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Review

Membrane fluidity-related adaptive response mechanisms of foodborne bacterial pathogens under environmental stresses

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ABSTRACT

The maintenance of bacterial membrane fluidity plays an important role in a variety of cell physiological functions such as nutrient transport, protection from external adverse environments, and cell morphology. The fluidity of membranes is modified in response to several environmental cues, enabling bacterial survival in otherwise unfavorable conditions. Many foodborne bacterial pathogens are able to survive a variety of food preservation treatments used to prevent microbial contamination. These pathogens are able to successfully exploit membrane fluidity-related adaptation strategies under unfavorable conditions, resulting in food hygiene failures. Factors involved in food preservation include pH, temperature, osmotic stress, antimicrobial agents, and high pressure. The fluidity of bacterial membrane lipid bilayer is altered mainly via the adjustment of membrane fatty acid composition. Under undesirable conditions, Gram-negative bacteria alter their membrane fluidity primarily by regulating the ratio of unsaturated fatty acids (UFAs) to saturated fatty acids (SFAs) and, to a lesser extent, the levels of cyclopropane fatty acids (CFAs), or by *cis*/*trans* isomerization. Gram-positive bacteria typically alter their membrane fluidity with changes in fatty acyl chain length or by forming branched-chain fatty acids (BCFAs), besides changes to the ratio of UFA to SFA. This review encompasses various modulators of membrane fluidity, particularly with respect to foodborne pathogens, which often survive even the hostile environments associated with food processing.

Contents

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1. Introduction

Microbial membranes are essential for survival because bacteria are unable to insulate themselves from various external physical and chemical factors (Mykytczuk, Trevors, Leduc, & Ferroni, 2007). In addition, the bacterial cytoplasmic membrane functions predominantly as a permeable barrier, controlling the transport of biological substances including solutes into and out of the cell. Hence, the membrane at fluid status transports important metabolites, including nutrients, into the cytoplasm. Thus, membrane fluidity is regulated to ensure the biologically active state of the membrane. However, when unfavorable compounds such as toxic agents are present, the fluidity of the membrane decreases in order to prevent their passage into the cells (Murínová & Dercová, 2014). As such, the physiological architecture of the membrane is continuously changing according to its surrounding environment, allowing bacteria to adapt successfully to potentially detrimental situations. Modification of membrane phospholipids plays a major role in regulating membrane fluidity in order to withstand external environmental conditions. Fluidity is associated with the degree of geometrical packing of the phospholipid membrane, a process governed by polar head group composition and fatty acyl chain conformation. Head groups of glycerophospholipids commonly found in bacteria are phosphatidylserine, phosphatidylethanolamine, and phosphatidylglycerol (Weber & de Bont, 1996). The size and charge of the head groups determine the extent of interfacial area between the head groups of membrane glycerophospholipids, eventually modulating membrane fluidity. However, alterations in polar head groups occur less frequently in comparison with changes in fatty acid composition and are less efficient in changing membrane fluidity (Russell, 1984). Therefore, this review focuses on illustrating the modulation of membrane fluidity through fatty acid composition.

As described earlier, the extent of membrane fluidity is affected by changes in fatty acid composition within membrane phospholipids. For example, membranes containing long-chain fatty acids are densely packed, thus lacking fluidity, whereas those composed of UFAs are loosely arranged and more fluid (Moorman et al., 2008). The ratio of UFAs to SFAs is the most important parameter affecting fluidity and rigidity of membranes in most bacteria. However, there are other modulators, including the presence of CFAs, BCFAs, and *cis*/*trans* isomerization of UFAs. The amounts of certain fatty acids are increased or decreased according to external stresses, as a microbial adaptive mechanism.

Changes in membrane fluidity resulting from alteration of fatty acyl composition can be measured by various tools such as X-ray diffraction, differential scanning calorimetry (DSC), electron spin resonance (ESR), nuclear magnetic resonance (NMR), and fluorescence polarization (reviewed in Mykytczuk et al., 2007). Among these, fluorescence polarization is a virtual real-time technique for observing membrane fluidity in response to stress conditions (Trevors, 2003).

Foodborne pathogens are frequently exposed to growth-inhibiting conditions due to food preservative processing measures, implemented for the prevention of microbial contamination. Factors resulting in adverse conditions for microbial growth include pH, temperature, osmotic pressure, and antimicrobial substances, all of which are controlled and used in food processing plants. However, many pathogens present in edible products can survive under stressful growth conditions and often cause foodborne illnesses. Changes in cell membrane fluidity are known to be closely related to adaptation to a variety of environmental stresses such as temperature, pH, osmotic stress, high pressure, nutrient availability, and toxic compounds, e.g., disinfectants, gas composition, ions, and bacterial growth phase (Denich, Beaudette, Lee, & Trevors, 2003; Mykytczuk et al., 2007).

Therefore, this review explains how foodborne bacteria adapt to adverse treatments and provides an opportunity to suggest countermeasures against such adaptation.

2. Modulators of membrane fluidity

Generally, regulation of membrane fluidity occurs through fatty acid changes under various environmental perturbations. Among these, changes in temperature are one of the most widely studied perturbations. Increases in temperature exert a membrane-fluidizing action and alter the fatty acyl chains within the membrane lipids, resulting in a disordered and non-lamellar membrane phase, whereas decreases in temperature solidify the membrane to a gel phase state; both scenarios result in a loss of membrane biological function (Hazel & Williams, 1990). Similar to low temperature, high pressure results in more tightly packed membrane phospholipids (Hazel & Williams, 1990). Toxic chemical compounds, especially hydrophobic molecules, accumulate within the membrane lipids, modify chemical interactions between the fatty acyl chains, and disorganize the membrane phospholipids. In addition, hydrocarbons of chemicals are assimilated to the interior of membrane and contribute to the expansion of the phospholipid bilayers (Antunes-Madeira, Videira, Klüppel, & Madeira, 1995; Denich et al., 2003). In other words, chemicals have a fluidizing effect on membranes, similar to that seen for high temperatures (Denich et al., 2003). Under highly ionic environment, charged molecules interact with the polar head group of the phospholipids within the membrane. Interaction with exogenous positively charged ions such as sodium or hydrogen leads to increased negative charge of the membrane phospholipids, thereby causing the phospholipids to become acidic. Furthermore, this alters the permeability of membrane and results in the swelling or shrinking of bacterial cells (Quinn, 1986; Thiemann & Imhoff, 1991). Bacterial membranes are also influenced by the growth phase, such that the membrane of *Escherichia coli* cells in the stationary growth phase contains lipids with lowered mobility and an increase in lipid–protein interactions, resulting in stabilized membrane (Souzu, 1986). Similar to this, nutrient starvation reduces membrane fluidity by increasing membrane lipid viscosity because of decrease in cell size and reduces the activity of metabolic enzymes, resulting in a retarded growth rate (Mykytczuk et al., 2007).

In response to unfavorable environmental factors, bacteria modify the fatty acyl chains of their membrane phospholipids by (i) alteration of the UFA to SFA ratio, (ii) CFA synthesis, (iii) BCFA formation, and (iv) conversion of *cis*- to *trans*-UFA.

2.1. Changes in the ratio of UFAs to SFAs

UFAs play a critical role in maintaining the fluidity of bacterial membranes. While bacteria increase membrane fluidity using the looser packing of UFAs in membrane phospholipids to adapt to low temperatures and hydrostatic pressures, they decrease membrane fluidity with the more closely packed SFA-containing phospholipids in response to various challenges such as osmotic stress and the presence of toxic compounds. In other words, the ratio of UFAs to SFAs in membrane lipids determines the degree of membrane fluidity and constitutes a major adaptive mechanism in the presence of environmental stresses. For instance, the phospholipid membranes of *E. coli* are mainly composed of three different fatty acids: an SFA, palmitic acid ($C_{16:0}$), and two UFAs, palmitoleic acid ($C_{16:1}$) and *cis*-vaccenic acid ($C_{18:1}$) (Mansilla, Cybulski, Albanesi, & de Mendoza, 2004). When these bacteria are grown at an optimal temperature, palmitic acid and palmitoleic acid are primarily found at positions 1 and 2 of the phospholipid, respectively.