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LACTIC ACID BACTERIA ENZYMES: CHARACTERISTICS, CLASSIFICATION AND BIOTECHNOLOGICAL SIGNIFICANCE

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- **AIM.** To summarize current knowledge on the classification, characteristics, and biotechnological significance of enzyme systems of lactic acid bacteria (LAB).
- **MATERIALS AND METHODS.** A narrative review of scientific literature indexed in PubMed/MEDLINE, Scopus, and Web of Science was conducted using comparative and analytical approaches.
- **RESULTS.** The main enzyme systems of LAB were analyzed, including proteolytic enzymes, glycoside hydrolases, lipolytic enzymes, and enzymes involved in exopolysaccharide synthesis. Particular attention was paid to cell-envelope proteinases, intracellular peptidases, β-galactosidase, phosphoketolase, glucosyltransferases, esterases, and lipases. Their roles in proteolysis, carbohydrate metabolism, flavor and aroma formation, lactose hydrolysis, and texture development in fermented dairy and meat products were characterized. The industrial significance of LAB enzymes in the production of cheese, yogurt, kefir, sourdough bread, lactose-free products, galactooligosaccharides, and dextran was discussed.
- **CONCLUSIONS.** LAB enzyme systems determine the technological and functional properties of fermented foods and represent promising targets for modern food biotechnology.
- **KEYWORDS:** *lactic acid bacteria, enzymatic activity, proteolytic enzymes, food biotechnology.*

ФЕРМЕНТИ МОЛОЧНОКИСЛИХ БАКТЕРІЙ: ХАРАКТЕРИСТИКА, КЛАСИФІКАЦІЯ ТА БІОТЕХНОЛОГІЧНЕ ЗНАЧЕННЯ

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- **МЕТА.** Узагальнити сучасні дані щодо класифікації, характеристик і біотехнологічного значення ферментних систем молочнокислих бактерій (МКБ).
- **МАТЕРІАЛИ І МЕТОДИ.** Проведено наративний огляд наукової літератури, індексованої в базах даних PubMed/MEDLINE, Scopus та Web of Science, із застосуванням порівняльного та аналітичного підходів.
- **РЕЗУЛЬТАТИ.** Проаналізовано основні ферментні системи МКБ, зокрема протеолітичні ферменти, глікозидгідролази, ліполітичні ферменти та ферменти синтезу екзополісахаридів. Особливу увагу приділено клітинно-зв'язаним протеїназам, внутрішньоклітинним пептидазам, β-галактозидазі, фосфокетолазі, глюкозилтрансферазам, естеразам і ліпазам. Охарактеризовано їхню роль у протеолізі, метаболізмі вуглеводів, формуванні смаку й аромату, гідролізі лактози та формуванні текстури ферментованих молочних і м'ясних продуктів. Розглянуто промислове значення ферментів LAB у виробництві сирів, йогурту, кефіру, заквасочного хліба, безлактозних продуктів, галактоолігосахаридів і декстрану.
- **ВИСНОВКИ.** Ферментні системи LAB визначають технологічні та функціональні властивості ферментованих продуктів і є перспективними об'єктами сучасної харчової біотехнології.
- **КЛЮЧОВІ СЛОВА:** *молочнокислі бактерії, ферментативна активність, протеолітичні ферменти, харчова біотехнологія.*

INTRODUCTION

Lactic acid bacteria (LAB) are a heterogeneous group of Gram-positive facultatively anaerobic microorganisms that produce lactic acid as the major end product of carbohydrate fermentation. This group includes representatives of the genera *Lactococcus, Lactobacillus, Streptococcus, Leuconostoc,* and related taxa [1, 2].

LAB are widely used as starter cultures in the production of fermented dairy products, cheeses, fermented vegetables, sourdough bread, and fermented meat products due to their technological and probiotic properties [3, 4].

The technological importance of LAB is primarily associated with their enzyme systems. LAB enzymes participate in the hydrolysis of proteins, carbohydrates, and lipids, ensuring nutrient acquisition and contributing to the formation of flavor, aroma, texture, and functional properties of fermented foods [5].

Recent advances in genomics and biotechnology have significantly expanded knowledge regarding

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the organization and regulation of LAB enzyme systems [6, 7].

Despite considerable progress, several aspects of LAB enzymatic activity remain insufficiently understood, particularly regulatory responses to technological stress and the interaction of enzymes involved in flavor formation.

The aim of this article is to summarize current knowledge on the classification, characteristics, and biotechnological significance of LAB enzyme systems.

MATERIALS AND METHODS

This article is a narrative review based on a systematic analysis of scientific literature indexed in the PubMed/MEDLINE, Scopus, and Web of Science databases. The search included the keywords lactic acid bacteria, enzyme systems, proteolytic system, β-galactosidase, lipase, esterase, exopolysaccharide, and starter cultures.

The collected data were comparatively analyzed using literature review methods. Enzyme classification was based on the principles of the International Union of Biochemistry and Molecular Biology (IUBMB). Information regarding substrate specificity, cellular localization, and industrial applications of LAB enzymes was also considered.

To evaluate the distribution of enzymatic activities among LAB species, published phenotypic data and genomic information from public databases including GenBank, UniProt, and KEGG were analyzed.

REVIEW

General characteristics and classification of LAB enzymes. The enzyme systems of lactic acid bacteria include several functional classes that differ in catalytic activity, localization, and physiological role [1, 8]. The major groups comprise hydrolases (proteinases, peptidases, glycoside hydrolases, lipases, esterases), oxidoreductases, transferases, and isomerases. Among them, hydrolases are the most important for food biotechnology because they participate in the degradation of proteins, carbohydrates, and lipids during fermentation [1, 3].

According to cellular localization, LAB enzymes may be surface-associated, cytoplasmic, or extracellular. Most enzymes are intracellular and become active in food systems mainly after bacterial cell lysis [5, 9]. Surface-associated enzymes, particularly cell-envelope proteinases, initiate the hydrolysis of milk proteins, whereas extracellular glucansucrases synthesize exopolysaccharides from sucrose.

Table 1. **Major enzyme systems of LAB and their characteristics**

Enzyme	EC number	Localization	Substrate	Main function	Practical significance
CEP proteinase (PrtP)	3.4.21.96	Cell surface	αS1-, β-casein	Initiation of proteolysis, nitrogen nutrition	Cheese ripening, flavor peptides
Endopeptidase PepO	3.4.24.-	Cytoplasm	Oligopeptides	Hydrolysis of oligopeptides	Flavor formation
Aminopeptidase PepN	3.4.11.2	Cytoplasm	Lys-, Ala-, Arg-containing peptides	Release of N-terminal amino acids	Bitterness/flavor development in cheese
β-Galactosidase (LacZ)	3.2.1.23	Cytoplasm	Lactose	Hydrolysis of lactose to Glc+Gal	Lactose-free products, GOS formation
Phospho-β-galactosidase	3.2.1.85	Cytoplasm	Lactose-6-P	Hydrolysis of phosphorylated lactose	Lactose utilization in lactococci
Phosphoketolase	4.1.2.9	Cytoplasm	Xylulose-5-P	Pentose breakdown	Heterofermentatio, aroma formation
Esterase/lipase	3.1.1.1/ 563.1.1.3	Cytoplasm/ surface	Triglycerides, fatty acid esters	Lipolysis, ester synthesis	Flavor of cheese and meat products
Glucansucrase (dextransucrase)	2.4.1.5	Extracellular	Sucrose	Dextran synthesis	Thickener, food additive
NADH oxidase	1.6.3.4	Cytoplasm	NADH, O_2	Protection against O_2-stress	Probiotic survival

Comparative genomic studies indicate that the general organization of LAB enzyme systems is relatively conserved among different species, although enzymatic activity and substrate specificity vary considerably at the strain level [7]. These differences largely determine the technological properties of starter cultures, including flavor development, texture formation, and exopolysaccharide production.

Proteolytic system of LAB. The proteolytic system is one of the best-characterized enzyme systems of LAB and plays a crucial role in bacterial growth in milk, where the concentration of free amino acids is limited [7, 10]. The system functions through three main stages: extracellular protein hydrolysis, peptide transport into the cell, and intracellular peptide degradation.

• *Cell-envelope proteinases.* Cell-envelope proteinases (CEP) are surface-associated serine endoproteinases responsible for the initial hydrolysis of casein into oligopeptides [5, 11]. These enzymes differ in substrate specificity among LAB species and strains, which significantly influences cheese ripening and flavor development. Lactococcal and lactobacillar CEPs exhibit similar mechanisms of action despite taxonomic differences, reflecting the conserved nature of the proteolytic system [10, 11].

The genes encoding CEPs are commonly associated with regulatory elements controlling enzyme expression under peptide-limited conditions [11]. Increased proteolytic activity enhances nutrient availability and contributes to the accumulation of flavor-forming peptides and amino acids in fermented dairy products.

• *Peptide transport systems.* Peptides generated by extracellular proteolysis are transported into the bacterial cell by ATP-dependent transport systems, mainly Opp, Dpp, and DtpT [7]. Among these, the Opp system is considered the most important because of its broad substrate specificity and ability to transport oligopeptides of different lengths.

Studies have demonstrated that defects in peptide transport systems significantly reduce bacterial growth in milk, confirming their essential role in LAB metabolism and adaptation to dairy environments [12].

• *Intracellular peptidases.* Inside the cell, peptides are hydrolyzed by intracellular peptidases that release free amino acids used for metabolism and aroma formation [7, 9]. LAB possess aminopeptidases, endopeptidases, and proline-specific peptidases differing in substrate specificity and catalytic properties.

PepN is one of the most widespread aminopeptidases and participates in the degradation of a broad range of peptides [9]. Proline-specific peptidases are particularly important because proline-rich casein peptides are resistant to hydrolysis and may contribute to bitterness in cheese when insufficiently degraded [12].

Endopeptidases such as PepO and PepF further hydrolyze oligopeptides into smaller fragments involved in flavor formation during cheese ripening [7]. Overall, the coordinated activity of CEPs, peptide transporters, and intracellular peptidases determines the efficiency of proteolysis and strongly influences the sensory properties of fermented dairy products.

Glycoside hydrolase systems of LAB. Carbohydrate metabolism in LAB depends on the coordinated activity of transport systems and glycoside hydrolases. Lactose is the principal carbohydrate substrate in dairy fermentations, and its metabolism is among the best-characterized enzymatic processes in LAB [13, 14].

• *β-Galactosidase and lactose metabolism.* In many LAB species, including *Streptococcus thermophilus* and *Lactobacillus bulgaricus*, lactose is transported into the cell and hydrolyzed by β-galactosidase into glucose and galactose [13]. Glucose enters glycolysis directly, whereas galactose is metabolized through the Leloir pathway.

Besides lactose hydrolysis, β-galactosidase can catalyze transgalactosylation reactions leading to the formation of galactooligosaccharides (GOS), which exhibit prebiotic properties and stimulate the growth of beneficial intestinal microbiota [14, 15]. Therefore, LAB β-galactosidases are widely applied in the production of lactose-free and functional dairy products.

• *Phospho-β-galactosidase pathway.* In *Lactococcus lactis* and related species, lactose uptake occurs through the phosphotransferase system (PEP-PTS), where lactose is phosphorylated during transport [13]. The resulting lactose derivatives are hydrolyzed by phospho-β-galactosidase. This pathway is characteristic of lactococci and represents an alternative mechanism of lactose utilization in LAB.

• *Phosphoketolase and heterofermentative metabolism.* Heterofermentative LAB, including *Leuconostoc* and *Weissella* species, metabolize carbohydrates through the pentose phosphate pathway. The key enzyme of this pathway is phosphoketolase, which contributes to the formation of lactate, ethanol or acetate, and carbon dioxide [16].

These metabolic products are important for the development of flavor, aroma, and texture in fer-

mented products such as kefir, Gouda cheese, and fermented sausages.

• *Glucosyl- and fructosyltransferases.* Glucosyltransferases and fructosyltransferases catalyze the synthesis of polysaccharides such as dextran and levan from sucrose [17]. These exopolysaccharides are widely used as thickeners, stabilizers, and prebiotic ingredients in food biotechnology.

Dextran synthesized by *Leuconostoc mesenteroides* has additional pharmaceutical applications, including use as a plasma volume expander and chromatography matrix material [17, 18].

Lipolytic enzymes of LAB. Lipolytic enzymes of LAB include lipases and esterases that hydrolyze triglycerides and fatty acid esters [19]. Although their activity is lower than that of fungi such as *Penicillium* and *Aspergillus*, LAB lipolysis contributes significantly to flavor development in fermented dairy and meat products through the formation of free fatty acids and volatile aroma compounds [19, 20].

Most LAB possess intracellular esterases that become active after bacterial cell lysis during product ripening [19]. The released fatty acids influence sensory properties: short-chain fatty acids contribute to characteristic cheese flavors, whereas excessive accumulation of long-chain fatty acids may cause off-flavors.

• *Esterases and aroma formation.* LAB esterases belong to the α/β-hydrolase family and preferentially hydrolyze short-chain fatty acid esters [19]. In addition to hydrolysis, these enzymes catalyze ester synthesis and transesterification reactions involved in aroma formation.

Several esterases have been identified in *Lactobacillus plantarum*, including cold-active enzymes that retain activity at low temperatures and are potentially useful in cheese production and low-temperature fermentations [21].

• *LAB lipases in fermented products.* Lipase activity has been detected in strains of *L. plantarum*, *L. casei*, *L. helveticus*, and *L. fermentum* [19]. These enzymes participate in the release of fatty acids that serve as precursors for aldehydes, ketones, and lactones responsible for characteristic aromas of cheeses and fermented sausages [20].

In fermented meat products, LAB act together with endogenous meat enzymes, contributing to lipolysis, texture development, and flavor formation during ripening.

Enzymes involved in exopolysaccharide synthesis. LAB exopolysaccharides (EPS) are synthesized through two major mechanisms. Heteropolysaccharides are produced intracellularly by glycosyltransferases and subsequently secreted outside the cell, whereas homopolysaccharides such as dextran and levan are synthesized extracellularly by glucansucrase and fructansucrase enzymes [17, 22].

The structure and properties of EPS are determined by strain-specific eps gene clusters encoding enzymes involved in polysaccharide biosynthesis [22]. These polymers play important technological roles in fermented foods by improving viscosity, texture, and water-holding capacity.

EPS-producing strains of Streptococcus thermophilus and Lactobacillus bulgaricus are widely used in yogurt production because they enhance consistency and reduce whey separation [22, 23].

Industrial applications of LAB enzyme systems. LAB enzyme systems constitute the molecular basis for the development of the organoleptic, textural, and technological properties of a wide range of fermented products. The specific complement of enzymes possessed by individual LAB species and strains determines the extent of proteolysis, lipolysis, aroma compound formation, exopolysaccharide synthesis, and other biochemical processes that directly influence the quality of the final product [3, 4]. The roles of the major LAB enzyme systems in the production of various fermented foods are summarized in *Table 2*.

Cheese making represents the most important field of application for the proteolytic and lipolytic systems of LAB. The ripening of Cheddar cheese (12–24 months) depends largely on the proteolytic activity of starter *Lc. lactis* ssp. *cremoris* cultures and adjunct *L. helveticus* strains. Endopeptidases PepO and PepF, together with several peptidases including PepN, PepQ, and PepX, are responsible for the degradation of β-casein-derived oligopeptides and the accumulation of free amino acids, which serve as markers of ripening progression. These amino acids are subsequently catabolized into characteristic aroma compounds: methionine is converted to methional, phenylalanine to phenylacetaldehyde, and leucine to isovaleric acid [9, 25].

In Gouda- and Edam-type cheeses, heterofermentative *Leuconostoc* spp. (particularly *Leu. mesenteroides*) play an important role. Through the phosphoketolase pathway, these bacteria produce CO_2, which is responsible for the formation of the characteristic eye structure, as well as diacetyl and acetoin, compounds that impart the characteristic buttery flavor to the product [16]. A technological evaluation of 128 LAB strains for cheese-making applications demonstrated that *Lb. delbrueckii* P10,

Table 2. **Enzyme systems of LAB in the production of specific products**

Product	LAB species / strain	Key enzymes	Role in quality formation
Cheddar cheese	Lc. lactis ssp. cremoris	CEP (PrtP), PepN, PepO, PepQ	Ripening, flavor, aroma
Gouda/Edam cheese	*Lc. mesenteroides*	Phosphoketolase, β-galactosidase	Eye formation («holes»), creamy flavor
Yogurt	*S. thermophilus* + *Lb. bulgaricus*	β-Galactosidase, CEP, EPS synthases	Acidity, aroma, texture
Kefir	*Lc. lactis* + *Leuconostoc* + yeasts	Phosphoketolase, lipase, proteases	Carbonation, characteristic flavor
Salami/sujuk	*Lb. sakei*, *Lb. curvatus*	Lipase, esterase, aminopeptidase	Lipolysis, aroma, texture
Lactose-free milk	*Lb. acidophilus*, *Lc. lactis*	β-Galactosidase	Lactose hydrolysis
GOS (prebiotic)	*Lb. bulgaricus*, *Lb. acidophilus*	β-Galactosidase (transgalactosylation)	Synthesis of galactooligosaccharides
Sourdough bread	*Lb. sanfranciscensis*, *Lb. fermentum*	Phosphoketolase, fructansucrase	Aroma, dough structure
Dextran (medical use)	*Lc. mesenteroides* B-512F	Dextransucrase	Plasma expander synthesis

Lb. rhamnosus P50, and *Lc. lactis* Q5C6 exhibited the highest PepN and PepX activities and were therefore recommended as promising adjunct cultures [25].

Yogurt production is based on the protocooperation between two species: *S. thermophilus* and *L. bulgaricus*. The former ferments lactose via the β-galactosidase-dependent (permease-mediated) pathway and produces lactic acid and acetaldehyde, whereas the latter, in addition to acid production, plays a crucial role in the proteolysis of milk casein, releasing free amino acids that serve as essential growth factors for *S. thermophilus*. This microbial mutualism results in a substantially higher fermentation rate when the two cultures are used in combination than when either is grown as a monoculture [26].

EPS-producing strains (*S. thermophilus* S-3, *Lb. bulgaricus* OLL1073R-1) provide yogurt with its characteristic ropy consistency. The polysaccharides synthesized by enzymes encoded within the *eps* gene cluster interact with casein micelles and whey proteins, forming a three-dimensional gel matrix with enhanced water-holding capacity [22, 26].

In fermented sausage products (salami, sujuk, and mettwurst), LAB perform four key functions: (1) acidification to inhibit pathogenic microorganisms; (2) nitrate/nitrite reduction; (3) proteolysis of muscle proteins, contributing to texture softening; and (4) lipolysis leading to the formation of aroma compounds. The dominant species include *Lb. sakei*, *Lb. curvatus*, and *Pc. pentosaceus*, as well as *Lb. plantarum* in traditional products [20, 24].

Within the meat matrix, the enzymatic systems of LAB act synergistically with endogenous meat proteases (calpains and cathepsins) and lipases. In particular, LAB lipases release unsaturated fatty acids, such as linoleic and arachidonic acids, which serve as substrates for lipid peroxidation reactions. These reactions generate aldehydes and ketones that contribute characteristic aroma notes often described as «roasted meat» and «nutty» flavors [20].

The production of lactose-free dairy products — one of the most rapidly growing market segments (CAGR ≈9% during 2020–2025) — is based on the use of industrial β-galactosidases, including those derived from LAB. Strains of *Lb. acidophilus* and *Lc. lactis* are among the principal producers of β-galactosidases for food industry applications [14, 15].

The synthesis of GOS — prebiotic galactooligosaccharides — represents a promising application of the transgalactosylation activity of LAB β-galactosidases. The GOS content of commercial prebiotic preparations typically ranges from 50% to 97%. Studies have demonstrated that strains of *Lb. bulgaricus*, *Lb. acidophilus*, and certain *Lc. lactis* isolates exhibit higher transgalactosylation activity than the industrial β-galactosidase from *Kluyveromyces lactis* under specific reaction conditions [15].

Dextran synthesized by *Leu. mesenteroides* through the action of dextransucrase is used in medicine (e.g., the plasma volume expander Dextran-70), the food industry (as a structure-forming agent in bakery products and a fat replacer), and

biochemistry (as the matrix material for Sephadex chromatography media). Levan produced by *L. sanfranciscensis* is employed as a texturizing agent and prebiotic ingredient [17, 22].

CONCLUSIONS

The enzyme systems of lactic acid bacteria encompass proteolytic, glycoside hydrolase, lipolytic, transferase, and oxidoreductase enzymes that determine the technological properties of LAB in fermented products. Proteolytic and lipolytic systems play a key role in the development of the flavor, aroma, and texture of cheeses, fermented dairy products, and fermented meat products, whereas β-galactosidases are responsible for lactose metabolism and the synthesis of prebiotic galactooligosaccharides. Glucosyl- and fructosyltransferases mediate the synthesis of exopolysaccharides that influence product consistency. Antioxidant enzymes enhance the resistance of LAB to technological stress, while modern genomic, proteomic, and bioengineering approaches provide opportunities for the development of strains with tailored enzymatic properties. The broad spectrum of enzymatic activities exhibited by LAB also highlights their considerable potential for the fermentation of plant-based substrates and the production of functional foods.

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ІНФОРМАЦІЯ ПРО КОНФЛІКТ ІНТЕРЕСІВ

Автори заявляють про відсутність конфлікту інтересів щодо публікації цієї статті.

ВИКОРИСТАННЯ ГЕНЕРАТИВНОГО ШТУЧНОГО ІНТЕЛЕКТУ

Автори заявляють, що під час підготовки рукопису використовувалися інструменти генеративного штучного інтелекту виключно для мовного редагування, покращення стилю викладу та перекладу тексту. Генеративний штучний інтелект не використовувався для створення, аналізу чи інтерпретації наукових результатів. Уся відповідальність за зміст статті, достовірність даних і висновків покладається на авторів.

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