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Stress response in bacteria originated from dairy products

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Abstract. In some bacteria, the stress adaptation response, a defence mechanism against low pH, can also induce a number of physiological and genetic resistance mechanisms that provide advantages for bacteria to resist other environmental factors. This phenomenon is called cross-protection, which can potentially have serious consequences for food safety. In some fermented, acidified foods, low pH can provide a favourable environment for the growth of bacteria. Bacteria can adapt to acidic environments and become able to survive various factors that occur during storage and processing such as salt, antibiotics, or technological effects.

The microbiota of dairy products includes beneficial microorganisms, spoilage bacteria, and foodborne pathogens. The most common bacteria on various dairy products are *Escherichia coli*, *Enterococcus* sp., *Staphylococcus* sp., and *Bacillus* sp.

The aim of this research is to determine the resistance of the identified bacteria (16S rDNA-based bacterial identification) to antibiotics and osmotic pressure as a consequence of their possible defence mechanisms adapted to the acidic environment.

Keywords and phrases: cheese, acidic condition, osmoregulation, antibiotic resistance

1. Introduction

Stress refers to any adverse factor or condition that affects microbial growth and survival. Bacteria on food are exposed to various stress factors during food

production, processing, and storage, which can cause inactivation or adaptation of microbial cells. Stress factors include physical treatments such as heat, pressure, or osmotic shock, chemical treatments such as acids or disinfectants, and biological stresses such as bacteriological stresses, e.g. bacteriocins, bacterial contamination (*Begley & Hill*, 2015; *Ding et. al.*, 2022). Bacteria sense changes in their environment and respond with altered gene expressions. Stress adaptation changes the virulence properties of pathogens and contributes to *in vivo* survival during infection.

A number of studies have shown that inactivation of foodborne pathogens or various stressors can trigger adaptive mechanisms and even lead to cross-protection mechanisms. The widespread use of antibiotics, herbicides, and sanitizers can lead to antibiotic-resistant pathogens. These bacteria become tolerant to the stress factors of food processing with increased viability. Antibiotic-resistant zoonotic bacteria are transmitted from animals (their products) to humans through food or skin contact, which leads to the development of antibiotic resistance through gene transfer (*Woode et al.*, 2020). Acquired tolerance is the result of chromosomal mutations, phenotype development through horizontal gene transfer or co-resistance/cross-protection phenomena (*Oniciuc et. al.*, 2019). The exact molecular mechanisms of the stress adaptation in food-borne pathogens are not yet well known, but their understanding is essential for the development and implementation of effective control measures (*Begley & Hill*, 2015).

Sodium chloride is a fairly common food preservative for inactivating microorganisms. The presence of salt in food creates an osmotic gradient between the intracellular and extracellular environment of bacterial cells that may lead to cell death. However, many pathogenic bacteria evolve cellular response systems, which respond by altering cell morphology, modulating of regulatory genes, and expressing different proteins. Another survival strategy comprises the osmoprotectants that control the osmotic pressure (*Malakar et al.*, 2022).

The presence of certain antibiotic resistance genes in bacteria increases osmoregulation. Multi-drug-resistant *Listeria monocytogenes* were found to be more resistant to osmotic stress than strains resistant to a single antibiotic. Similarly, antibiotic-resistant *Staphylococcus aureus* shows resistance to osmotic stress (*Woode et al.*, 2020). The general stress responses include specific proteins that are activated as a reply for stresses protecting the cell against multiple stresses. The best-characterized general stress response is the alternative sigma factors.

In Gram-negative bacteria (*E. coli*, *Salmonella* sp., and *Vibrio* sp.), the alternative sigma factor RpoS regulates general stress responses, whereas in Gram-positive bacteria (*L. monocytogenes*, *Bacillus subtilis*, and *S. aureus*) the stress response is regulated by the alternative stress sigma factor SigB. These factors play a central role in the development of a coordinated response to stress and have been shown to be involved in tolerance to low pH, increased osmolarity, temperature, bacteriocins, antibiotics, ethanol, and prolonged starvation (*Begley & Hill*, 2015).

Prior to exposure to acidic conditions, some bacteria develop tolerance to acidified environments. Survival in acidic conditions is due to several molecular mechanisms including proton efflux pump, alteration of membrane composition, control of iron uptake, basification of the cytoplasm *(Dawan & Ahn*, 2022; *Xu et. al.*, 2022).

The aim of this research is to determine the resistance of identified bacteria (16S rDNA-based bacterial identification) to antibiotics and osmotic pressure as a consequence of their possible defence mechanisms adapted to acidic environments.

2. Materials and methods

Bacteria from different cheeses (caraway cheese, fresh cheese, feta-type cheese, cottage cheese, whey cheese, salted cheese, and cheddar) were isolated on different selective media such as Pseudomonas Agar Base for isolation of the genus *Pseudomonas*, Mannitol Salt Agar for the isolation of *Staphylococcus aureus*, TBX (Tryptone Bile X-glucuronide Agar) for the detection of *Escherichia coli* and coliforms.

A stock suspension was prepared in physiological solution (0.9% NaCl). 10 g of sample was weighed into 90 ml of physiological solution. 0.1 ml of each stock suspension was spread on the selective agar mediums and incubated at 37°C for 24 hours.

The molecular identification of the bacteria strains at the species level was performed by 16S rDNA sequence analysis (*Tóth et al.*, 2018; *György et al.*, 2022).

To determine the acid tolerance of the selected bacterial strains, bacterial cultures prior to incubation at 37°C for 24 hours were centrifuged at 6,000 g for 5 minutes. After centrifugation, the pellets were resuspended in nutrient broth with different pHs: 3, 3.5, and 5.5, adjusted with 1 M HCl and lactic acid, respectively, and incubated for 1 h at 37°C without shaking. After incubation, the cells were inoculated into nutrient broth at pH 7, and bacterial survival was determined by optical density (OD) at 595 nm after 24 hrs. The bacterial survival rate was calculated as follows: OD sample/OD control 100 incubation (*Horlbog et al.*, 2018; *Nath et al.*, 2020; *György et al.*, 2022).

To determine osmotolerance, bacterial strains were inoculated into nutrient broth containing 0%, 2%, 4%, 6.5%, 10%, 15%, and 20% NaCl. After incubation for 24 hrs at 37°C, the optical density (OD) of the bacterial culture was measured at 595 nm. Bacterial survival rate/growth rate was calculated as OD sample/OD control*100 (Horlbog et al., 2018; Nath et al., 2020; György et al., 2022).

The susceptibility of the selected identified bacteria to eight different antibiotics (ampicillin (AMP 25), kanamycin (K 30), clindamycin (CD 2), streptomycin (S 10), erythromycin (E 15), chloramphenicol (C 30), gentamicin (GEN 10),

tetracycline (TE 10)) was determined by the agar diffusion method. The size of the inhibition zones was measured. Based on the size of the inhibition diameters, the susceptibility or resistance of the bacteria was determined according to the recommendations of the European Committee for Antibiotic Susceptibility Testing (*EUCAST 2023*).

3. Results and discussions

The bacterial colony counts on selective media from commercial and artisanal dairy products obtained with different technologies are shown in *Table 1*. Bacteria were detected on Pseudomonas selective media only from caraway cheese. The bacterial counts of the dairy products tested ranged from $1.5 \cdot 10^2$ CFU/g for cottage cheese and from $2.68 \cdot 10^4$ CFU/g for feta-type cheese.

Table 1. Viable counts of some selected cheeses

Cheese samples	**Selective media**			
	Czapek – Dox	**TBX**	**Mannitol – Salt**	**Pseudomonas**
	CFU/g			
Caraway cheese	-	-	-	$6.5 \cdot 10^2$
Salted cheese	-	$8.8 \cdot 10^3$	$1.5 \cdot 10^2$	$1.45 \cdot 10^4$
Feta-type cheese	-	$4.9 \cdot 10^2$	$2.68 \cdot 10^4$	$7.6 \cdot 10^3$
Fresh cheese	$8.4 \cdot 10^2$	$1.12 \cdot 10^4$	$9.9 \cdot 10^3$	$1.76 \cdot 10^3$
Whey cheese	$< 10^3$	$7.3 \cdot 10^3$	$3.9 \cdot 10^3$	$2.8 \cdot 10^3$

Dairy products, including cheese and cottage cheese, are susceptible to microbial contamination because they provide ideal conditions for the growth and survival of microorganisms. Several studies summarize that improperly handled raw materials, non-hygienic and different production conditions contribute to microbial contamination, posing a health risk for consumers. *Studenica et al.* (2022) have shown in artisanal cheeses the presence of several pathogenic bacteria: *Escherichia coli*, *Staphylococcus aureus*, *Listeria monocytogenes*, and *Salmonella* sp., reaching a cell count 10^6. The isolated bacterial strains were identified based on 16S rDNA gene sequence similarity – sequences > 95% similarity were identified on the genus level, whereas sequences > 97% identity were identified on the species level (*Tóth et al.*, 2018; *Johnson et al.*, 2019).

The identified bacterial strains belong to different genera such as *Staphylococcus*, *Citrobacter*, *Bacillus*, *Actinobacteria*, *Alkalihalobacillus*, *Micrococcus*, and *Enterococcus* (*Table 2*).

Table 2. Identified bacterial strains ant their sequence similarity %

Bacterial strains	**Similarity (%)**
Staphylococcus saprophyticus	98.61
Citrobacter freundii	98.69
Enterobacter mori	87.14
Bacillus cereus	97.94
Bacillus sp.	99.72
Bacillus sp.	98.94
Bacillus sp.	98.95
Staphylococcus xylosus	99.07
Staphylococcus xylosus	99.42
Bacillus sp.	98.90
Actinobacterium sp.	97.04
Enterococcus faecalis	99.05
Bacillus toyonensis	98.35
Citrobacter youngae	98.91
Micrococcus endophyticus	96.40
Bacillus cereus	99.63
Alkalihalobacillus clausii	95.52
Bacillus licheniformis	97.31
Bacillus sp.	98.53
Bacillus thuringiensis	99.34

The two main sources of bacteria in cheese are the starter culture and the raw milk microbiota. However, cheese can be contaminated with microorganisms from the processing environment, sometimes affecting the ripening and the organoleptic properties of the product. Bacterial strains are essential for the development of cheese characteristics and are responsible for organoleptic properties such as flavour (*György & Laslo*, 2021). The composition and production technology of cheese is extremely diverse. The quality and processing of the milk, the environmental conditions (temperature, humidity, salinity), and the technological parameters used influence the prevalence, quantity, and diversity of microbial species. There are more microbial species on the surface of the cheese than in the inside of

the product. The most commonly found bacteria on cheese are *Escherichia coli*, *Enterococcus* sp., *Shigella* sp., *Proteus* sp., *Staphylococcus* sp., *Bacillus* sp., and *Listeria* sp. It has been shown that the surface of cheese is characterized by aerobic bacteria such as *Brevibacterium* sp., *Bacillus sp.*, and *Micrococcus sp*. The predominant microbes inside the cheese are anaerobic or facultatively aerobic microorganisms such as *Escherichia coli* (*György & Laslo*, 2021).

Amplicon-based sequencing of 16S rRNA revealed that *Streptococcus* sp. species were most prevalent in Provolone (72–85%) and Swiss cheese (60–67%), whereas *Lactococcus* sp. species were dominant in Cheddar cheese (27–76%). Species diversity varied considerably. Alpha diversity analysis showed that soaked Cheddar cheese had the highest heterogeneous microbial diversity, while smoked Provolone cheese had the lowest. The microbial diversity of the cheese rind region was higher than that of the core region, as the smoking and soaking processes affected the rind of each cheese. Within a given cheese type, the microbial composition was very similar regardless of the sampling location (*Choi et al.*, 2020). Changes in the acidity of cheese stimulate the growth of certain coliforms and foodborne pathogens. The presence of coliforms in white ripened cheese is responsible for premature bloating and the formation of large gas holes in the cheese mass (*Hayaloglu, 2016*; *György & Laslo*, 2021).

The smear-ripened cheese microflora contained mainly coryneform bacteria, followed by staphylococci and micrococci, which were able to grow in the presence of 10% NaCl. The most common staphylococci were the *Staphylococcus equorum*, *S. saprophyticus*, *S. caseolyticus*, and *S. xylosus* (*Hayaloglu*, 2016). Our results regarding the identified bacteria were in agreement with *Martin et al's* 2021 results – similar bacteria were found in cheeses such as *Enterobacter aerogenes*, *C. braakii*, and *C. freundii*. Coliforms are indicator bacteria resulting from poor hygienic conditions. They are responsible for premature bloating of cheeses causing gas formation and deformation of the cheese paste. The presence of spore-forming bacteria are associated with the raw milk environment. The presence of the potentially pathogenic bacteria *Citrobacter freundii* has been detected in several cheeses and dairy products (*Gaglio et al.*, 2021; *Gücükoğlu et al.*, 2023).

The inorganic (hydrochloric acid, HCl) and organic (lactic acid) acid stress tolerance of identified bacteria at 37°C was determined by preliminary adaptation step. The frequent use of low pH as an additive or preservative in foods may exert a selective pressure on bacterial growth, leading to acid tolerance in bacterial strains. The acid tolerance of bacterial strains was characterized by determining the survival rate (*Table 3*). The analysed pH values resulted in different survival rates. At pH 5.5, adjusted with lactic acid and HCl, bacterial growth was almost above 50%. Some of the tested bacteria survived the acid shock, and some of them are adaptive acid-tolerant such as *Staphylococcus xylosus* or *Bacillus* sp.

At pH 3, adjusted with HCl, *Staphylococcus saprophyticus* showed a survival rate of 50.15% and *Enterococcus faecalis* 82.47%. Some of the *Bacillus* species showed good survival rate at the tested pHs.

Table 3. Identified bacterial strains survival rate (%) in acidic conditions

Isolated bacterial strains	pH – 3 HCl	pH – 5,5 HCl	pH – 3,5 Lactic acid	pH – 5,5 Lactic acid
	Survival rate (%)			
Staphylococcus saprophyticus	50.15	55.41	6.46	71.02
Citrobacter freundii	37.78	60.56	8.89	79.82
Enterobacter mori	48.88	56.86	12.72	59.23
Bacillus cereus	15.71	53.68	24.55	60.64
Bacillus sp.	45.08	70.86	11.03	67.75
Bacillus sp.	134.44	98.89	25.56	437.78
Bacillus sp.	20.54	62.68	36.74	62.79
Staphylococcus xylosus	55.90	88.33	7.95	80
Staphylococcus xylosus	54.10	75.84	18.54	89.818
Bacillus sp.	51.17	100	17.58	100
Actinobacterium sp.	9.81	45.61	12.36	56.18
Enterococcus faecalis	82.47	50.52	5.73	56.08
Bacillus toyonensis	47.63	54.50	6.41	78.78
Citrobacter youngae	31.64	66.98	10.90	52.80
Micrococcus endophyticus	39.73	61.33	34.52	61.04
Bacillus cereus	44.09	45.90	9.32	51.04
Alkalihalobacillus clausii	35.94	15.40	9.60	80.58
Bacillus licheniformis	61.87	82.58	12.07	66.26
Bacillus sp.	60.20	48.33	17.80	57.73
Bacillus thuringiensis	39.23	51.21	11.74	59.81

Horlbog et al. (2018) reported that resistance to acid is an important factor in the survival and infection of pathogenic bacteria. Strains belonging to *Enterococcus* genus are acid-tolerant and maintain the intracellular pH homeostasis (*Gaca & Lemos*, 2019). In *Enterobacteriaceae*, acid shock induces acid shock proteins. Gram-positive bacteria respond to the acid and osmotic stress with responsive σb and σ3 factors (*Marmion et al.*, 2022). Acid tolerance response is determined by different environmental and growth factors, also the type of the acid (*Xu et al.*, 2022).

The NaCl tolerance (0%, 2%, 4%, 6.5%, 10%, 15%, and 20%) of the tested bacterial strains was characterized by survival rates (*Table 4*). In the presence of

2–6.5% NaCl, the growth of *Staphylococcus xylosus* was moderate. The higher concentrations of NaCl inhibited growth completely.

10% and 15% of NaCl inhibited the growth of the isolated bacterial strains, except for *Bacillus sp.*, *Staphylococcus xylosus*, and *Staphylococcus saprophyticus*, where the growth was lower.

Li et al. (2021) reported that increased NaCl concentrations inhibited the growth patterns of bacterial species. The salt tolerance, osmoregulation of bacteria is a complex process involving increased uptake of potassium ions or the production of various metabolites. The use of NaCl for spoilage prevention is based on the low resistance of spoilage and pathogenic bacteria to high osmotic pressure. Adaptation to higher salt concentrations has recently been described for a number of bacteria, including those that are harmful to human health such as *Bacillus cereus* or *Enterococcus faecalis*.

Table 4. Survival rates (%) in the presence of NaCl of the selected bacterial strains

Bacterial strains	**Survival rate (%)**					
	2%	**4%**	**6.5%**	**10%**	**15%**	**20%**
Staphylococcus xylosus	31.94	30.69	58.04	1.04	1.88	2.71
Actinobacterium sp.	67.41	74.66	40.86	32.07	18.97	0.86
Citrobacter freundii	58.24	114.78	18.63	11.78	3.64	1.28
Bacillus cereus	53.01	56.93	67.17	61.14	59.64	25.30
Citrobacter youngae	65.09	43.39	18.20	11.47	13.22	5.49
Staphylococcus xylosus	100.46	89.66	90.11	55.63	39.08	4.60
Enterococcus faecalis	97.16	94.54	65.28	19.43	6.55	0.87
Staphylococcus saprophyticus	47.44	53.91	69.00	49.60	39.35	1.08
Alkalihalobacillus clausii	31.43	28.57	54.90	7.35	2.45	0.00

Bacterial strains with antibiotic resistance could be a source of antibiotic resistance genes. Bacterial susceptibility/resistance was determined according to the EUCAST recommendations based on the diameter of the inhibition zones.

Resistance to ampicillin was found in *Citrobacter freundii* isolated from fresh cheese and in *Staphylococcus saprophyticus* and *Alkalihalobacillus clausii* as originated from cottage cheese.

Resistance to tetracycline was detected in *Bacillus* sp. isolated from cottage cheese and whey cheese and in *Enterococcus faecalis* and *Alkalihalobacillus*

clausii as originated from cottage cheese. Metagenomic analysis of tetracycline resistance in cheese bacteria summarized that raw-milk cheeses were considered a source of tetracycline resistance genes that could be shared via horizontal gene transfer (*Flórez et al.*, 2017).

Resistance to clindamycin was detected in *Citrobacter youngae* isolated from whey cheese, in two *Staphylococcus xylosus* isolated from Cheddar and fresh cheese, and in *Bacillus* sp. isolated from salted cheese.

Resistance to erythromycin was found in two *Bacillus sp.*, in *Enterococcus faecalis* from cottage cheese, and in *Staphylococcus xylosus* from fresh cheese. Enterococci with antibiotic resistance genes, virulence genes, and biofilm-forming capacity were found in traditional dairy products as a result of poor food hygiene practices (*Amidi-Fazli & Hanifian*, 2022).

Citrobacter freundii from whey cheese and *Alkalihalobacillus clausii* from cottage cheese showed resistance to streptomycin.

Alkalihalobacillus clausii and a *Bacillus* sp. were also resistant to kanamycin, and *Alkalihalobacillus clausii* was resistant to chloramphenicol and gentamicin.

The broad spectrum of resistance was observed in the case of *Alkalihalobacillus clausii*, which was susceptible to only two tested antibiotics. *Alkalihalobacillus clausii,* with the old name *B. clausii*, was detected in ropy bread spoilage. Strains of these bacteria with probiotic potential possessed genes encoding multiple antibiotic resistance, but these genes were not located on mobile elements (*Pacher et al.*, 2022; *Dhakephalkar et al.*, 2022).

The overuse of antibiotics for prophylaxis or treatment of infectious diseases is connected with the emergence of antibiotic resistance and the dissemination of this phenomenon. Resistant bacteria can be transmitted through the consumption of livestock products, milk, or related foods. Types of antibiotic resistance are intrinsic and acquired. Acquired antibiotic resistance can result from mutation and horizontal gene transfer (conjugation, transformation, transduction). Dairy products, including fresh cheese, have been shown to contain phage particles with antibiotic resistance genes (*Blanco-Picazo et al.*, 2022).

4. Conclusions

The microbial analysis of tested cheeses showed high microbial load. However, the results are in line with microbiological limits; among and identified bacteria, there are pathogenic and spoilage bacteria. These bacteria are *Bacillus cereus*, *Citrobacter youngae*, *Staphylococcus xylosus*, *Enterococcus faecalis*, and *Staphylococcus saprophyticus*. Cheeses have been contaminated with the undesirable bacteria that are resistant to certain antibiotics, either through cross-contamination or as a result of poor hygienic conditions. Resistance to stress factors that may

appear during food production, such as different NaCl concentrations and pH, are characteristics of bacteria strains with antibiotic resistance. This is probably explained by the phenomenon of cross-protection. A further aim is to demonstrate the resistance of the bacterial strains to other food-related stresses.

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