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MINI-REVIEW

Exopolysaccharides produced by lactic acid bacteria: from health-promoting benefits to stress tolerance mechanisms

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Abstract A wide range of lactic acid bacteria (LAB) is able to produce capsular or extracellular polysaccharides, with various chemical compositions and properties. Polysaccharides produced by LAB alter the rheological properties of the matrix in which they are dispersed, leading to typically viscous and "ropy" products. Polysaccharides are involved in several mechanisms such as prebiosis and probiosis, tolerance to stress associated to food process, and technological properties of food. In this paper, we summarize the beneficial properties of exopolysaccharides (EPS) produced by LAB with particular attention to prebiotic properties and to the effect of exopolysaccharides on the LAB-host interaction mechanisms, such as bacterial tolerance to gastrointestinal tract conditions, ability of ESP-producing probiotics to adhere to intestinal epithelium, their immune-modulatory activity, and their role in biofilm formation. The pro-technological aspect of exopolysaccharides is discussed, focusing on advantageous applications of EPS in the food industry, i.e., yogurt and gluten-free bakery products, since it was found that these microbial biopolymers positively affect the texture of foods. Finally, the involvement of EPS in tolerance to stress conditions that are commonly encountered in fermented beverages such as wine is discussed.

Keywords Exopolysaccharides · Lactic acid bacteria · Prebiotic · Probiotic · Stress tolerance

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Introduction

The term "exopolysaccharide" (EPS) is generally related to all forms of polysaccharides present outside of the microbial cell wall. Several lactic acid bacteria (LAB) produce long chains of homo- or heteropolysaccharides, consisting of (branched) repeating units of sugars or sugar derivatives (Ruas-Madiedo et al. 2002; Zannini et al. 2016), which may be substituted with various chemical moieties (Kleerebezem et al. 1999). EPS can be either weakly or strongly bound to the bacterial cell surface and they are distinguished into capsular and secreted forms (Chapot-Chartier et al. 2011). In some cases, EPS confer and increased viscosity to their original environment (Fig. 1).

The physiological role that exopolysaccharides play in the ecology of LAB is not yet completely understood. EPS are thought to protect the bacterial cells against extreme conditions such as biotic stress and/or abiotic stresses, including temperature, light intensity, pH, or osmotic stress (Donot et al. 2012). EPS can also be involved in adhesion to surfaces and biofilm formation and to cell adhesion/recognition mechanisms (Ruas-Madiedo et al. 2002; Broadbent et al. 2003; Rozen et al. 2004). Several health benefits have been attributed to the microbial exopolysaccharides, such as immune-stimulatory (Vinderola et al. 2006; Hidalgo-Cantabrana et al. 2012; Matsuzaki et al. 2014) and antitumoral effects (Kitazawa et al. 1998; Nishimura 2014) or lowering blood cholesterol (Nakajima et al. 1992; Maeda et al. 2004b; Ryan et al. 2015). The different exopolysaccharides' chemical structure affects their potential prebiotic properties. Moreover, the EPS chemical structure could confer diverse probiotic and pro-technological characteristics to the bacterial producer strains (Kleerebezem et al. 1999; van Kranenburg et al. 1999a; Tallon et al. 2003; Zannini et al. 2016).

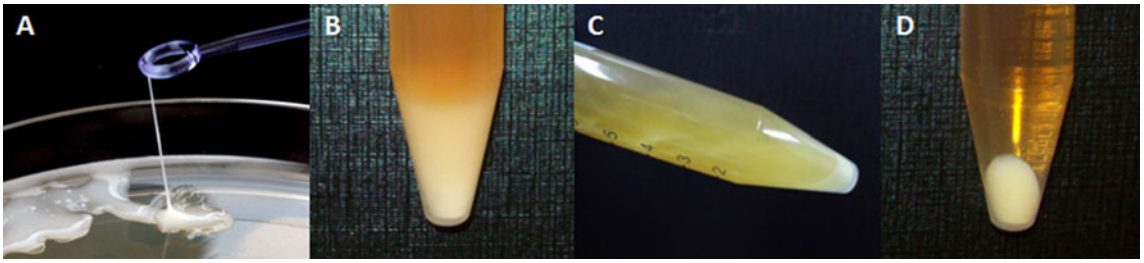

Fig. 1 Ropy phenotype of a *Lactobacillus plantarum* EPS-producing strain on de Man, Rogosa and Sharpe (MRS) plate (**a**) and MRS broth (**b**, **c**). MRS broth culture of a *L. plantarum* EPS-producing strain without ropy phenotype (**d**)

Exopolysaccharides' biosynthesis and chemical classification

The production of exopolysaccharides by LAB has been correlated to specific gene clusters tagged as *eps* or *cps*, located, as in *Streptococcus thermophilus* or *Lactobacillus plantarum*, mainly on the bacterial chromosome (Stingele et al. 1996; De Vuyst and Degeest 1999; Siezen et al. 2010) or in species such as *Lactococcus lactis* and *Pediococcus damnsosus* predominantly on plasmids (Van Kranenburg et al. 1997, 1999b). Remus et al. (2012) identified four *cps* genes clusters in the chromosome of *L. plantarum* WCFS1, which are associated with surface polysaccharide production. The *eps*/*cps* clusters include genes encoding both regulatory factors and enzymes involved in EPS biosynthesis, polymerization, and secretion, including glycosyltransferases, which are responsible for the assembly of the characteristic EPS-repeating unit (De Vuyst and Degeest 1999; Welman and Maddox 2003; Lebeer et al. 2009; Kleerebezem et al. 1999; Nierop Groot and Kleerebezem 2007) (Fig. 2).

The Wzx/Wzy-dependent assembly pathway is involved in biosynthesis of several surface polymers, including EPS (Yother 2011). The synthesis of the sugar units occurs in the cytoplasm; they are assembled on the lipid carrier molecule undecaprenyl phosphate through monosaccharides transfer from nucleotide sugars by specific glycosyltransferases; subsequently, Wzx (flippase) move the lipid-bound repeating units from the cytoplasmic face of the membrane to the outer face where they are polymerized by Wzy (Islam and Lam 2013). Several models of EPS assembly have been proposed for *L. lactis* (Kleerebezem et al. 1999; Laws et al. 2001), *Streptococcus pneumoniae* (Bentley et al. 2006), and *Lactobacillus rhamnosus* (Lebeer et al. 2009). However, in addition to the "flippase-like" route, it could be possible, in LAB, another route involving ABC transporters, although the export-polymerization pathway for EPS production in LAB has not yet been demonstrated.

Microbial exopolysaccharides are divided into two groups: homopolysaccharides (e.g., cellulose, dextran, mutan, alternan, pullulan, levan, and curdlan) and heteropolysaccharides (e.g., gellan and xanthan) (Welman and Maddox 2003; Zannini et al. 2016). Homopolysaccharides (HoPS) in LAB consist of repeating units of one kind of monosaccharide, such as D-glucose or D-fructose; they consist mainly in glucans and fructans, with molecular weights ranging from 10^5 to 10^6 Da (Ruas-Madiedo et al. 2002; Badel et al. 2011). Depending on the linkage type and the position of the carbon involved in the bond, HoPS can be classified as α-D-glucans (dextran, mutan, reuteran, and alternan) and β-D-glucans, whereas those containing fructose are fructans (levan and inulin-types) (Ruas-Madiedo and de los Reyes-Gavilan 2005). Glucans and fructans are found most frequently among the homopolysaccharides, and they are both applied as ingredient in the food industry (Anwar et al. 2008; Zannini et al. 2016).

Conversely, heteropolysaccharide (HePS) are composed commonly by glucose, galactose, and rhamnose and in some cases by *N*-acetyl-D-glucosamine and *N*-acetyl-D-galactosamine (Badel et al. 2011) but may also contain phosphate or other moieties in their polymeric structure (van Kranenburg et al. 1999a; Kleerebezem et al. 1999). The molecular mass is generally between 10^4 and 10^6 Da (Ryan et al. 2015). The exopolysaccharides yield and composition produced by some LAB appear to be significantly influenced by culture and fermentation conditions (i.e., pH, temperature, incubation time, and medium composition) (Dueñas et al. 2003; Torino et al. 2015; Zannini et al. 2016) while in some strains appear a relatively constant production of these polymers under a variety of conditions (Boels et al. 2003). To date, among LAB, the yield of heteropolysaccharides is quite variable (Tsuda 2013); one of the largest EPS producers is *L. rhamnosus* RW-9595M (2775 mg/L) (Macedo et al. 2002) and *Lactobacillus kefiranofaciens* WT-2B (2500 mg/L) (Maeda et al. 2004a) followed by *L. lactis* subsp. *cremoris* (80–600 mg/L), *S. thermophilus* (50–350 mg/L), *Lactobacillus delbrueckii* subsp. *bulgaricus* (60–150 mg/L), *Lactobacillus casei* (50–60 mg/L) (Cerning 1995), and *L. plantarum* (140 mg/L) (Tsuda and Miyamoto 2010).

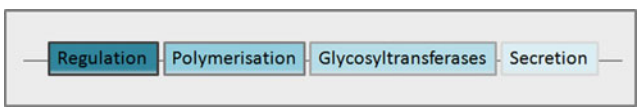

Fig. 2 Block representation of a generic *cps*/*eps* gene cluster, involved in exopolysaccharides biosynthesis

Prebiotic properties of exopolysaccharides

Although the definition of prebiotics has been altered over the years, a recently proposed definition is "a selectively fermented ingredient that results in specific changes in the composition and/or activity of the gastrointestinal microbiota, thus conferring benefit(s) upon host health" (Gibson et al. 2010).

A prebiotic effect has been observed for exopolysaccharides produced by LAB (Dal Bello et al. 2001; O'Connor et al. 2005), as they can be used by probiotic strains, if they possess enzymes capable to degrade the EPS (Tsuda and Miyamoto 2010). An increased growth of probiotic bacteria was elicited by an α-D-glucan produced by a strain *L. plantarum*, which showed a low digestibility by artificial gastric juice and displayed in vitro prebiotic activities, corroborated by the poor growth of non-probiotic bacteria such as *Enterobacteriaceae* (Das et al. 2014). A bifidogenic effect of levan-type EPS from *Lactobacillus sanfranciscensis* has also been reported (Dal Bello et al. 2001). Exopolysaccharides from *Weissiella cibaria*, *Weissiella confusa*, *L. plantarum*, and *Pediococcus pentosaceus* exhibited high resistance to gastric and intestinal digestions, selective enhancement of beneficial gut bacteria, in particular bifidobacteria, suggesting their prebiotic potential (Hongpattarakere et al. 2012). The growth of probiotic microorganisms, defined as "live microorganisms that, when administered in adequate amounts, confer a health benefit on the host" (Hill et al. 2014), may be positively modulated by β-D-glucan produced by *Pediococcus parvulus* (Russo et al. 2012). In contrast, purified EPS from *P. parvulus* were un- able to elicit prebiotic effects in a mouse model, although ingestion of live EPS-producing bacteria-antagonized *Enterobacteriaceae* without disturbing the homeostasis of the microbiota (Lindström et al. 2013).

Exopolysaccharides-host interactions

The consumption of probiotic bacteria has been proposed to be beneficial to human health. These bacteria have been suggested to contribute to nutrient digestion, development, and maintenance of appropriate mucosal immune functions. Furthermore, some microorganisms provide essential vitamins (e.g., folate, biotin, vitamin K) and produce short-chain fatty acids that are used as energy source by colon cells (Gerritsen et al. 2011; Bove et al. 2013; Arena et al. 2014)).

Tolerance to gastrointestinal stress, adhesion on the intestinal mucosa, the ability to inhibit pathogens, and the modulation of immune system are some of the criteria adopted for the selection of probiotics bacteria (Dunne et al. 1999).

Exopolysaccharides produced by LAB may be important on probiotic survival during the gastrointestinal transit. For instance, Stack et al. (2010) reported that β-glucan produced by *P. parvulus* confers to *Lactobacillus paracasei* higher survival during gastrointestinal passage or technological process conditions. Moreover, the addition of microbial glucans has been proven to enhance growth, stress tolerance, and probiotic potential of lactobacilli (Russo et al. 2012). In contrast, in *P. parvulus* and *L. lactis*, the presence of EPS did not confer advantage for bacterial cells survival in the human digestive tract (Fernández de Palencia et al. 2009; Looijesteijn et al. 2001). The differences observed may be due to the diverse structures and compositions of EPS produced by LAB as well as the strains specificity ability to use different EPS.

LAB-EPS also have a key role in biofilm formation and surfaces adhesion enabling the colonization of different environments (Dertli et al. 2015; Zannini et al. 2016). Ruas-Madiedo et al. (2006a) evaluated the effect of exopolysaccharides isolated from Scandinavian traditional fermented milk on probiotics adhesion and their interference of enteric pathogens bacteria adhesion on human intestinal mucus model. These authors observed a greater probiotic adhesion in absence of EPS, without differences in the pathogens' adhesion (Ruas-Madiedo et al. 2006a). Furthermore, exopolysaccharides from probiotic bacteria seem to adhere to intestinal mucus in dose-dependent manner; the ubiquity of *cps*/*eps* gene clusters on probiotic genomes suggests that such strains from the intestinal microbiota may produce these polymers in gut and that high EPS concentrations could be locally reached in the gastrointestinal tract (Ruas-Madiedo et al. 2006b; Salazar et al. 2015). EPS layer might shield specific adhesion factors on the bacterial cell surface and/or electrostatically interfere with the binding to receptors of mucosal surface, thus hindering the adhesion process and the recognition mechanisms which are required for stable adherence on animal cells (Lebeer et al. 2009; Denou et al. 2008; Remus et al. 2012; Dertli et al. 2015) **(**Fig. 3**)**. For example, changes in the genes involved in EPS synthesis in *Lactobacillus johnsonii* altered its surface properties and affect biofilm formation, cell adhesion, and autoaggregation, all important factors for bacterial colonization of the gut (Dertli et al. 2015). Therefore, the EPS removing might enhance bacterial attachment, thus exposing adhesins and/or other cell surface factors that favor the process of bacterial adherence. Moreover, EPS could interfere with adhesion to intestinal cells by a competitive inhibition mechanism (Ruas-Madiedo et al. 2006b). Nikolic et al. (2012) reported that non-ropy derivatives microorganism improved in vitro adhesion with respect to the parental strains. In contrast, β-glucans secreted by *P. parvulus* increased the adhesion of the EPS-producing bacteria (Fernández de Palencia et al. 2009; Garai-Ibabe et al. 2010), as well as exopolysaccharides produced by wine *P. parvulus* (García-Ruiz et al. 2014). In this regard, the ambivalent effect of EPS might depend on their specific chemical nature (Fernández de Palencia et al. 2009). However, the contribution of extracellular polysaccharides in bacterial in vivo adhesion to the intestinal epithelium has not

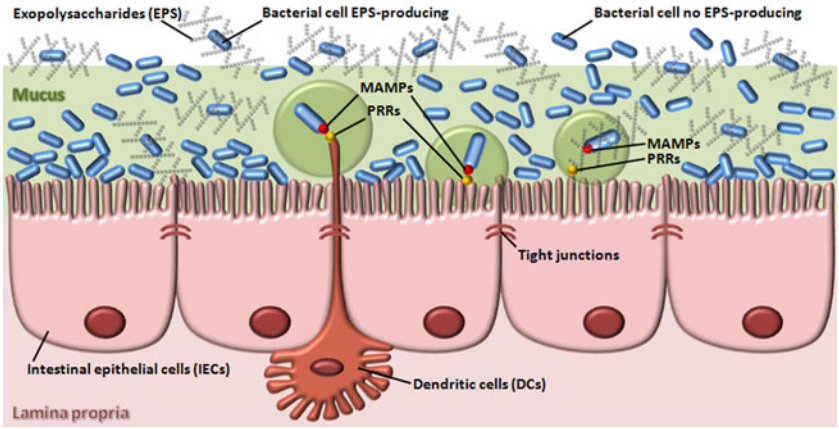

Fig. 3 Probiotic bacteria-intestinal epithelial cells (*IECs*) and dendritic cells (*DCs*) host interaction. Bacterial cells EPS-producing would adhere to intestinal cells less than bacterial cells unable to produce EPS as the surrounding layer of exopolysaccharides might shield specific factors on the bacterial cell surface, thus hindering the adhesion process and the recognition mechanisms with animal cells. Host pattern recognition receptors (*PRRs*) recognize the bacterial cells by microorganisms associated molecular patterns (*MAMPs*)

yet been validated (Ruas-Madiedo et al. 2008). Recently, the in vivo colonization and persistence of exogenous LAB including *L. plantarum* Lp90, an EPS-producing strain, have been reported, using zebrafish larvae (Russo et al. 2015). Even in this case, contrasting data exist regarding the role of EPS on bacterial adhesion passing from in vitro to in vivo models. For instance, Chen and Chen (2013) reported the inability to colonize permanently the intestine of germ-free mice due to the EPS produced by *L. kefiranofaciens*. By contrast, Lebeer et al. (2011) found a greater persistence of *L. rhamnosus* GG with respect to its EPS-mutant strain in a murine model, contrary to what was observed from a previous in vitro model (Lebeer et al. 2009).

The intestinal epithelial cells (IECs) or dendritic cells (DCs) can communicate with the human gastrointestinal microbiota through their pattern recognition receptors (PRRs), which detect microorganisms-associated molecular patterns (MAMPs) (Fig. 3). The interaction between MAMPs and PRRs results in the induction of signaling cascades, which determine a molecular response (i.e., cytokines, chemokines, and antimicrobial agents' immune-modulation) against the detected microorganisms (Lebeer et al. 2010). The Gram-positive bacteria cell wall contains several structural components including exopolysaccharides that are fundamental in the interaction mechanisms between probiotics and host receptors (Kleerebezem and Vaughan 2009).

Recently, it has been observed that some EPS present immunomodulatory properties, with a potential effect on human health (Fernández de Palencia et al. 2009; Liu et al. 2011; Hidalgo-Cantabrana et al. 2012, 2014; Notararigo et al. 2014). Remus et al. (2012) suggested a shielding role of surface polysaccharides *L. plantarum* cell envelope; likewise, the exopolysaccharides produced by *L. rhamnosus* GG may protect by shielding effect against intestinal innate factors, such as the antimicrobial peptide LL-37 (Lebeer et al. 2011). Chapot-Chartier et al. (2010) reported that a novel cell wall polysaccharide pellicle on the surface of *L. lactis* offers protective barrier to the cell wall against host phagocytosis by murine macrophages.

The ability of EPS to elicit immune responses is different between LAB species or strains, and such differences are tough to be related to the structure/size of EPS produced (Hidalgo-Cantabrana et al. 2012). For example, acidic HePS, characterized as having phosphate in their composition, are able to induce the immune response as previously reported in LAB used as starters in the dairy food industry (Kitazawa et al. 1996; Hidalgo-Cantabrana et al. 2012). In contrast, high molecular weight (HMW) HePS seem to act as suppressors of the immune response (Hidalgo-Cantabrana et al. 2012). Indeed, in *Lactobacillus casei* Shirota, the HMW HePS induced the production of various cytokines by macrophages, including IL-6 (Yasuda et al. 2008). However, knockout mutants of genes involved in the synthesis of a HMW polysaccharide were able to induce the production of TNFa, IL-12, IL-10, and IL-6 to a higher extent than the wild-type bacterium (Yasuda et al. 2008; Hidalgo-Cantabrana et al. 2012). Therefore, cell wall polysaccharide in *L. casei* Shirota may be considered as an internal "switcher" able to regulate (attenuate) the host immune response.

The ability of LAB to form biofilms and the relationship between this capacity and their probiotic properties have been recently reported. Although strain-specific, biofilm culture is associated with some of the beneficial properties that characterize probiotic bacteria. For example, biofilms are resistant to gastrointestinal environment-related conditions and produce extracellular factors that possess both immunomodulatory properties and the ability to inhibit the growth of pathogens (Rieu et al. 2014; Aoudia et al. 2016). Studies on the ability of

microbial exopolysaccharides to form biofilm have been carried out, although with conflicting results. Indeed, a negative effect on biofilm formation was observed from the galactose-rich cell wall-associated EPS produced by *L. rhamnosus* GG (Lebeer et al. 2009), while Dols-Lafargue et al. (2008) reported that the β-glucan-containing capsules of *P. parvulus* and *Oenococcus oeni* enhanced their adhesion capacities on abiotic surface. Therefore, the role of EPS in biofilm formation could be affected by the chemical structure, relative quantity and charge, properties of the abiotic surface, and surrounding environment (Van Houdt and Michiels 2010).

Exopolysaccharides application in food industry

The industrial applications of microbial exopolysaccharides are a topic of growing interest that has been smartly reviewed by Zannini et al. (2016). In this contest, we will only summarize some potentiality and critical aspects of EPS-producing LAB in an industrial contest. The EPS produced by LAB are able to modify the rheological properties, texture, and "mouthfeel" of food products; thus, they would find application in the food industry as viscosifiers, stabilizers, emulsifiers, or gelling agents (De Vuyst and Degeest 1999; Looijesteijn et al. 1999; Patel et al. 2012; Zannini et al. 2016). The availability of LAB starter cultures which produce exopolysaccharides in situ during fermentation could be a suitable alternative for products whose polysaccharides addition requires the specification as food additives, which is a condition not much appreciated by consumer. Moreover, LAB are "generally recognized as safe" (GRAS) due to their long history of safe use in food production, and many of them have the QPS (qualified presumption of safety) status (Lahtinen et al. 2011). Further research on the use of cheaper substrates, optimal fermentation conditions, and development of mutant strains with high yield of EPS would be of fundamental importance. Indeed, the cost of production and the low amount of EPS produced by LAB, compared to the commercial value of microbial exopolysaccharides, are limiting factors for their industrial applications (Nwodo et al. 2012; Zannini et al. 2016). Currently, the highest production of microbial exopolysaccharides is attributed to *Xanthomonas campestris*, which produces 30–50 g/L of xanthan gum, an extracellular heteropolysaccharide used as a food additive and rheology modifier and whose industrial use is considered convenient. Although the EPS yield produced by LAB is much lower, the in situ applications in the manufacturing sector may be sustainable (Tsuda 2013). There is a wide range of bacteria EPS producing with interesting industrial applications, but only xanthan and gellan are authorized for the use as additives in the food products in the USA and Europe (Donot et al. 2012).

In this regard, several authors studied the effect of LAB exopolysaccharides on the rheological and sensorial properties in yogurt (Hassan et al. 2003; Doleyres et al. 2005; Folkenberg et al. 2006; Yang et al. 2014), the product of fermentation of milk led by starter cultures of *L. delbrueckii* ssp. *bulgaricus* and *S. thermophilus* in ratio 1:1. Both bacteria produce exopolysaccharide from 30 to 890 mg/L for *S. thermophilus* and from 60 to 150 mg/L for *L. delbrueckii* ssp. *bulgaricus* (Bouzar et al. 1997; Marshall and Rawson 1999). It has been found that exopolysaccharides contribute to improve the viscosity and texture of yogurt and they do not alter the flavor of the final product (Jolly et al. 2002; Badel et al. 2011). In a recent report, the in situ production of EPS from *Lactobacillus mucosae* improved the textural and rheological properties, without affecting the yogurt starter cultures (London et al. 2015).

Since some decades, several studies on the influence of microbial exopolysaccharides produced in situ during the fermentation of bread were performed. Arendt et al. (2007) suggested that exopolysaccharides produced by sourdough LAB could be a valid and cheaper alternative to replace the more expensive vegetal hydrocolloids. Production of dextran by *Weissella confusa* significantly increased the viscosity of the sourdoughs, providing mild acidic wheat bread with a greater volume and softness of the loaf (Katina et al. 2009). Oligosaccharides produced by *W. cibaria* and *L. reuteri* have been used in order to evaluate the influence of in situ EPS secretion in dough rheology and quality of gluten-free sorghum bread, resulting in an improved bread-making potentials (Galle et al. 2012). This is a promising application of bacterial EPS, because one of the main problems of gluten-free bakery products regards to the rheological properties that are less satisfactory than conventional products. Furthermore, the addition of sourdoughs fermented with starter cultures producing exopolysaccharides could increase the prebiotic amount in gluten-free breads (Schwab et al. 2008).

EPS production by wine LAB: ropy and non-ropy phenotype

Although EPS-producing LAB are potentially important microorganisms for industrial application (Badel et al. 2011; Zannini et al. 2016), in alcoholic beverages such as wine, EPS-producing LAB are sometimes responsible of an alteration known as "ropiness" or "oiliness," characterized by a viscous texture and oily feel and responsible of considerable economic loss (Gindreau et al. 2001). In most cases, the ropiness develops slowly and became evident weeks or months after bottling. The ropiness appearance in wines is mainly due to the presence of wine LAB such as *P. parvulus* (Dols-Lafargue and Lonvaud-Funel 2009) and *Pediococcus damnosus* (Lonvaud-Funel 1999; Gindreau et al. 2001) harboring a "ropy" phenotype.

The biological role of the ropy phenotype in wine LAB is probably associated to the ability to tolerate or overcome stress commonly encountered in wine (Spano and Massa 2006). For example, some ropy strains of *P. parvulus* exhibited a strong resistance to harsh conditions in wine including ethanol, pH, and SO_2 stress (Lonvaud-Funel and Joyeux 1988; Lonvaud-Funel 1999; Velasco et al. 2006; Dols-Lafargue et al. 2008; Coulon et al. 2012). Dols-Lafargue et al. (2008) showed that wild or recombinant oenological bacterial strains, harboring a functional *gtf* (glycosyltransferase) gene, were more resistant to several stresses occurring in wine not only in alcohol, but also pH, and SO_2. By contrast, Walling et al. (2005) reported that EPS produced by *P. damnosus* were unlinked to ethanol stress.

The use of lysozyme in winemaking process has been legalized in some countries in alternative to sulfur dioxide addition in order to inhibit native LAB population and to delay malolactic fermentation (Lerm et al. 2010). Interestingly, Coulon et al. (2012) found a *P. parvulus* strain from ropy wine, able to synthesize a β-glucan, which confers tolerance to lysozyme stress by shielding effect of EPS around the cell wall.

A well management of the wine fermentation process may make the ropiness appearance in wines quite rare, although LAB with ropy phenotype may be even isolated from non-ropy wine. The ability to synthesize EPS by wine LAB in non-ropy wine is sometimes common. For example, *O. oeni*, one of the best adapted LAB to resist the harsh wine conditions and the most utilized species for commercial malolactic fermentation (MLF) starter preparation (Capozzi et al. 2010; Maitre et al. 2014; Betteridge et al. 2015), is able to release EPS into the wine during spontaneous as well as during induced MLF (Dols-Lafargue et al. 2007; Dimopoulou et al. 2014). Several *O. oeni* strains able to produce EPS are isolated from non-ropy wine without altering this product in a medium term (Ciezack et al. 2010). The EPS produced by *O. oeni* vary, depending on the strain and media used, and this variability is probably due to distinct biosynthetic pathways that can even coexist in some *O. oeni* strains (Ciezack et al. 2010; Dimopoulou et al. 2016). The natural propensity of some *O. oeni* strains to form a polysaccharide capsule is connected to an improved survival during production and conservation processes (Dimopoulou et al. 2016).

In addition to *O. oeni*, several studies indicate that wine *L. plantarum* strains retain excellent potential and characteristics that would make it suitable as MLF starter in wine (Berbegal et al. 2016). This feature is even associated to the ability of *L. plantarum* to overcome food stresses (Fiocco et al. 2007; Fiocco et al. 2009; Capozzi et al. 2011). *L. plantarum* strains with ropy phenotype were recently identified in non-ropy wine during spontaneous MLF. Preliminary results suggest that, compared to "non-ropy" strains, the ropy phenotype of *L. plantarum* is associated to low pH tolerance.

Although further works needed to unreveal the mechanisms responsible for the stress tolerance observed, the external barrier made by capsular and/or ramified EPS may physically protect cell wall by lysozyme, SO_2, and/or ethanol stress in wine LAB able to produce EPS or harboring a ropy phenotype (Fig. 4).

Conclusions

The industrial application of EPS-producing LAB or EPS from LAB, ranges from food fermentation to prebiotic/probiotic

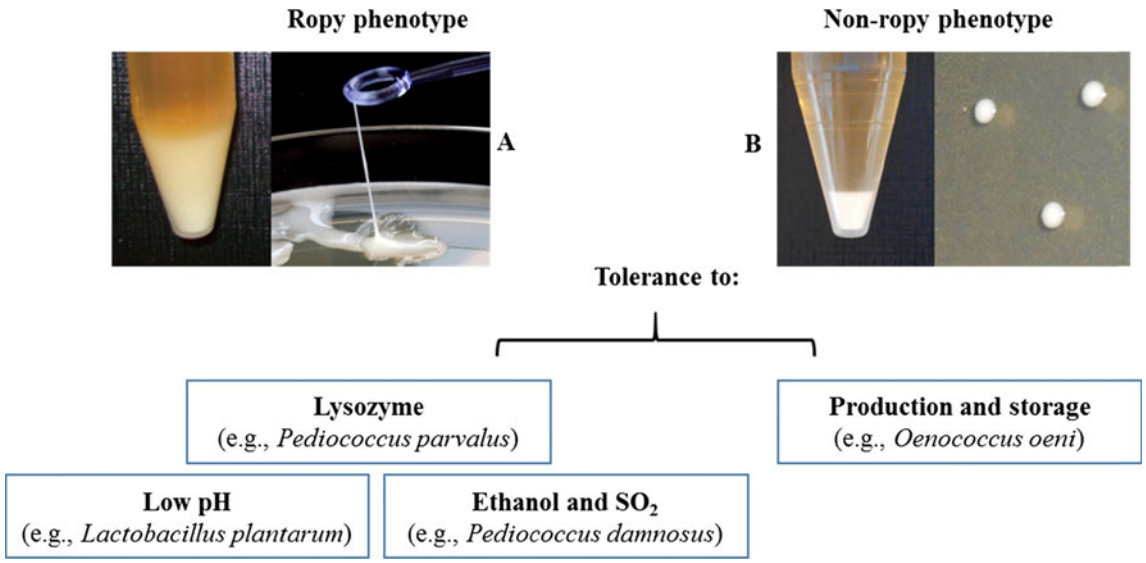

Fig. 4 EPS and stress tolerance. EPS-producing strains of lactic acid bacteria (LAB) isolated from induced or spontaneous malolactic fermentation (MLF) may tolerate stress commonly found in wine if they are able to display a "ropy phenotype" (**a**). The "non-ropy phenotype," but still EPS producer, has been recently associated to an improved tolerance to production and storage in the wine MLF starter *Oenococcus oeni* (**b**)

applications. For example, the use of EPS-producing LAB in the "in situ" fermentation process may improve the rheological and sensorial properties of fermented food. This aspect could be particularly advantageous for the food industries, as the microbial EPS could be used in substitution to the current hydrocolloids of plant origin. However, the low amount of EPS produced by LAB and the identification of high yields-producing strains with desirable properties linked to their use in food may be considered a critical step in such application (Zannini et al. 2016).

Prebiotics and/or probiotic properties are frequently attributed to LAB EPS or LAB-producing EPS. It has been claimed that some EPS reduce cholesterol levels, act as fermentable (prebiotic) substrates for intestinal microbiota, and modulate the immune response. However, contrasting finding are reported on the impact of microbial EPS on growth of probiotics or stimulation of intestinal epithelial cells as well as tolerance to human gastrointestinal tract transit. Therefore, the physicochemical characteristics of EPS must be the key parameters determining their biological and functional properties. The strains-dependent ability to use different EPS may be even responsible of the differences noted.

Finally, the EPS produced by LAB may be considered as an additional piece of the stress response machinery developed by LAB. This feature may be sometimes useful to improve robustness of microbial starters, taking in account that LAB displaying a ropy phenotype are sometimes associated with spoiled fermented beverages.

Compliance with ethical standards This article does not contain any studies with human participants or animals performed by any of the authors.

Conflict of interest The authors declare that they have no competing interests.

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