

Exopolysaccharides from Lactic Acid Bacteria: Functional Properties and Effects on Yogurt

Texture

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ABSTRACT

Exopolysaccharides (EPSs) are polysaccharides synthesized extracellularly by microorganisms and have positive effects on health. EPSs produced even at low concentrations have the effect of improving the structure of food products. Thus, it is possible to meet the needs and demands of consumers by developing the textural feature of the final product as desired without using any additives, as well as positive benefits for human health. The number of studies on the use of EPS-producing microorganisms in the production of fermented milk products is continuously increasing. However, the literature does not include sufficient number of studies that explains the interaction between caseins and EPSs in fermented milk products. In this review, EPSs, their functional properties and caseins and EPSs interaction that is critical factor for the formation of yogurt texture, and correspondingly their effects on some problems such as serum separation and poor texture have been handled.

Laktik Asit Bakterileri Tarafından Üretilen Ekzopolisakkaritler: Fonksiyonel Özellikleri ve Yoğurt Dokusu Üzerine Etkileri

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ÖZ

Ekzopolisakkarit (EPS)'ler, mikroorganizmalar tarafından hücre dışı olarak sentezlenen ve sağlık üzerinde olumlu etkileri olan polisakkaritlerdir. Düşük konsantrasyonlarda bile sentezlenen EPS, gıda ürünlerinin yapısını iyileştirme etkisine sahiptir. Böylece nihai ürünün dokusal özelliğini herhangi bir katkı maddesi kullanmadan istenilen şekilde geliştirerek, tüketicilerin ihtiyaç ve taleplerini karşılamakla birlikte insan sağlığına da çeşitli faydalar sağlamaktadır. EPS üreten mikroorganizmaların fermente süt ürünleri üretiminde kullanımına yönelik çalışmaların sayısı giderek artmaktadır. Ancak fermente süt ürünlerinde kazeinler ile EPS arasındaki etkileşimi açıklayan yeterli çalışma bulunmamaktadır. Bu derlemede, ekzopolisakkaritler, fonksiyonel özellikleri ve yoğurt dokusunun oluşumunda kritik faktör olan kazein ile EPS etkileşimi ve buna bağlı olarak serum ayrılması, gevşek yapı gibi istenmeyen sorunlara karşı etkileri ele alınmıştır.

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1. Introduction

Polysaccharides are used in foods as stabilizers, emulsifiers, gelling agents or water-binding agents. Polysaccharides obtained from plants and algae such as starch, galactomannan, pectin, carrageenan and alginate constitute the majority of the polysaccharides used in the food industry (Freitas et al.,

2011). Exopolysaccharides (EPSs) have been used to identify compounds known as extracellular polymeric substances (Rana and Upadhyay, 2020). EPSs are recyclable polymers with high molecular weight monosaccharides secreted extracellularly by microorganisms (Gupta and Diwan, 2017). In recent years, as an alternative to polysaccharides produced from plants and algae, interest on the use of microbial EPSs has increased as they form viscous solutions even at very low concentrations with their pseudoplastic structure (Andhare et al., 2014).

EPSs are essentially straight or branched, soluble ionic or non-ionic biopolymers in which monosaccharides are bound by glycosidic bonds and hexose and pentoses constitute the majority of their structures (Zhou et al., 2018; Moradi et al., 2021). Although EPSs can also be synthesized by plants, yeast, molds and archaea species, the use of bacteria is more preferred in quantity and variety as bacteria provides faster production without affection by geographic or seasonal conditions as there is no need for solar energy for microbial production. Additionally, bacterias can use a wide variety of organic sources as a fermentation sources (Ergene and Avcı, 2016). Among these microbial polysaccharides, EPS produced by lactic acid bacteria (LAB) is preferred for wide-ranging applications (Angelin and Kavitha, 2020). In addition, optimization of fermentation conditions and development of strains producing new biopolymers in high quantities with genetic arrangements can be brought in new starters in the dairy industry (Zhang et al., 2021a).

Microbial sourced EPSs are classified into two separate groups, demonstrated in Figure 1 (Angelin and Kavitha, 2020; Tiwari et al., 2021), as homopolysaccharides (HoPs) and heteropolysaccharides (HePs) in terms of chemical composition, biosynthesis mechanism, and molecular size according to simple sugars in their structures (Saadat et al., 2019). While HePs are synthesized in the cell, HoPs are synthesized by extracellular enzymes using sucrose (Minervini et al., 2011). HoPs are divided into two types: plain neutral glucans, containing a single type of bond, polyanionic homopolymers containing acyl groups, and cyclerglucans containing repeating 1,6- α -D-glycosyl (Korcz and Varga, 2021). HePs refer to long-chain polysaccharides produced by repeating units containing D-glucose, D-galactose, L-rhamnose, or rarely N-acetylglucosamine, N-acetylgalactosamine, and glucuronic acid or derivatives thereof (Kumari et al., 2020). HePs mostly used in the industry can exist in two different forms: capsular (associated with the bacterial cell surface) and ropy or slimy (Abarquero et al., 2021). EPS produced from different LAB: It varies in terms of many properties such as chemical composition, electrical charge, three-dimensional structure, coagulation stability, and ability to interact with proteins (Ruas-Madiedo and De Los Reyes-Gavilán, 2005). In addition to its physical characteristics, the interactions between EPS and various structures contribute to the development of the final product (Werning et al., 2012).

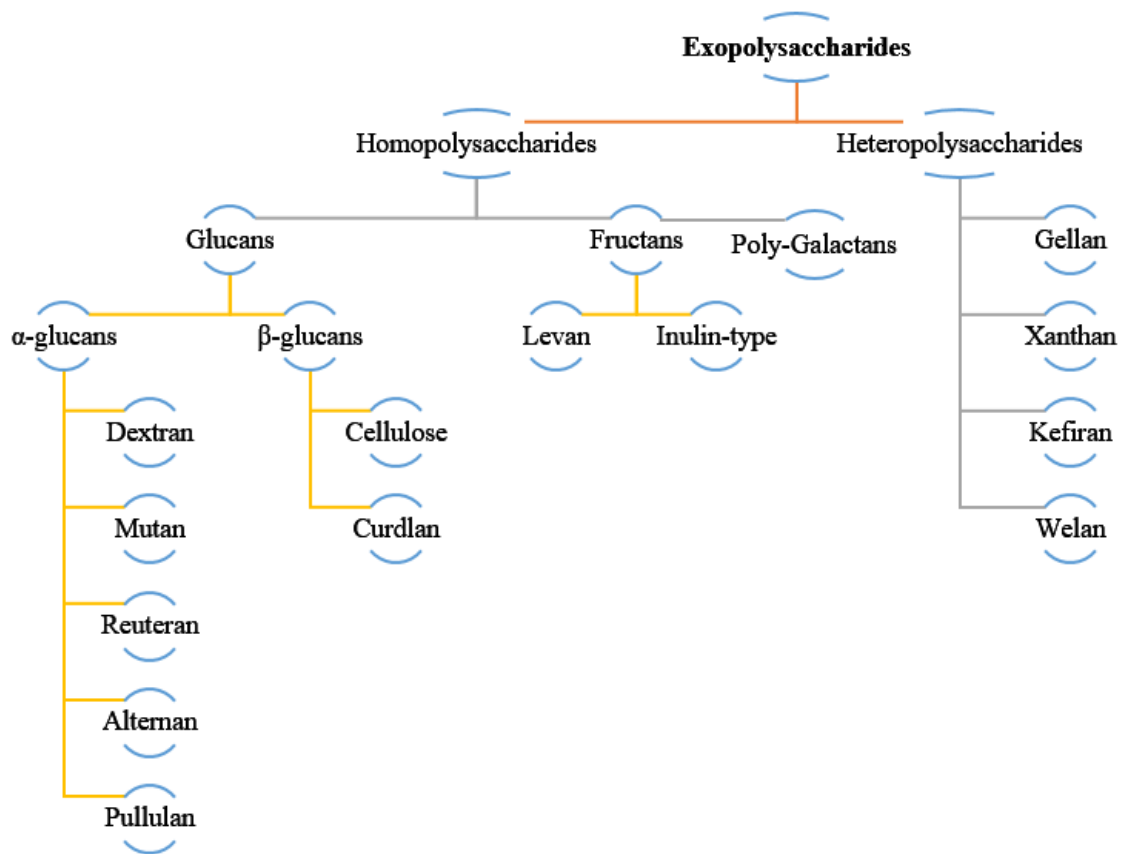


Figure 1. Classification of EPSs

LAB stand out among EPS-producing bacteria in the human diet because of their generally recognized as safe (GRAS) status, ability of producing antimicrobial substances, resistance to acid and bile, and ability to produce EPSs that can be involved in probiotic activity (Ayyash et al., 2020; Rajoka et al., 2020). In Table 1, various LAB capable of producing EPSs have been shown (Angelin and Kavitha, 2020; Kavitate et al., 2020; Patel et al., 2021; Jurášková et al., 2022). Since the use of stabilizers is prohibited in most of the European Union (EU) countries, the use of thickener culture is quite common. In the dairy industry, starter cultures containing thickener LAB are sold in the market as commercial cultures in EU countries and US. Consumer demands for foods with low fat-sugar contents and without inorganic food additives have led manufacturers to foods with high EPS content (Ergene and Avci, 2016; Das et al., 2019).

Table 1. LAB that can produce EPS

EPS	Monomer Units	Species
Dextran	Glucose	<i>Lactobacillus reuteri</i> , <i>Lactobacillus casei</i> , <i>Lactobacillus sakei</i> , <i>Lactobacillus parabuchneri</i> , <i>Lactobacillus fermentum</i> , <i>Lactobacillus curvatus</i> , <i>Leuconostoc mesenteroides</i> , <i>Leuconostoc mesenteroides subsp. dextrtanicum</i> , <i>Streptococcus mutans</i> , <i>Streptococcus downei</i> , <i>Streptococcus sobrinus</i> , <i>Streptococcus salivarius</i> , <i>Streptococcus gordonii</i> , <i>Weissella cibaria</i> , <i>Leuconostoc pseudomesenteroides</i> , <i>Leuconostoc citreum</i>
Mutan	Glucose	<i>Streptococcus mutans</i> , <i>Streptococcus downei</i> , <i>Streptococcus sobrinus</i> , <i>Lactobacillus reuteri</i>
Alternan	Glucose	<i>Leuconostoc mesenteroides</i> , <i>Leuconostoc citreum</i>
Reuteran	Glucose	<i>Limosilactobacillus reuteri</i>
β-glukan	Glucose	<i>Pediococcus damnosus</i> , <i>Pediococcus parvulus</i> , <i>Lactobacillus diolivorans</i>
Poly-galactans	Galactose	<i>Lactococcus lactis</i> , <i>Lactobacillus delbruecki</i>
Levan	Fructose	<i>Lactobacillus reuteri</i> , <i>Lactobacillus frumenti</i> , <i>Lactobacillus sanfranciscensis</i> , <i>Leuconostoc mesenteroides</i> , <i>Streptococcus sobrinus</i> , <i>Streptococcus salivarius</i>
Inulin	Fructose	<i>Lactobacillus reuteri</i> , <i>Leuconostoc citreum</i> , <i>Streptococcus mutans</i> , <i>Lactobacillus johnsonii</i>
Kefiran	D-Glucose, D-Galactose	<i>Lactobacillus kefirianofaciens</i> , <i>Lactobacillus kefirgranum</i> , <i>Lactobacillus parakefir</i> , <i>Lactobacillus kefir</i> , <i>Lactobacillus delbrueckii subsp. bulgaricus</i>

1.1. Biosynthesis of EPSs

Numerous enzymes and regulatory proteins are involved in the biosynthesis of microbial EPS. EPS-producing microorganisms use sugars as energy sources, ammonium salts and amino acids as nitrogen sources. The production of EPS by the microorganism mainly depends on the ratio of carbon and nitrogen availability in the environment. Although low nitrogen concentration leads to high EPS production, optimal C/N ratio for maximum EPS production is 10:1 (Wu et al., 2012). The production of HePs is different and somewhat more complex than the production of HoPs. Their production requires precursors or intermediates (such as lipid phosphate esters and isoprenoid alcohols). After the synthesis of the side groups is made in the cell wall, they are transported to the intercellular environment with the help of the mentioned intermediates, and combined enzymatically and synthesized. Glucosyl transferase, galactosyl transferase, 1,2 glucuronic acid transferase and polymerase enzymes are involved in this synthesis (Ruas-Madiedo et al., 2002). EPS derived from LAB can be formed ex situ as an additive in food after purification or in situ by LAB, which generate EPS in the food matrix. Compared to ex situ production and use of EPS, in situ synthesis process is less controllable, and the food matrix and optimum conditions in which EPS-producing microorganisms grow affect the quality and yield of EPS. Among these factors, carbon and nitrogen

sources, mineral salts, trace elements, microorganism type, temperature, pH and oxygen concentration are important (Hundscheil and Wagemans, 2019).

1.2. Challenges Associated with Biosynthesis of EPSs

The biosynthesis of EPS is highly affected by the ambient and growth conditions (Gientka et al., 2016). There may be challenges limiting the growth of LAB and the production of EPS. Caused by the conditions of production and microorganism itself; high temperature, drying, freezing, high pressure, acidic or alkaline media, anaerobic growth conditions, rich nutrient requirement, oxygen, pH, inhibitors and competitive microorganisms are the factors preventing the growth of LAB (Farnworth, 2008). EPS production is increased by protect microbial cells under stress conditions. In a study in which different concentrations of NaCl were added to the bacterial growth medium, all strains showed good growth in the presence of NaCl at 28 °C. However, it was determined that LAB strains produced more EPS at different NaCl concentrations than under optimal conditions (Grosu-Tudor and Zamfir, 2014). Various carbon sources such as sucrose, glucose, lactose, maltose, mannitol, sorbitol, starch, fructose, ribose, arabinose, raffinose, methanol are used in EPS production. EPS biosynthesis yield and molecular size may vary depending on the carbon source. For example, it has been reported that alginate is produced from fructose and glucose at a molecular weight of 500 kDa and 276 kDa, respectively, after 48 hours of incubation (Conti et al., 1994). Most bacterial EPS production takes place under aerobic conditions, so aeration is required for maximum EPS production. However, some EPS, such as bacterial alginate, occur under microaerobic conditions (Freitas et al., 2011). Bensmira et al. (2010) in the study of the effect of different process conditions on the rheological properties of kefir and the production of EPSs have determined that the combination of homogenization pressure of 19 MPa, incubation temperature of 24 °C and incubation period of 18 hours gives better results than other combinations in terms of rheological properties of kefir and EPS production in kefir. In a study it is reported that *Lactobacillus lactis* can produce the maximum amount of EPSs in the presence of nitrogen sources such as maltose, ammonium sulfate, casein, skimmed milk, and 1 % (w/v) oatmeal added (Almalki, 2020).

2. Interaction between EPSs and Milk Proteins

Microstructures of cheese, yoghurt, ice cream, cream and dairy desserts affect quality parameters such as texture, solubility, flow, visco-elasticity and brittleness. The microstructure is generally shaped by the common interaction of proteins, carbohydrates, lipids and other structural components at the micro scale. Milk proteins, which are the basic microstructure components and have high nutritional value, are widely used in foods with their functional properties; improving the textural properties of foods, increasing the consistency, strengthening the gel formation, forming emulsion, preventing water-retention, serum separation, aroma formation and heat stability (Ramirez-Santiago et al., 2010; Xiao et al., 2020). The properties of the gel in the structure of fermented milk can be determined by

examining the microstructure and microscopic images. Evaluation is mostly characterized by protein bindings, their amounts and pore size distribution (Hassan et al., 1995). It is stated that the interaction between EPSs and milk proteins is an important factor for the formation of yogurt texture. The interaction between EPSs and milk proteins can produce a dense network structure with higher elasticity through Van der Waals force and electrostatic repulsion. EPS does not interact with casein if it is neutral but may interact depending on pH if it is charged. In addition, EPS may interfere with the association between the casein micelles and result in a less firm coagulum (Ruas-Madiedo et al., 2002). EPS synthesis increases protein network aggregation and interaction between EPS and casein matrix in yoghurts, whereas it potentially prevents protein-protein interaction (Yilmaz et al., 2015). As the incubation temperature increases, the hydrophobic interactions between the casein molecules increase and a denser structure is formed. With the decrease in incubation temperature, the hemholtz activation energy required for gelation in yogurt increases. Since the Hemholtz activation energy is desired to be at a minimum level for gel formation with suitable physical properties, the decrease in incubation temperature weakens the curd stability in yogurt (Lee and Lucey, 2003). Birch et al. (2017) reported that with the increase of pH from 4.0 to 5.5, the ability of HePs to bind milk proteins decreases, while HoPs cause a decrease in syneresis, increase in viscosity and a brighter surface in cream and fermented milk products. In another study, EPS-casein complex was formed by adding EPS at different rates (0%, 0,25%, 0,50%, 0,75%, and 1%) into 20 mL of simulated milk ultrafiltrate containing 3% casein. According to the results of the analysis, it was observed that the textural properties of yoghurt improved as the EPS concentration increased (Zhang et al., 2021b).

2.1. Applications of EPS in Dairy Product

EPSs produced by LAB strains are used as natural ingredients as viscosity and thickener, syneresis reducing, stability and emulsifier, and excess water binder in fermented dairy products such as yogurt, cheese, kefir and low-fat cheese to increase the desired sensory features (Mende et al., 2016). In a study it has also been reported that *Weissella cibaria* CH2 isolated from Western Himalayan cheese shows maximum EPS production (81.3%) with sucrose at 20°C. It also shows β -galactosidase production, vitamin and essential amino acid biosynthesis, and antimicrobial activity against pathogenic bacteria in the gastrointestinal tract. Therefore, it can be used as an important probiotic source in fermented dairy products (Kumari et al., 2020). Abushelaibi et al. (2017) have also reported that *Lactobacillus plantarum* KX881772 and KX881779 strains isolated from camel milk had the best EPS production and can be used as probiotics. The first study to determine the microbial diversity and EPS production capacity in Thai milk kefir states that 24 out of 85 isolates are *Bacillus* species and they can produce EPS on 8% glucose, sucrose, and lactose but the appearance of EPS varies depending on the bacteria and sugar type. This study of the components of the Thai milk kefir community and its EPS-producing bacteria suggests that it may be important for the development of

new kefir grains or starter cultures with desired properties as functional foods or probiotic products (Luang-In and Deeseenthum, 2016). In a different study, it is stated that the EPS (Kefiran) isolated from *Lactobacillus kefiranofaciens* has strong potential, advantageous biological, physicochemical and rheological properties for agro-food and biomedical industries (Tan et al., 2020). The EPS-producing starter culture *Streptococcus thermophilus* MYE92 is used to improve the texture properties of low-fat Turkishcheese (Şanlı et al., 2013).

2.2. Functional Properties of EPSs

In recent years, with the awareness of consumers, the tendency of human health protection through nutrition has increased. The positive results of studies examining the effects of yogurt on health have made yogurt production and consumption increasingly widespread all over the world, especially in Europe (Kızılaslan and Solak, 2016; Bilginer and Çetin 2019). In addition, new concepts related to probiotics such as postbiotics and para-probiotics have been used to describe non-viable microorganisms or cell-free extracts that may benefit the host by offering additional bioactivities to probiotics. EPSs are examples of these metabolites (Barros et al., 2020; Amiri et al., 2021). Fermentation is the most common source of postbiotics in food technology. Some foods that are naturally rich in postbiotics, such as yogurt, kefir, pickled vegetables, sauerkraut, kimchi, are rich in postbiotics (Tomasik and Tomasik, 2020). In this context, the multifunctional effect of EPSs has increased the interest of functional properties of yogurt. Generally, functional properties of EPSs are shown in Figure 2 (Korc et al., 2018). EPSs belonging to lactic acid bacterial strains isolated from different products have also been shown to be used as a substitute for antitumor drugs that damage cytotoxicity and the nervous system since they are products obtained from natural sources with low toxicity and minimal side effects (Di et al., 2017). A study shows that *Lactobacillus rhamnosus* ZFM231, which is part of the gut microflora of healthy people and can produce large amounts of EPSs, can be used as effective ingredients in foods to prevent diseases due to its positive effects on human and health (Zhu et al., 2020). Xu et al. (2011) has reported that EPS derived from *B. animalis* RH increase the antioxidant capacity in the blood and Glutathione S-transferase in the liver. In addition, Guo et al. (2013) have reported that EPS derived from *Lactococcus lactis subsp. lactis* reduces lipid peroxidation in blood and liver. A study emphasized that EPS produced by *Lactobacillus kefir* MSR101 isolated from Chinese kefir grains can be used as natural anti-tumor agents in various functional food products (Rajoka et al., 2020). Another study reports that EPS produced with *Lactobacillus plantarum* C70 isolated from camel milk has anticancer, antidiabetic, and antioxidant activity (Ayyash et al., 2020). It has been reported that *Lactobacillus paracasei* M7 isolated from breast milk is an important potential source for EPS production and the EPS produced exhibits versatile biological activities such as ipcholesterolemic, antioxidant and antibiofilm, and also has significant potential on versatile industrial applications for emulsification and polymer film formation (Bhat and Bajaj, 2019). Ale et al. (2019) reports that when EPS from *Lactobacillus fermentum* Lf2 is

added as a food ingredient to yogurts, it plays a prebiotic role by causing an increase in the levels of bacterial groups known to produce health-beneficial short-chain fatty acids. In a study on yogurt, it was determined that EPS produced by *Lactobacillus plantarum* RS20D strain isolated from a homemade Sichuan paocai sample improved the texture of yogurt and in vitro regulated the immune system (Zhu et al., 2019).

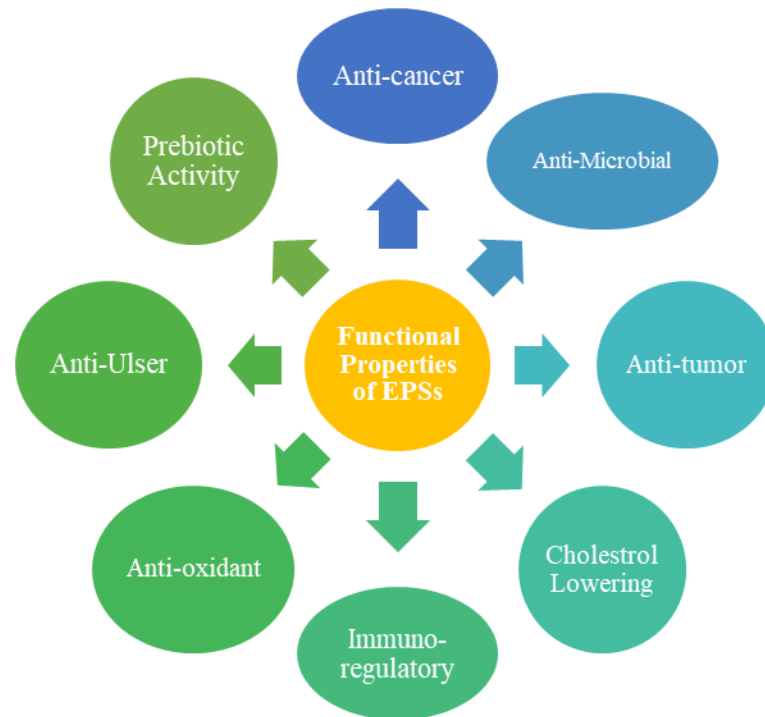


Figure 2. Functional Properties of EPSs

2.3. Effect of EPSs on Textural Properties of Yoghurt

Yogurt is a fermented dairy product preferred by consumers due to its nutritional, sensory, and health benefits. The fermentation conditions and the fermentation strains used are important for the quality of yogurt. Undesirable problems such as serum separation, poor texture may be encountered in yogurt production (Lee and Lucey, 2010). In industry, stabilizers such as gelatin and pectin are often added to fermented milk as additives to prevent syneresis and improve texture in yoghurts (Girard and Schaffer-Lequart, 2008). As an alternative to food additives, starter cultures that produce EPS are used during fermentation to maintain fermentation conditions and improve the textural properties of yogurt. Thus, it can eliminate the need for additional stabilizers (Tiwari et al., 2021). Various positive effects of EPSs on the structural properties of yoghurt are shown in Figure 3 (Han et al., 2016). Depending on the strain combination and hence the types of EPS, yogurt texture and structure will change. Combining the *Lactobacillus* CHCC-10935 strain with the *Streptococcus thermophilus* CHCC-13140 strain that produces negligible amounts of EPS increases the water holding capacity in yogurt in fermentation after a moderate mechanical treatment. For this reason, *Streptococcus thermophilus* strain

selection (CHCC-13140) is important in determining the rheological properties of yogurt produced. Because the incompatibility between the existing EPS and milk protein reduces the water holding capacity and exhibits a more porous structure. In addition, while extracellular type EPS of *Lactobacillus* CHCC-10935 strain increases serum viscosity, capsule type EPS increases gel hardness (Zhang et al., 2016). In a study, *Lactobacillus paracasei* was used as a starter to prepare yogurt under optimum fermentation conditions. It was determined that the viscosity of yogurt increased with EPS production, and to clarify this phenomenon, the binding of EPS-S11 extracted and purified from yogurt to casein was evaluated by turbidity and particle size analysis, zeta potential study, and confocal laser scanning microscopy. According to the results of the study, with the addition of EPS-S11, the turbidity and particle size of the casein solution decreased in a dose-dependent manner, while the zeta potential increased depending on the dose, suggesting that EPS-S11 might inhibit the aggregation of casein and thus increase its effect (Li et al., 2020). In a different study investigating the effects of EPSs produced in-situ on the textural properties of yoghurt produced from goat milk, it was observed that EPS production significantly improved the quality properties of goat milk yoghurt. In situ EPS production of the starter cultures resulted in goat milk yogurt with low syneresis, high viscosity and improved sensory qualities. During this study, the lowest syneresis values were observed in the starters producing medium EPS, while the highest value was observed in the starters producing high EPS. It was determined that the viscosity values increased in direct proportion with the amount of EPS (Madhubasani et al., 2020). In a study by Gentès et al. (2011) the effect of fermented milk on gel formation and rheological/physical properties (hardness, apparent viscosity, elastic modulus, syneresis) was compared with different EPS structures produced in situ. As a result of the study, it was determined that the gel formation and physical properties of fermented milk were changed by the structural properties of EPS, especially negative charge, flexibility, degree of branching and molecular weight. In the study conducted by Hassan et al. (2001) a decrease in the water release rate of yoghurts produced with gelling cultures was observed. In addition to commercial culture (1.5%), EPS production was detected. Higher EPS production was determined in yoghurts produced with *Lactobacillus bulgaricus* B3 and *Streptococcus thermophilus* W22 strains. In terms of viscosity values, it was stated that yoghurts using these strains were more viscous. In a study examining the effect of 0.01% to 0.03% EPSs on the texture and microstructure of buffalo yoghurt, it was stated that while the casein micelles were denser with the addition of EPS, a better stability was demonstrated when 0.01% EPS was added on water holding capacity, viscosity, hardness and gumminess properties (Yang et al., 2014). It was stated that ropy type EPSs were synthesized higher in yoghurt samples than non-ropy type EPSs and samples produced with ropy type EPS producing strain had the lowest whey separation and the highest density and viscosity (Güler-Akın et al., 2009).

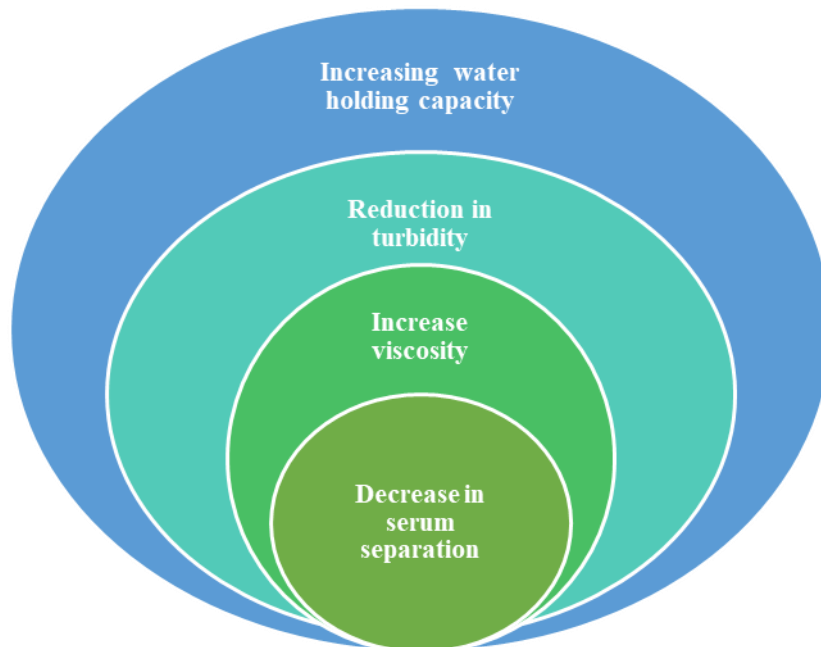


Figure 3. Various improve structure in yogurt provided by EPS

3. Conclusions

LAB have an important role in the fermented food industry. They are especially important for yogurt production. LAB in yogurt improves structure, viscosity and water holding capacity. LAB producing EPS is important in the dairy industry as it contributes to the consistency and rheological properties of fermented milk products. EPS produced by LAB and with GRAS status are applied on an industrial scale in the fermentation of raw food products such as meat and vegetables, especially in the dairy industry. While EPS increases the functional properties and quality of fermented milk products, they also protect bacteria against toxic compounds, phage attacks, and osmotic stress. However, the mechanism of positive effect of EPS on the quality of yogurt has not been clearly defined. The most suitable synthesis for the physical structure of yoghurt should be optimized according to the ambient conditions of the EPS efficiency and interaction with the casein micelles. As a result, the interaction of casein and EPSs is directly effective in improving the rheological properties of yogurt produced in in situ conditions, and it should focus on studies that will determine the optimum conditions according to various processes, challenges and characteristics of milk. In this way, the positive effects of EPSs, which are included in the postbiotic group, which has recently entered the literature and whose research topic is increasing, will be provided both on the structural properties of yogurt and on the health of the consumer.

Statement of Conflict of Interest

Author has declared no conflict of interest.

Author's Contributions

The contribution of the author is 100%.

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