

Impact of quorum sensing on the quality of fermented foods

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The quality of fermented food highly depends on the microorganisms involved, their metabolic activities and interactions. Recently, focus has been on quorum sensing (QS) being a cell density-dependent mechanism allowing adaptive responses. Specific QS molecules in prokaryotes and eukaryotes, respectively, mediate the transcriptional changes. For food-borne microorganisms QS regulated traits include biofilm formation, acid stress tolerance, bacteriocin production, competence, adhesion, morphological switches and oriented growth. QS has been reported for microorganisms involved in the production of a number of different fermented foods such as fermented vegetables, sourdough, dairy products, wine, and so on suggesting that QS plays a role in the fermentation of these fermented foods.

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Introduction

The complex microbial communities living in fermented foods, their proliferation, metabolic activity and interactions determine the quality of fermented foods [1]. Some of these microorganisms are deliberately introduced as starter cultures while others are part of the in-house microbiota or introduced by, for example raw materials. The flavour, texture and safety of fermented foods dependent on enzymes and secondary metabolites produced actively by the microorganisms or released to the food matrix by cell lysis [1]. The microorganisms and their functions are strongly influenced by extrinsic and intrinsic factors, the latter including microbial interactions taking place among the members of the microbial community. A detailed understanding of these interactions is therefore a prerequisite in order to optimise and control the quality of fermented foods [2].

Several interaction mechanisms have been described extensively for food-borne microorganisms including nutrient competition, production of organic acids, alcohols, bacteriocins, killer toxins and so on [2]. These types of interactions are common among microorganisms in fermented foods and have been described for fermented foods as kefir, yoghurt, sourdough, surface ripened cheese and wine [3,4]. Meanwhile, knowledge regarding more complex interaction mechanisms such as cell-to-cell communication is lacking behind. One recently described type of microbial cell-to-cell communication is quorum sensing (QS), which is a cell density-dependent type of communication mediated by QS molecules allowing an adaptive switch in gene transcription. QS can be more or less specific and has been reported to occur at both the intraspecies and interspecies level [5].

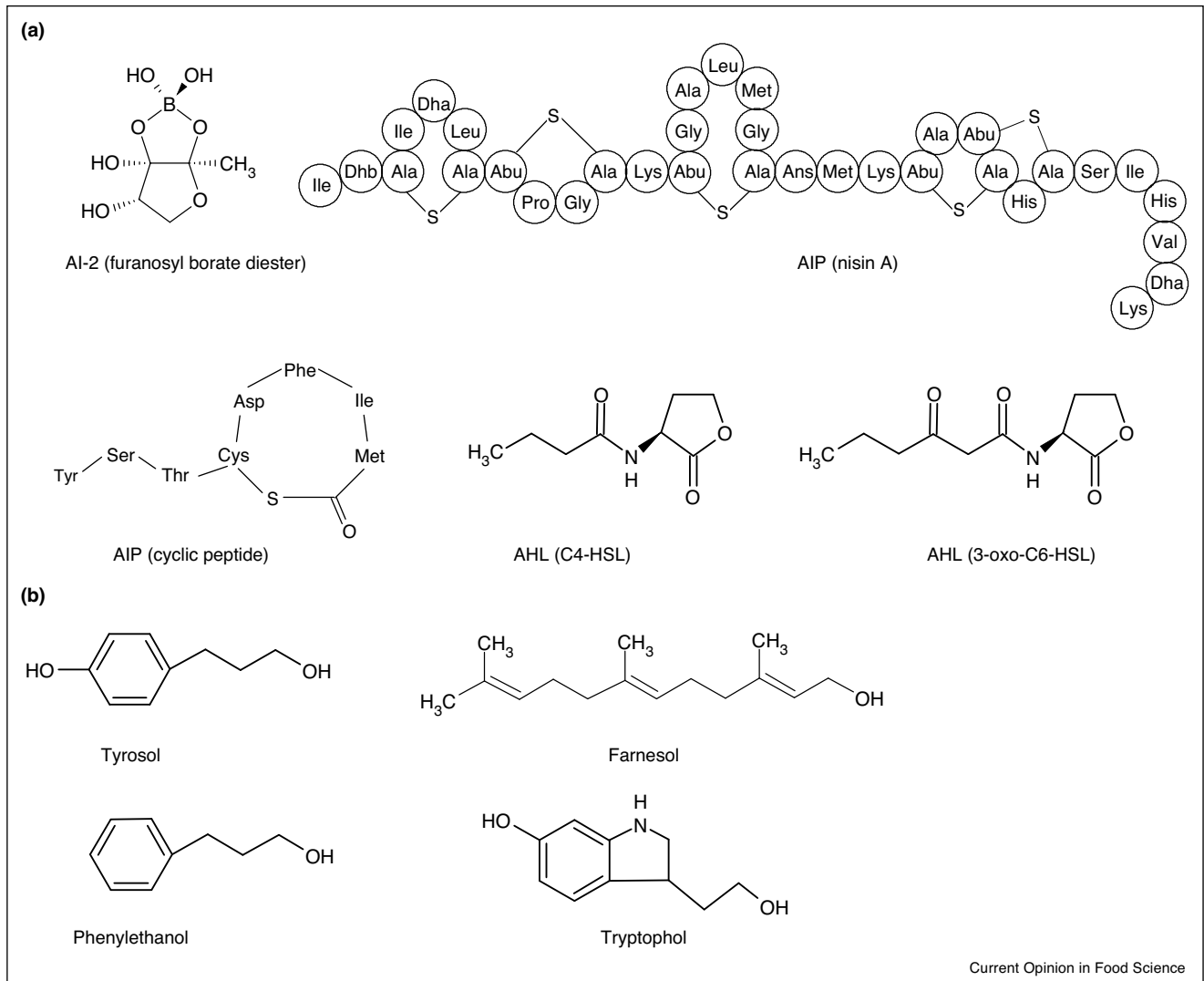
Here, we review recent research on QS for food related microorganisms focusing on the different QS systems identified, microbial traits regulated, effects in the food matrix and potential impacts on the quality of fermented foods.

QS systems in prokaryotes and eukaryotes

QS involves production, secretion and detection of signalling molecules. In its simplest form, proliferating microorganisms produce QS molecules, which are secreted to the extracellular environment. The extracellular concentration of QS molecules increases proportionally to the cell density. At an empirically observed critical threshold various responses are triggered in the cells, able to sense the QS molecules leading to synchronised changes in gene expression [5,6]. Even though QS appears to be rather universal, different QS systems exist for prokaryotes and eukaryotes. Firstly discovered in bacteria, four main groups of QS molecules have been identified, and for most bacterial QS systems the mode of action has been elucidated [5]. On the contrary, less knowledge exists when it comes to eukaryotic QS systems [7]. The structures of various QS molecules are shown in [Figure 1](#).

Autoinducer-2 (AI-2) is produced by more than 100 Gram positive and Gram negative bacterial species. The biosynthetic pathway for AI-2 production is highly conserved among bacteria and caused by its non-specific nature AI-2 has been proposed to function in both intraspecies and interspecies communication [8]. The *luxS* gene, involved in the synthesis of AI-2 has been identified in food-borne LAB [9], in probiotic strains of *Lactobacillus*

Figure 1



Representative structures of quorum sensing (QS) molecules. **(a)** Prokaryotes; autoinducer-2 (AI-2) from *V. harveyi*, autoinducer peptide (AIP) nisin A from *L. lactis* (Abu: aminobutyrate, Dha: dehydroalanine, Dhb: dehydrobutyryne), cyclic AIP from *S. aureus*, acylhomoserine lactones (AHLs) from *P. aeruginosa* (C4-HSL) and *V. fischeri* (3-oxo-C6-HSL). **(b)** Eukaryotes; aromatic alcohols. Tyrosol and farnesol are produced by, for example *C. albicans* whereas phenylethanol and tryptophol are produced by, for example *S. cerevisiae*.

spp. [10], in *Bacillus* spp. [11] and in food-borne pathogens [12^{*}]. In *Vibrio* spp. AI-2 is detected by binding to a receptor protein (LuxP), which interacts with a sensor kinase (LuxQ) initiating a phosphor-transfer cascade resulting in bioluminescence (Figure 2a). Other receptor systems exist in, for example *Escherichia coli* [5]. Autoinducer-3 (AI-3) has been identified in the Gram negative bacteria enterohemorrhagic *E. coli* (EHEC) as well as *Klebsiella pneumoniae*, *Shigella* spp., *Salmonella* spp., *Enterobacter cloacae* and in non-pathogenic *E. coli* [13]. The synthesis pathway and structure of AI-3 is still poorly known [13].

Autoinducer peptides (AIPs) constitute a peptide-mediated QS system in Gram positive bacteria, which has been identified in more than 40 species [14]. AIPs are characterized by a small size, high stability, specificity and diversity. They are ribosomally synthesized as precursor peptides and posttranslationally modified to the active AIP signalling molecules. AIPs are recognised by cognate two-component sensor kinase proteins that upon binding interact with response proteins, which induce transcription of QS regulated target genes [15^{*},16]. Nisin A is known to be an AIP in *Lactococcus lactis*, acting in a QS-dependent manner (Figure 2b).

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