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Exopolysaccharides from Lactic Acid Bacteria: A Review on Functions, Biosynthesis and Applications in Food Industry

Tuğba Karabekmez Erdem[1,a], Hazel Dilşad Tatar[2,b], Sermet Ayman[2,c], Yekta Gezginç[2,d,*]

[1]*Department of Food Processing, Vocational School of Technical Sciences, Kahramanmaraş Sütçü Imam University, 46000 Kahramanmaraş, Türkiye*
[2]*Department of Food Engineering, Faculty of Engineering and Architecture, Kahramanmaraş Sütçü Imam University, 46000 Kahramanmaraş, Türkiye*
[*]*Corresponding author*

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A B S T R A C T

Lactic acid bacteria are the substantial source for producing polysaccharides used in technological applications as thickeners and viscosifiers in the food industry. A broad variety of lactic acid bacteria species secrete structurally diverse exopolysaccharides that contribute to their surface attachment, protection against abiotic or biotic stress factors and nutrient uptake. The exopolysaccharides are produced naturally during fermentation process by living lactic acid bacteria cells and accepted as postbiotic for these metabolites having various physiological health-promoting effects. Exopolysaccharide producer lactic acid bacteria encode a great number of enzymes and regulatory proteins involved exopolysaccharide biosynthesis process. This process is a complex and occurs through presence of multiple genes. However, it is crucial the understanding of structure, composition, function, chemical, and physical properties of exopolysaccharides which vary from one type of bacteria to another via chemical analysis methods. In this review, the use of lactic acid bacteria exopolysaccharides, their structures, genetic modules and biosynthesis, and the use of exopolysaccharides derived from lactic acid bacteria in the food industry are described, discussed and focused on recent developments.

[a] *tkarabekmez@hotmail.com* *https://orcid.org/0000-0001-6361-4796*
[b] *dilshadtatar@hotmail.com* *https://orcid.org/0000-0002-2615-7992*
[c] *sermetayman@hotmail.com* *https://orcid.org/0000-0002-7521-8712*
[d] *yekgan@ksu.edu.tr* *http://orcid.org/0000-0002-3230-2850*

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Introduction

Lactic acid bacteria (LAB) are essential industrial microorganisms and are frequently used in food fermentations. Apart from the food industry, LAB are used in various industries for their ability to produce important compounds. LABs are commonly utilized as starter cultures in food production and are responsible for the fast acidification of dairy products via lactic acid fermentation. During fermentation, LAB produce mainly lactic acid along with other compounds such as organic acids, aromatic compounds, exopolysaccharides (EPSs) that they are also called postbiotic (Smid and Kleerebezem, 2014; Malashree et al., 2019). Postbiotics are beneficial substances released by living LAB during the fermentation process and are also known as "simply metabolites" or "cell-free supernatants" (Izuddin et al., 2018). The studies for EPS derivatives have shown that these compounds directly interact with the host and can have several bioactivities (Cuevas-González et al., 2020).

EPSs are high molecular weight polymers made up of repeated sugar units and released extracellularly by several microorganisms including algae, fungi, bacteria and yeasts (Taylan et al., 2019). These microbial cells produce extracellular substances that vary in form and structure consisting of proteins, fats, nucleic acids, and metal ions settled in the slimy extracellular matrix. The EPS acts as a protective barrier, preventing the interaction of foreign substances with the cell membrane and cellular stress caused by unfavorable environmental conditions and exposure to toxins. The nutrient composition of the medium (carbon, nitrogen, phosphate, oxygen levels, and carbon/nitrogen ratio), environmental conditions such as pH and temperature, and cell-growth phases both can affect the quantity and composition of EPS produced by cells. Since EPS polymerization and translocation require active nucleotides as an energy source, it is abundantly synthesized during active sugar intake, and EPS accumulation occurs significantly during the stationary phase (Sanlibaba and Cakmak, 2016).

EPSs are produced by cells as in capsular or free form. Capsular EPSs (cEPSs) remain attached to the cell wall (directly attached to phospholipid or lipid a particle by covalent bonding) after synthesis, and free EPSs (or slime EPSs –sEPSs) are independent secretions released from the cell wall into the medium. Depending on the strain, either free or both forms of EPS can be observed. For LAB, cEPS lead to ropiness, whereas sEPS enhances viscosity of growth medium without causing ropiness (Rajoka et al., 2020) and based on this property EPS-producing LAB strains can be classified as ropy phenotype and mucoid phenotype (Zannini et al., 2016). LAB produce various EPSs with different structures such as monosaccharide composition (homo-heteropolysaccharides), link types (α-glucans, β-glucans), degree of branching, molecular weight (Figure 1). EPS gene clusters, which can be expressed on chromosomes or plasmids, encode enzymes implicated in EPS production. The diversity of EPS generated by LAB is broad, seeing that eps gene clusters are strain-specific. This structural diversity makes EPS a major metabolite and provides substantial opportunity to be used in commercial applications since the structure determines the physicochemical properties (emulsifier, stabilizer, viscosifier, texturizer) and bioactivities (antitumor, wound healing, cholesterol lowering, immunomodulating, antimicrobial, antioxidant activities) of EPS (Patel et al., 2012; Zhou et al., 2019; Gezginç et al., 2022). In recent years many EPS-producing LAB species have been used in fermented milk and food products to avoid syneresis and to replace stabilizers. Streptococcus, Lactobacillus, Lactococcus, Pediococcus, Bifidobacterium, Weissella, Oenococcus and Leuconostoc are some EPS-producing bacterial genera that have been successfully used to produce fermented foods with varied physicochemical and biological improvements (Adesulu-Dahunsi et al., 2018; Dimopoulou et al., 2018; Kılınc and Gezginc, 2019; Taylan et al., 2019; Kumar et al., 2020; Milanović et al., 2020).

This review presents an overview of lactic acid bacterial exopolysaccharides, their chemical compositions, biosynthesis pathways, and genetic modules within current research. Methods developed for the characterization of EPS production and proposed novel methods have been compared. Furthermore, contemporary LAB application areas in the food industry are defined and explored within the context of ongoing investigations.

Chemical Composition and Characteristics of Exopolysaccharides

EPSs are divided into two different groups homopolysaccharides (HoPSs) and heteropolysaccharides (HePSs) depending on their monomer composition. HoPSs are consist of just one type of monosaccharide, such as glucose or fructose and possess a molecular weight (MW) within the scope of 10^5-10^6 Da. They comprise repeating units of a type of monosaccharide and therefore are split to two sample groups, glucans (α-glucans, β-glucans) and also fructans (Rajoka et al., 2020).

α-glucans are synthesized by *Streptococcus mutans, Streptococcus salivarius, Limosilactobacillus reuteri, Lacticaseibacillus casei, Latilactobacillus sakei, Limosilactobacillus fermentum, Leuconostoc mesenteroides* and *Weissella cibaria.* and that may be distinguished in accordance with their linkage; glucan (α-1,2), mutan (α-1,3), reuteran (α-1,4), dextran (α-1,6), and alternan (α-1,6 along with α-1,3 linkages). β-glucans are synthesized by *Lentilactobacillus diolivorans, Levilactobacillus brevis, Pediococcus damnosus* and *Pediococcus parvulus.* Microbial fructans are mainly synthesized by Streptococcus, Leuconostoc, Lactobacillus, and Weissella spp. All these HoPS include chains of fructosyl units with different bond types e.g., levan (β-2,6) and inulin (β-2,1). HePSs are actually produced by using several duplicates of oligosaccharides and possess two or more unlike monosaccharides (commonly through two to eight varied monosaccharides) each of them causes polysaccharides to become more complicated. The most common monosaccharides within HePSs are L-rhamnose, D-galactose, and D-glucose. Fructose, fucose, N-acetylglucosamine (GlcNAc), N-acetylgalactosamine (GalNAc), glucuronic acid (GlcA); substituted monosaccharides (phosphate, glycerol or maybe acetyl groups) take place less often. HePS possess a molecular mass generally ranging between 10^4 and 10^6 Da. HePSs are actually produced by a number of mesophilic and thermophilic LAB. Some of the LAB strains producing EPSs are given in Table 1 (Saadat et al., 2019; Mende et al., 2020; Rajoka et al., 2020;).

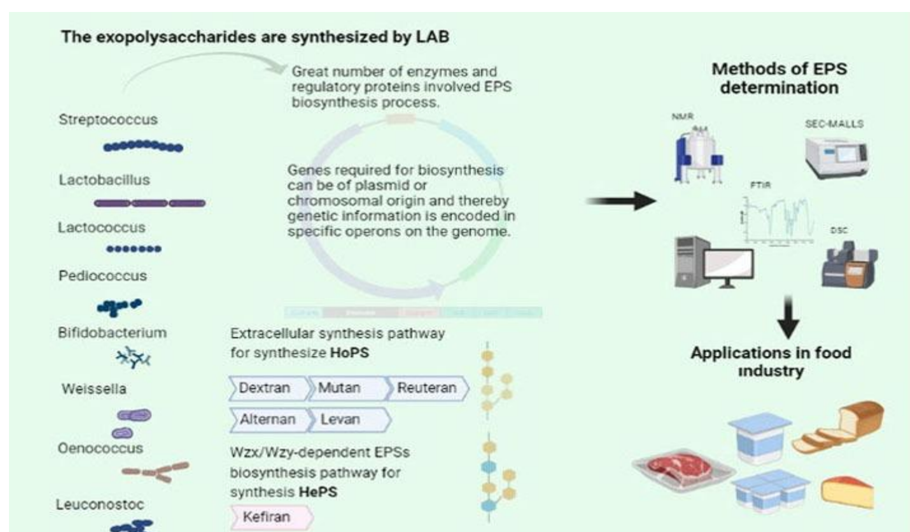

Figure 1. General overview of the EPS biosynthesis, methods of EPS determination and its applications in food industry

Table 1. Overview of LAB strains generating extracellular polysaccharides (EPSs)

Strains	References
Lactobacillus acidophilus 606	Kim and Choi (2010)
Lactobacillus acidophilus LA1	Abd El Ghany et al., (2015)
Lactobacillus acidophilus 10307	Deepak et al., (2016)
Lactobacillus delbrueckii subsp. *bulgaricus* B3	Durlu-Özkaya et al., (2007)
Lactobacillus delbrueckii subsp. *bulgaricus* A13	Sengül et al., (2006)
Lactobacillus delbrueckii ssp. *bulgaricus* (BioLb94, BioLb155, BioLb159)	Kılınç and Gezginç, (2019)
Lactobacillus casei 01	Liu et al., (2011)
Lactobacillus confuses TISTR 1498	Surayot et al., (2014)
Lactobacillus coagulans RK-02	Kodali and Sen (2008)
Lactobacillus fermentum Bz2	Milanović et al., (2020)
Lactobacillus gasseri strains	Sungur et al., (2017).
Lactobacillus kefiranofaciens DN1	Jeong et al., (2017)
Lactococcus lactis NCR112	Nguyen and Nguyen (2014)
Lactobacillus paracasei NFBC 338 & *mucosae* DPC 6426	London et al., (2014)
Lactobacillus paracasei subsp. *paracasei* NTU 101	Liu et al., (2011)
Lactobacillus paraplantarum BGCG11	Nikolic et al., (2012)
Lactobacillus plantarum C88	Zhang et al., (2013)
Lactobacillus plantarum 70810	Wang et al., (2014)
Lactobacillus plantarum RJF4	Dilna et al., (2015)
Lactobacillus plantarum YW32	Wang et al., (2015)
Lactobacillus plantarum EPLB	Mahdhi et al., (2017)
Lactobacillus plantarum-group (LPG)	Huang et al., (2017)
Lactobacillus plantarum NCU116	Zhou et al., (2017)
Lactobacillus plantarum MTCC 9510	Ismail and Nampoothiri, (2013)
Lactobacillus reuteri DSM17938	Kšonžeková et al., (2016)
Lactobacillus. reuteri TMW1.656	Chen et al., (2016).
Lactobacillus rhamnosus KL37 (EPS37)	Ciszek-Lenda et al., (2013)
Lactobacillus rhamnosus YHOC 137	Thapa and Zhang, (2009)
Lactobacillus rhamnosus KL37	Ciszek-Lenda et al., (2011).
Lactobacillus rhamnosus RW-9595M	Bleau et al., (2010)
Lactobacillus sanfranciscensis Ls-1001	Zhang et al., (2019)
Lactobacillus sakei MN1	Nácher-Vázquez et al., (2015)
Leuconostoc mesenteroides NTM048	Matsuzaki et al., (2015)
Leuconostoc mesenteroides RTF10	Nácher-Vázquez et al., (2015)
Leuconostoc citreum L3C1E7	Domingos-Lopes et al., (2017)
Streptococcus salivarius ssp. thermophilus (BioSt33, BioSt166)	Kılınç and Gezginç (2019)
Streptococcus salivarius ssp. thermophilus AR333	Ren et al., (2016)
Weissella cibaria GA44	Adesulu-Dahunsi et al., (2018)
Weissella confusa	Adebayo-Tayo et al., (2018), Adesulu-Dahunsi et al., (2018)

EPSs' physio-biological activities stem from their particular structure and source. The presence and length of side chains, and frequency of branching all affect the intensity or rigidness of the EPS, possibly affecting the rheological properties of fermented dairy products such as yogurt, kefir, cheese (Kılınç and Gezginç, 2019; Jurášková, et al., 2022). The EPS-producing LAB strains have been progressively investigated for the manufacturing of fermented products owing to the ability of theirs to improve rheology, texture, and mouth feel, and decrease thermal and physical shock and syneresis of the products. The addition of EPS producing LAB to fermented products (sauerkraut, fermented cereal beverages, sausage, sourdough bread, cheese, and fermented milk) has become a trend lately and in time, different EPS producing LAB strains may be used as functional starter cultures specific to certain fermented products (Velasco et al., 2021; Xu et al., 2021; Bancalari et al., 2020; Milanović et al., 2020).

Lactic acid Bacterial Exopolysaccharides

Dextran is a water-soluble HoPS consisting of the main chain of α-1,6 linked glucose monomers and branches with α-(1,2), α-(1,3) or α-(1,4) links. Dextran is produced by species of Lactobacillus (*Latilactobacillus sakei*, *Liquorilactobacillus mali*, *Lb. Liquorilactobacillus hordei*, *Lacitilactobacillus nagelii*, *Limosilactobacillus fermentum)* (Nácher-Vázquez et al., 2015; Xu et al., 2018; Llamas-Arriba et al., 2019), Leuconostoc (*Leu. meseteroides*, *Leu. citreum*, *Leu. pseudomesenteroides*, *Leu. carnosum*, *Leu. lactis*) (Nácher-Vázquez et al., 2015; Yang et al., 2015; Llamas-Arriba et al., 2019; Wang et al., 2019; Besrour-Aouam et al., 2021), Streptococcus (*S. mutans*) (Iliev et al., 2006)**,** Weissella (*W. cibaria, W. confuse*) (Besrour-Aouam et al., 2021), Oenococcus (*O. oeni*) (Dimopoulou et al., 2014) genera from sucrose via dextransucrase activity. The degree of branching involving

α-1,2, α-1,3 and α-1,4 linkages in dextrans vary according to the origin of dextransucrase. Dextran is a functional hydrocolloid due to its bending structure, high water solubility, and biodegradable properties and has many applications in food industry, i.e, they are added to bakery products and confectionery to improve softness or moisture retention, to prevent crystallization, and to increase viscosity, rheology, texture and volume (Ateş, 2015; Zarour et al., 2017; Taylan et al., 2019).

Mutan is a water-insoluble, adhesive, branched HoPS, consisting of mixed α-1,3 and α-1,6 linked glucose monomers, and synthesized by mutansucrase in the presence of sucrose (Wiater et al., 2012). Mutan is mainly produced by *S. mutans* along with *Streptococcus sobrinus* (Wiater et al., 2005) and some Leuconostoc, Lactobacillus and Bifidobacterium species. The structure of mutan varies with the organism and the type of mutansucrase. Also, properties of mutan can be altered via chemical modifications. It was reported that carboxymethylation enhanced water solubility and antioxidant properties of mutan and carboxymethyl derivatives could find uses in food industry (Boddapati et al., 2020).

Reuteran is a water soluble, highly branched HoPS consisting α-1,4 and α-1,6 glycosidic linkages and produced by *Limosilactobacillus reuteri* via reuteransucrase enzyme activity from sucrose. The degree of α-1,4 and α-1,6 linkages in reuteran vary according to type of reuteransucrase involved. Reuteran is used in the food industry for improving the technological properties of sourdough, textural properties and shelf life of bread (Chen et al., 2016).

Alternan is a branched HoPS with a unique structure consisting α-1,3 and α-1,6 linked glucose units. Special structure brings alternan high solubility, low viscosity, hydrolysis resistance properties. Alternan is produced by *Leu. mesenteroides* strains via alternansucrase activity from sucrose (Zannini et al., 2016; Saadat et al., 2019).

Kefiran is a water-soluble branched HePS containing equal amounts of D-glucose and D-galactose monomers. Kefiran is the major EPS found in kefir grains and produced by Lactobacillus species especially *Lactobacillus kefiranofaciens* (Júnior et al., 2020). Kefiran improves texture of fermented foods with its water binding property. Besides texture improvement, kefiran can be used to produce edible films for food packing. Also, kefiran is reported to have antitumor, wound healing, cholesterol lowering antimicrobial activities (Zannini et al., 2016; Hussain et al., 2017).

Levan is a highly water-soluble branched HoPS consisting D-fructosyl units linked with β-2,6 and β-2,1 bond. Levan is produced by *Lb. reuteri*, *S. salivarius*, *Leu. mesenteroides*, and *Fructilactobacillus sanfranciscensis* via levansucrose activity. Levan has many uses in food, chemical, cosmetics and pharmaceutical industries due to its adhesive, non-calorie, water soluble and film-forming abilities. Levan is also reported to has health benefits such as anti-cancer, antioxidant, cholesterol-lowering, and prebiotic activities (Yildiz and Karatas, 2018; Huang et al., 2021).

Biosynthesis and Genetics of Exopolysaccharides

Comprehensive understanding of LAB's biochemistry, biosynthesis pathways, genetics and regulation mechanisms are essential to further exploit their ability to produce polysaccharides (Ateş, 2015). EPS consists mainly of carbohydrates, as well as some non-carbohydrate substances such as proteins, pyruvate, phosphate, acetate and succinate (Rana and Upadhyay, 2020). Exopolysaccharide biosynthesis process involves a great number of enzymes and regulatory proteins. Besides, EPS biosynthesis pathway changes depending on whether produced EPS is HoPS or HePS. The EPS biosynthesis pathway can be divided into three major stages: (i) synthesizing the precursor substrate (sugar nucleotides) (ii) polymerization and transporting cytoplasmic membrane and (iii) exporting through the outer membrane (Nouha et al., 2018; Nguyen et al., 2020).

First stage is synthesis of precursor substrate; the conversion of intermediate sugar metabolites into the EPS precursor, such as nucleoside diphosphate sugars. They aid in an initialized transmitter for the glycosyl transferase-catalyzed transfer of the sugar to a carbohydrate (Becker, 2015). In the second stage, the precursor is transferred to the polymer. In the next stage the sugar nucleotide complex formed, the monosaccharide activation is performed by sequential addition of sugars and acyl groups to isoprenoid lipid receptors in the cytoplasmic membrane via specific sugar transferase enzymes. Repeating oligosaccharide units with acetyl, pyruvyl and acyl groups attached are polymerized. After attaching units, the chain is removed from the outer membrane, which can be coordinated with cytoplasmic proteins, outer membrane proteins and periplasmic proteins (Nouha et al., 2018).

The exopolysaccharides are synthesized by LAB via four different biosynthesis pathways (1) extracellular EPSs biosynthesis pathway; (2) ATP-binding cassette transporter dependent EPSs biosynthesis pathway; (3) synthase-dependent EPSs biosynthesis pathway; and (4) Wzx/Wzy-dependent EPSs biosynthesis pathway. The extracellular synthesis pathway and the Wzx/Wzy-dependent pathway are the universal EPS biosynthesis pathways in LAB (Rajoka et al., 2020; Rana and Upadhyay, 2020).

In extracellular EPSs biosynthesis pathway, the polymer is extended via addition of monosaccharides, fragments of di- or tri-saccharides, for other pathways, precursor molecules required for the gradual extension of strands are generated by various enzymatic reactions, following the same concept of producing sugars/sugar acids (Schmid et al., 2015). The participating enzymes of EPS production are classified into four groups; (i) intracellular enzymes such as hexokinase that participate in various cellular metabolisms; (ii) enzymes catalyzing the conversion of sugar nucleotides, such as UDP -glucose pyrophosphorylase; (iii) glycosyltransferases (GTFs) that transfer sugar nucleotides to the repeating unit attached to the glycosyl carrier lipid and are found in the cell periplasmic membrane; (iv) enzymes participating in polymerization and located outside the cell (Ateş, 2015).

Firstly, LAB use the extracellular synthesis pathway only to synthesize HoPS. The extracellular pathway of HoPS, as defined in the Weissella, Leuconostoc, Lactobacillus and Pediococcus strains, usually occurs in the extracellular position. The process involves two steps: The polymerization is conducted via transferring monosaccharides to the growing chain by responsible

enzymes such as fructansucrase and glucansucrase. And, then HoPS chain is released directly into the environment (Zhou et al., 2019).

In a second way, the carrier-bound ATP binding cassette (ABC) pathway involves in the synthesis of capsular polysaccharide (CPS). In this way, capsular polysaccharides are synthesized by glycosyltransferases in the inner membrane linking to the ABC transporter (Rajoka et al., 2020).

As a third way, the synthase-dependent pathways are often used to couple homopolymers consisting same sugar precursors. Finally, the translocation and polymerization processes in this pathway are carried out by a single synthase protein, for alginate and cellulose a subunit of the envelope-spreading multiprotein complex (Schmid et al., 2015).

HePSs, which have a more complex structure than HoPS, are synthesized via EPS biosynthesis pathways connected to Wzx/Wzy. The Wzx/Wzy-dependent EPS biosynthesis pathway includes the phases of phosphorylation and transportation of disaccharides as well as monosaccharides, activation of monosaccharides and sugar nucleotide formation, conversion of repetitive subunits via flippase (Wzx) from the inner side of the membrane to the outer surface and polymerization of repetitive subunits via polymerization protein (Wzy), and finally subsequent release of polymer to the environment (Zhou et al., 2019; Rajoka et al., 2020).

EPS biosynthesis is a complex process that occurs through the presence of multiple genes. These genes required for biosynthesis can be of plasmid or chromosomal origin and thereby genetic information is encoded in specific operons on the genome (Werning et al., 2012). It was reported 146 EPS gene clusters were detected in 106 Lactobacillus strains. The three EPS gene clusters from *Lb. plantarum* 16, *Lb. buchneri* CD034 and *Lb. buchneri* NRRL B-30929 were found to be located on the plasmids whereas the rest were encoded by the chromosomal genome (Deo et al., 2019). In the biosynthesis of exopolysaccharide by *L. lactis* subsp. *cremoris* SMQ-461, the gene products provide functions via eps genes encoded by *epsA*, *epsB*, *epsC*, *epsD*, etc. that are located on the gene cluster. The determination of the length of the EPS chain is predicted to be carried out by the gene products of *epsA*, *epsB*, *epsC* and *epsD*. They share a high identity (89 to 97%) with *EpsA*, *EpsB*, and *EpsC* from *L. lactis* subsp. *Cremoris* NIZO B40 (Dabour and LaPointe, 2005).

According to Péant et al. (2005) it was claimed that the exopolysaccharide biosynthesis gene clusters of four *Lacticaseibacillus rhamnosus* strains consist of chromosomal DNA regions of 18.5 kb encoding 17 ORFs, was highly similar (99 %) among the strains. The variation in EPS production levels observed among these *L. rhamnosus* strains has been associated with differences in central metabolism and the presence of sugar precursors. The central portion of the locus is occupied by five of the six genes (welF, welG, welH, welI, welJ and welE) encoding potential glycosyltransferases. Because of a high correlation between glycosyltransferase gene presence and EPS repeat-unit structure, it can be used in future for screening *L. rhamnosus* strains for novel EPS structures (Soumya and Nampoothiri, 2021).

Chemical Methods of EPS Determination

Instrumental analysis and chemical methods strategies are often coupled to evaluate the structure of LAB-generated EPSs. Traditional chemical analysis methods consist of methylation, Smith degradation, periodate oxidation, and acid hydrolysis that happen to be primarily employed for the proportion of EPSs produced by LAB as well as dedication of the monosaccharide composition. Raditional substance analysis techniques provide a judgment regarding the glycosidic bonds of EPSs produced by LAB besides the linkage modes, and this forms the basis of the instrumental analysis techniques (Wei et al., 2018).

Nuclear magnetic resonance (NMR) spectroscopy is widely used technique for determining the structure of EPS. It is a method depending on the absorption of radio wavelengths within the existence of magnetic areas. This particular method is commonly used to investigate the conformation of particles in formula and enables elucidation of the type of the structure and glycosidic linkages of the repeating unit (Ruas-Madiedo and De Los Reyes-Gavilán, 2005). Two-dimensional NMR (2D NMR) techniques for examining the chemical composition of exopolysaccharides include Nuclear Overhauser Effect Spectroscopy (NOESY), Absolute Correlation Spectroscopy (TOCSY), and Correlation Spectroscopy (COSY) (Rana and Upadhyay, 2020). In these techniques small variants to come down with magnetic areas caused by the electrons orbiting the nucleus induce a change contained electrical power amount as well as resonance indicators, that is distinctive of the substance connect of a certain nucleus. The above-mentioned chemical change enables the substance evaluation as well as structure perseverance of big particles (such as EPS). The 1H (proton) is essentially the most widely used proton due to the high natural abundance of its as well as substantial MR awareness (Neu et al., 2010).

The configuration of glycosidic bonds is evaluated primarily by 1H NMR. Also 1H NMR further differentiate their qualities based on the setup qualities of various glycosidic bonds within the structural evaluation on the EPSs (Botelho et al., 2014). 13C NMR enables to figure out the displacement of different carbons, the sorts, ratios, branching locations and substitution sites of monosaccharide residues and to differentiate conformations and configurations of EPSs (Yu et al., 2016). Ever since, one-dimensional NMR (1D NMR) technology has been frequently applied in the structural studies of EPSs, with reports of effective measurements of several structural properties for LAB-produced EPSs (Li and Lee, 2017). Wang et al. (2014) used 1D NMR and methylation to investigate the linkage modes of the main and side chains of EPS produced by *Lb. plantarum* 70810. Polak-Berecka et al. (2014) evaluated the impact of five different carbon supply media on *Lb. rhamnosus* E/N EPSs structures. In that particular research, the bond sequences and the five EPSs glycosides modes of primary along with edge chains have been driven by methylation, ROESY, 1D-NMR, 2D NMR and heteronuclear multiple bond correlation (HMBC).

Practical applications and unexpected discoveries have developed as a result of recent advancements in unique analytical approaches. Specifically, methods associated

with purification and isolation, advanced structural identification, primary structure as well as computer programs (CASPER) coupled with NMR applied to the use of monitoring LAB generated EPSs are discussed. This kind of information is going to provide the necessary kind new guide substance just for the upcoming utilization as well as fundamental study investigations in to the field of LAB generated EPSs (Wei et al., 2018).

For the extraction and purification of LAB-derived EPSs, centrifugation to seperate bacteria, enzymatic deproteinization, and organic substance precipitation are all required. It has become easier to achieve improved purification of LAB generated EPSs thanks to recent advances in chromatography technology. Typically, the first isolation of EPS fractions in crude extracts with various qualities was carried out using DEAE Sepharose Fast Flow chromatography (Miao et al., 2014).

Traditional detection methods are limited by the complicated structure of microbial EPSs. Multiangle laser light scatter, static light scatter, and dynamic light scatter meters have all been shown to be easy and effective techniques for measuring the advanced structure and molecular weight of EPSs. (Xu et al., 2015). Shao et al., (2015) used a combination of multi angle laser light scattering and dynamic light scattering (SEC-MALLS) to determine the EPSs fraction S2 structure formed by *L. rhamnosus* KF5 in solution (Rana and Upadhyay, 2020). X Ray diffraction (XRD), Differential Scanning Calorimetry (DSC) and Thermal Gravimetric Analysis (TGA) as thermoanalytical techniques are also applied to study the exopolysaccharide structure (Hubbard et al., 2012; Zhang et al., 2015).

Fourier Transform Infrared (FTIR) is a powerful analytical tool for detecting different types of functional groups and characterizing bonds in EPS structures. It is based on the idea that bonds vibrate at specific frequencies. By comparing best matches with libraries of spectra reported for known materials, it is possible to predict the information obtained from the FTIR spectrum of unknown materials (Finore et al., 2014).

Commercial Applications of LAB EPSs' in Food Industry

There is a wide spreading request for low calorie healthy foods without additives in consumer market and LAB-based EPS, as an inartificial alternative to chemicals, may be used to meet the consumer demands without impairing the textural properties of the food products (Korcz et al., 2018).

EPS producer LAB are exploited extensively in manufacturing of fermented dairy and bakery products for EPS synthesized in fermentation improves viscosity, texture and structure of the product and reduces syneresis (Sandra et al., 2012; Bachtarzi et al., 2019).

LAB produce EPS in low quantities and EPS purification is costly. However, EPS would be obtained in high quantities and use of pure EPS in food production may become common with the development of efficient production and purification techniques and supporting studies on LAB EPSs' technological properties. Llamas-Arriba et al., (2019) reported that dextran obtained from *Leuconostoc carnosum* with a production yield of 3.65 ± 0.21 g/L and from *Liquorilactobacillus mali* with 11.65 ± 1.15 g/L yield and for its shear-thinning rheological properties, EPS is suitable to be used in food production and may improve sensory properties of foods as mouth feel and flavor release. Yang et al., (2015) studied the dextran obtained from *Leuconostoc citreum* (yield of 23.5 g/L) and stated that the EPS had high water solubility (72.0 g/L) and water retention properties (21.52% of water holded) and has potential to be used as a water-binding agent. Wang et al., (2019) reported that dextran obtained from *Leuconostoc pseudomesenteroides* (30.5 g/L yield) exhibited excellent thermal stability with a degradation temperature of 304.9 °C and possessed high viscosity at high concentration (21954.3 mPas at 60 mg/mL conc.), at low temperature and acidic pH, making it promising to be used in thermal processed foods and fermentation of acidic food products. In a study on EPS which produced by *Weissella cibaria* (35.27 ± 2.19 g/L yield) it was found that dextran has low branched structure, and high emulsifying property with capacity to maintain hydrocarbon emulsion in water by 73.38 ± 2.34% of emulsion. Also, EPS had high water solubility (95.23 ± 4.45% of dry amount), water holding capacity (287.84 ± 16.23% of dry weight), strong antioxidant (86.36 ± 2.09% of hydroxyl radical scavenging activity compared to 91.47 ± 2.71% activity of vitamin C) properties. It was stated that EPS could be evaluated as water-binding, stabilizer and antioxidant agent for industrial applications (Ye et al., 2018). Chen et al. (2016) compared the effects of dextran and reuteran to bread quality and reported that effects of dextran on bread volume and texture were superior to reuteran but modified reuteran (high α-(1→4) linkage and low molecular weight) was as efficient as dextran in bread quality improvement. *Lactiplantibacillus plantarum* isolated from homemade dairy products conferred optimal viscosity and texture to the skimmed milk due to their capability to synthesize EPS in fermentation (İspirli et al., 2020). Also, EPS crude extract from *Lb. fermentum* Lf2 is proposed as a potential techno-functional ingredient for the design of novel foods (Bachtarzi et al., 2019). İspirli et al. (2020) studied the effect of α-glucan of *Limosilactobacillus reuteri* E81 on sourdough rheology and bread characteristics and reported that glucan synthesis in sourdough fermentation improved rheological properties of sourdough and bread texture. Cao et al. (2021) studied a heteropolysaccharide, with the constituents of glucose, galactose, N-acetyl-D-galactosamine, and rhamnose, synthesized by *Streptococcus thermophilus* ZJUIDS-2-01 and found that the EPS had high emulsifying activity (48% emulsification index value) than commercial EPS xanthan gum (XG) (42% emulsification index value) for the O/W system consisting of olive oil and high flocculating activity (85.52%) than XG (75.71%). EPS also reported to had promising antioxidant property (34.5 ± 0.73% DPPH free radical scavenging ability compared to 94.7 ± 0.07% activity of vitamin C) which was close to XG (38.54 ± 1.65%) and showed antibacterial activity against *Staphylococcus aureus* CMCC 26003 and *Listeria monocytogenes* CMCC 54007. It was stated that EPS had potential to be used as emulsifier and bio-flocculant for industrial applications.

Use of biodegradable packaging material for food packing is a topic of interest (Ale et al., 2019). Consumer's

demand for foods without chemical preservatives led researchers to investigate new bio-based material for food packaging to extend shelf life. LAB EPS have good film-forming properties and can be used to design edible packing. The use of glycerol as a plasticizer to kefiran provides low water vapor permeability, exceptional flexibility, and is even more flexible than low density polyethylene for food packaging. (Hasheminya and Dehghannya, 2020). Utilization of LAB EPS (etc. kefiran-based films) with antioxidant and antimicrobial properties for film development may allow the reduction of additives required to preservation of foods (Júnior et al., 2020; Moradi et al., 2021).

LAB EPSs offers great potential to be used in the food industry because they are natural polymers, possess bioactivities and have suitable technological properties. Function of a compound is determined by its structure and LAB EPSs have high diversity in chemical structure that can even vary between producer strains also alterable by growth conditions. This great variety makes these polymers an attractive subject of research for diversity in structure affects functions. In this context, with the expanding knowledge on structure-function relationship, it could be expected the use of LAB EPS in food and related industries will be more common.

Conclusions

LAB EPSs is attracting the scientists with their diverse chemical structure, unique properties, structure-function relationships. The diversity of LAB EPSs is large and offer significant potential as use in commercial applications for many industries due to their novel and distinct properties. And extensive investigations to be conducted on genes responsible for EPS biosynthesis will allow to increase the EPS production and to modify the structure of EPS produced and eventually enable its commercial use to become more widespread. The naturally occurring capacity of LAB to release significant amounts of bioactive compounds makes them potentially attractive hosts for the synthesis of new molecules. They have an especially important place in the food industry for edible food film and food packaging purposes. The amount of research on the use of EPS to produce LAB in the food industry is steadily increasing, and it is expected that this increase will lead to higher quality food substances on the shelves.

Many LAB EPSs have recently been used in commercial applications, including alginate, xanthan, dextran, and pullulan. EPS can be used in a variety of areas, including biomedicine, cosmetics, food, and pharmaceuticals. Novel EPS with interesting properties have been published in a large number of journals, and possible applications of EPS have been discovered. LAB generated EPSs can change their characteristics in response to a number of environmental stimuli. As a result, EPS could be modified to become stimuli-responsive EPS (smart EPS), which could be used in biotechnological and biomedical applications. LAB EPSs are also useful materials for developing micro or nanoparticles that can be used in a variety of applications, including drug delivery, food, medicine, the environment, and agriculture. Bioactive EPS extracted from LAB could be developed as micro or nanoparticles to interact with a variety of targets. Currently, research into biomaterials derived from bioactive EPS is in its early stages.

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