. Sodium nitrate did not have any appreciable effect, even at 200 ppm. These results may change the real function role of food preservatives and its interaction with the mechanism of QS of bacteria (Lu *et al*., 2004).

Furthermore, extracts of vanilla, garlic, and other medicinal plants have also anti-quorum sensing activity (Bjarnsholt *et al*., 2005, Choo *et al*., 2006). Recently it was found that fatty acids of poultry meat such as linoleic acid, oleic acid, palmitic acid and stearic acid had inhibition effect to autoinducer-2 (AI-2) (Widmer *et al*., 2007).

Girennavar *et al*. (2008) reported that naturally occurring furocoumarins from grapefruit showed > 95% inhibition of AI-1 and AI-2 activities based on the *V. harveyi* autoinducer bioassay. Grapefruit juice and furocoumarins also inhibited biofilm formation by *Escherichia coli* O157: H7, *Salmonella typhimurium* and *Pseudomonas aeruginosa*.

So, further studies are needed to know whether processed and natural foods contain AIs, AI-like "mimic" compounds, or quorum-sensing inhibitory molecules. Also, it is need to have a clear understanding of how these foods and food components influence microbial cell signalling.

Finally, understanding the relationships that exist between the food ingredients, food processing, handling, and food consumption methods, and the cell-signalling-based microbial activity of pathogens and spoilage bacteria is critical because such understanding can be important in formulating the next generation of foods that are microbiologically safe and have extended shelf life.

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الحس الجماعي البكتيري والغذاء: استعراض مرجعي

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أدى اكتشاف قدرة البكتيريا على التواصل مع بعضها البعض إلى إحداث تغير كبير في إحساسنا بعديد من الكائنات وحيدة الخلية التي تعيش في عالمنا. تستطيع البكتريا أن تتواصل فيما بينها مستخدمة مركبات صغيرة الوزن الجزيئي يطلق عليها "محفزات ذاتية" (Autoinducers). يتم ذلك من خلال نظام إشارات يعتمد على كثافة الخلايا يعرف بـ "الحس الجماعي" (Quorum sensing QS). المكونات الرئيسية التي تشكل دورة الحس الجماعي هي نوعان من الجينات المنظمة يطلق عليهما *LuxI* و*LuxR* إلى جانب الأوبرون Operon المستهدف وهذا عادة ما يتكون من جينات مختلفة.

ويمكن من خلال الحس الجماعي للبكتريا أن تنظم من سلوكياتها والتي تتمثل في العديد من أنشطتها الحياتية المختلفة. بصفة عامة تستخدم البكتريا الحس الجماعي في نموها والمحافظة على بقائها وسميتها في العديد من بيئات النمو المختلفة – ومن بينها الغذاء. وبناء على ذلك فإن استهداف واختراق دورة الحس الجماعي يمكن أن يكون الاتجاه الفعال لمواجهة نمو وسمية البكتريا.

فساد الأغذية عملية معقدة وكميات متزايدة من الغذاء تفقد بسبب الفساد الميكروبي. وقد وجد أن تحلل كثير من مكونات الغذاء مثل البروتينات والدهون والبكتين والسيليولوز والذي يكون مصاحباً لفساد كثير من الأغذية – يتم تنظيمه من خلال الحس الجماعي للبكتريا. وقد تم اكتشاف أنواع متعددة من المحفزات الذاتية في كثير من المنتجات الغذائية الفاسدة. وعلى ذلك فإن اختراق دورة الحس الجماعي له دور بالغ في التحكم في التعبير الجيني للبكتريا المرتبطة بفساد الغذاء.

وقد كان لإكتشاف وتطوير مثبطات نظام الحس الجماعي –بهدف تثبيط تخليق جزئيات المحفزات الذاتية أو إيقاف أو حجب دروها في التواصل بين الخلايا- دوراً هاماً قد يؤدي إلى منع أو التحكم في الفساد الميكروبي وتكوين الأغشية الحيوية وكذلك انتقال الأمراض عن طريق الغذاء.