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The adaptive response of bacterial food-borne pathogens in the environment, host and food: Implications for food safety

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ABSTRACT

Bacteria are constantly faced to stress situations in their ecological niches, the food and the host gastrointestinal tract. The capacity to detect and respond to surrounding changes is crucial for bacterial pathogens to survive or grow in changing environments. To this purpose, cells have evolved various sophisticated networks designed to protect against stressors or repair damage caused by them. Challenges can occur during production of foods when subjected to processing, and after food ingestion when confronted with host defensive barriers. Some pathogenic bacteria have shown the capacity to develop stable resistance against extreme conditions within a defined genomic context and a limited number of generations. On the other hand, bacteria can also respond to adverse conditions in a transient manner, through the so-called stress tolerance responses. Bacterial stress tolerance responses include both structural and physiological modifications in the cell and are mediated by complex genetic regulatory machinery. Major aspects in the adaptive response are the sensing mechanisms, the characterization of cell defensive systems, such as the operation of regulatory proteins (e.g. RpoS), the induction of homeostatic and repair systems, the synthesis of shock response proteins, and the modifications of cell membranes, particularly in their fatty acid composition and physical properties. This article reviews certain strategies used by food-borne bacteria to respond to particular stresses (acid, cold stress, extreme pressure) in a permanent or transient manner and discusses the implications that such adaptive responses pose for food safety.

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1. Introduction

Foods are complex environments in which microorganisms may face natural stress conditions such as limited nutrient availability, adverse pH, osmolarity, oxidation, and extreme temperatures, among others. In addition, industrial food preservation regimes commonly rely upon imposing extreme physical and chemical stresses with the aim to inactivate or limit the growth of pathogenic bacteria. Thus, a variety of preservation technologies such as thermal processing, high hydrostatic pressure, pulsed electric fields, radiation, refrigeration, drying, etc. impose a challenge to bacterial cells and can determine the fate of food-borne pathogens along the food chain. Modern strategies in food preservation seek to use mild treatments that inhibit permanently stressed or injured microorganisms by using multiple barriers, especially in the case of minimally processed foods. However, cells adapted to stress, hardened, could be able to withstand further treatments or even the passage through the stomach and intestinal barriers when confronted with host defensive barriers. Other concern is represented by the difficulty of detection during the microbiological

analysis of injured cells because they are not able to grow in conventional microbiological media, when inhibitory compounds are used or an appropriate environment for resuscitation is absent. In this regard, the situation could lead to an overestimation of the lethality of treatments, or to the failure in the detection of pathogens during routine quality control of foods or outbreak investigations.

Bacteria have evolved a range of adaptive strategies to cope with rapidly changing environmental conditions and ensure their survival in inhospitable niches. The stress responses are global, complex systems of defence. They comprise networks to adapt to changing environments and to survive under adverse conditions. Adaptations sometimes derive from the acquisition of stochastic genomic mutations which are positively selected and fixed in the microbial population due to the beneficial phenotype they confer under selective pressure environments (Rando and Verstrepen, 2007). In other occasions, a transient stress response generally consisting of a characteristic change in the pattern of gene expression occurs (Abee and Wouters, 1999). Bacteria are able to do so by upregulating certain genes and down regulating others in order to maintain viability. If the environment surrounding the cell is modified, the changing conditions are sensed by the cell, and the adaptive response is triggered. The genetic regulation involves a series of

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switches controlling the coordinated expression or repression of genes. In the end, a series of physiological responses occur with changes in proteins, DNA, lipids, etc. The response includes the initiation of homeostatic systems, induced synthesis of stress proteins which repair damaged DNA and proteins, and activation of enzymatic systems with specific stress-counteracting activities. Transient stress responses can also occur through modulation of the envelopes and other cellular structures to keep functionality. These transient stress responses help to protect vital processes and to restore cellular homeostasis, to repair the damage, to counteract or eliminate the stress agent, and/or to increase the cellular resistance against subsequent stress challenges.

2. Acquisition of permanent stress tolerance through adaptive mutagenesis

The known edges of the biosphere are typically delineated by extremophilic bacteria that manage to resist the severe physical and chemical conditions encountered in these environments. However, further to the existence of extremophiles, some mesophilic bacteria have shown the capacity to develop resistance against extreme environments within a defined genomic context and a limited number of generations, in a clear example of bacterial adaptability (Vanlint et al., 2011). Such adaptability could be the basis for the existence or persistence of classic mesophilic bacteria in extreme environments that so far have been reported as inaccessible by current experimental techniques.

High hydrostatic pressure (HHP) processing is becoming a valuable non-thermal food pasteurization technique. While the degree of natural HHP resistance has already been shown to vary greatly among and within bacterial species, a still unresolved question remains as to what extent different food-borne pathogens can actually develop HHP resistance, and how this impacts food safety of HHP processed products. Vanlint et al. (2011) used a direct evolution approach to assess the potential of the mesophilic model bacterium *Escherichia coli* to acquire stable resistance to extreme high temperatures or pressures. They observed that while heat resistance could only marginally be increased, piezoresistance (i.e. resistance to high pressures) could readily and reproducibly be extended into the Gigapascal range. The currently recognized maximum pressures for growth or survival of any vegetative microorganisms (including *E. coli*) are in the range of 120 MPa and 800–900 MPa, respectively (Zeng et al., 2009; Jofré et al., 2010). Indeed, it was generally assumed that vegetative microorganisms would never be able to survive exposures in the GPa range (Daniel et al., 2006). However, in the study by Vanlint and co-workers the acquired piezotolerance was extraordinary, since the upper pressure limit for survival increased from the initial 600 MPa to 2 GPa, thereby greatly exceeding the currently recognized maximum high pressure for growth or survival, and the pressure levels commonly used in food industries for food preservation.

Acquisition of extreme piezotolerance among food-borne pathogens might not be limited to *E. coli*. Vanlint et al. (2012) examined the potential for HHP resistance development among strains of *E. coli*, *Shigella flexneri*, *Salmonella* Typhimurium, *Salmonella* Enteritidis, *Yersinia enterocolitica*, *Aeromonas hydrophila*, *Pseudomonas aeruginosa* and *Listeria innocua* and reported that extreme HHP resistance was only observed in some *E. coli* strains. These authors concluded that a specific genetic predisposition could be required for HHP resistance development. However, piezotolerant variants have been found by other research groups in other food-borne pathogens such as *Listeria monocytogenes* and *Staphylococcus aureus* (Karatzas and Bennik, 2002; Karatzas et al., 2005, 2007; Van Boeijen et al., 2010). In the study by Karatzas and Bennik (2002) a piezotolerant strain of *L. monocytogenes* was isolated after a single HHP treatment of 400 MPa for 20 min. This isolate showed morphological alterations, including increased cell size and lack of flagella and also presented increased stress tolerance to heat, acid and hydrogen peroxide treatments. This resistant phenotype was attributed to a

single codon deletion in a glycine-encoding repeat region of the *ctsR* gene, which encodes a class 3 heat shock response regulator. In a subsequent study Karatzas et al. (2005) exposed wild type cultures of *L. monocytogenes* EGDe to 350 MPa for 20 min and evaluated the piezotolerance of individual surviving isolates, finding 33 isolates with a stable piezotolerant phenotype. Interestingly, 21 of these 33 piezotolerant variants had mutations in the *ctsR* gene. These mutations mainly consisted of deletions or codon insertions in the glycine repeat region of the *ctsR* gene. However, a piezotolerant phenotype could not be linked to mutations in the *ctsR* gene for the rest of variants, which evidenced that other unknown mechanisms may also lead to stable piezotolerance in *L. monocytogenes*. Similarly, Van Boeijen et al. (2010) isolated 24 *L. monocytogenes* LO28 stress-resistant variants after HHP treatment. Genetic analysis of these variants revealed two variants with deletions in the upstream region of *ctsR* and seven variants with mutations in the *ctsR* gene itself. Interestingly, all variants were more resistant to heat than the wild type strain. Piezotolerant variants have been also found for *S. aureus* by Karatzas et al. (2007) following a HHP treatment of a clonal culture at 400 MPa for 30 min. The majority of these isolated variants showed increased thermotolerance, impaired growth and reduced antibiotic resistance as compared to the wild type. However, no mutations in the *ctsR* gene were detected for any of the variants, which suggests that genes and regulatory mechanisms involved in acquisition of resistance to HHP by *S. aureus* may differ from those of *L. monocytogenes*.

Selection of resistant variants has been also reported for certain food-borne pathogens after exposure to other stress conditions or food processing technologies different to HHP. Van Boeijen et al. (2011) isolated highly heat-resistant variants for two strains of *L. monocytogenes* by using a kinetic modelling-based sampling scheme. Interestingly, they revealed for one of these strains the presence of heat-resistant variants under industrially relevant conditions, i.e. through growth in ultra-high temperature (UHT)-processed whole milk followed by heat treatment cycles at 72 °C. Variants thus obtained showed high resistance to standard pasteurization conditions. Several of the highly heat-resistant variants had also mutations in the *ctsR* gene, while the mechanisms leading to increased resistance in the rest of variants were not elucidated. Karatzas et al. (2008) showed that exposure of cells of *S. Typhimurium* and *S. Enteritidis* to extreme acid environments (15 cycles of exposure to pH 2.5 for up to 4 h followed by growth at pH 7.0 for 48 h) gave rise to an increase in the population acid resistance by three to four fold. In addition, these authors isolated from those acid-exposed populations variants with a stable increased acid resistance, which also showed increased heat resistance, reduced virulence and changes in colony morphology, expression of fimbriae, and growth. Moreover, stable highly acid resistant variants of *L. monocytogenes* have been recently isolated by Metselaar et al. (2013) after exposure of late-exponential phase cells to pH 3.5 for 90 min. Sixteen of the twenty-three variants isolated by these authors were highly resistant to a treatment at pH 2.5 for 3.5 min, showing less than 1 log reduction after acid treatment, compared to an average of 4 log reductions for the wild type strain. Nevertheless, the genetic shifts behind the acquisition of stable extreme acid resistance in these bacterial populations have not been unravelled yet.

3. Transient adaptive responses to stress

Apart from the above discussed stable and selection-driven acquisition of high resistance to stress, microorganisms can respond to adverse conditions in a transient manner, i.e. once the stressor disappears the bacterial population recovers its conventional tolerance to the particular stress agent. A good example of a transient response to stress are the stress tolerance responses, which can be defined as the induced resistance to normally lethal stress conditions following growth or short-term exposure at mild sub-lethal stress conditions. Stress tolerance responses are commonly mediated through activation of particular

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