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REVIEW PAPER

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POTENTIAL OF BACTERIOCINS FROM LAB TO IMPROVE MICROBIAL QUALITY OF DRY-CURED AND FERMENTED MEAT PRODUCTS

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ABSTRACT

Meat and meat products are an important component of the daily diet. Nevertheless, they are perishable goods and are prone to microbial contamination, which leads to an increased risk to the health of consumers as well as economic losses in the meat industry. Fermentation has been used for thousands of years to preserve meat. As a result of extensive biochemical reactions occurring in meat during fermentation and ripening, the conditions inhibiting the growth of pathogenic and spoilage bacteria are formed. These changes are catalyzed by endogenous meat enzymes and exogenous enzymes derived from natural contaminating bacteria or starter cultures applied. In dry-cured and fermented meat products they are represented mainly by lactic acid bacteria (LAB) that produce a wide range of compounds, such as bacteriocins, directed against other microorganisms. The use of bactericidal peptides does not affect the sensory quality of foodstuffs, so that they attract attention as alternative means of preserving the stability and safety of dry-cured products.

Keywords: LAB, bacteriocins, dry-cured meat products

INTRODUCTION

Ensuring the high level of microbial quality of food is the main task of food producers. New preservation technologies, such as high hydrostatic pressure (HHP), and new packaging systems, like modified atmosphere packaging (MAP) and active packaging (AP) based on non-thermal inactivation of microorganisms, are widely used to increase food safety (Zhou et al., 2010). Scientists are also interested in natural antimicrobial compounds that can ensure the natural taste and fresh appearance of food, while eliminating pathogenic and spoilage microorganisms.

The quality of dry-cured and fermented meat products is the result of biochemical, microbiological, physical and sensorial changes occurring during their manufacture and subsequent ripening at specific conditions (temperature, relative humidity, use of smoke or not). These processes may take from a few weeks up to 24 months, depending on the product (Kołożyn-Krajewska and Dolatowski, 2009; Toldrá, 1998). When they are performed in appropriate technological conditions, they generally do not pose a health risk. This is due to the selection of suitable additives (salt, spices), and the presence of natural and/or inoculated microflora, resulting in a decrease in pH and water activity, thereby limiting the growth of undesirable pathogenic or spoilage microorganisms. Nevertheless, the possible contamination of raw meat used for the production and the ability of some microorganisms

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to adapt easily to unfavorable environmental conditions can pose a microbiological hazard (Casaburi et al., 2016). In particular, *Listeria monocytogenes* can survive the commercial dry sausage manufacturing process despite various obstacles, such as low pH, salt and nitrites, and can lead to foodborne illness (Fontana et al., 2015; Martin et al., 2011). About 10% of dry fermented sausages in Chile and France were observed to be contaminated by *L. monocytogenes* (Thévenot et al., 2005). As shown by Mataragas et al. (2015), depending on the fermentation temperature, pH and water activity are the crucial factors with regard to the growth and subsequent survival rate of the pathogens. However, if the initial contamination of raw materials is high, they are not sufficient for the complete pathogen elimination, particularly in the case of Gram-positive bacteria. Therefore, it is necessary to seek additional ways to control and/or eliminate undesirable microflora growth.

This paper presents an overview of the bacteriocins produced by lactic acid bacteria (LAB), thus emphasizing their importance as an effective tool to improve food safety, particularly in dry-cured meat products.

BACTERIOCINS PRODUCED BY LAB – GENERAL CHARACTERISTICS

Bacteriocins are produced by Gram-positive bacteria such as *Lactobacillus, Lactococcus, Leuconostoc, Pediococcus, Propionibacterium, Enterococcus* and Gram-negative bacteria, especially *Escherichia coli* (colicins), *Enterobacteriaceae* (microcins). Colicin was the first bacteriocin reported by Gratia (1925), who observed inhibition of *E. coli* φ by *E. coli V*. Meat borne strains of *Lactobacillus sakei* and *Lactobacillus curvatus* has been described as the main source of this antimicrobial compounds, referred as sakacines and curvacines, respectively (Barbosa et al., 2015; Casaburi et al., 2016; Fontana et al., 2015; Todorov et al., 2013).

Bacteriocins are ribosomally synthesized, extracellularly released bioactive peptides or peptide complexes, with bactericidal or bacteriostatic activity against species closely related to the bacteriocin producer. It has been found that more than 99% of bacteria can produce at least one bacteriocin. So far the number of identified bacteriocins has reached almost 230, and is not limited. However, only approximately 50% of these were well-characterized and sequenced at the protein or DNA levels. Some bacteriocins appear to inhibit Gram-positive food spoilage and food-poisoning bacteria, such as *Bacillus* spp., *Clostridium* spp., *Staphylococcus* spp., and *Listeria* spp. Bacteriocin producing LAB strains protect themselves against the action of its own bacteriocin by the expression of a specific immunity protein, which is generally encoded in the bacteriocin operon (Gwiazdowska and Trojanowska, 2005; Klaenhammer, 1993; Słońska and Klimuszko, 2010; Tagg et al., 1976; Yang et al., 2014).

Bacteriocins produced by LAB are categorized into four classes according to their biochemical and genetic properties: the lantibiotics; the small heat-stable non-lantibiotics; large, heat-labile proteins; and complex proteins whose activity depends on the presence of carbohydrate or lipid moieties (Jack et al., 1995; Klaenhammer, 1993).

Currently, there is a discussion in the literature with regard to the number of classes of bacteriocins. Woraprayote et al. (2016) pointed to two classes of bacteriocins: class I and class II with a, b, c and d subclasses. Recently, Alvarez-Sieiro et al. (2016) proposed three classes of bacteriocins: heat-stable class I with six subclasses, heat-stable class II with four subclasses and thermo-labile class III with two subclasses. In turn, Cotter et al. (2005) excluded bacteriolysins (non-bacteriocin lytic proteins) from the bacteriocin definition and proposed two classes of bacteriocins. The main classes and their characteristics are listed in Table 1.

LAB bacteriocins of class I and II are by far the most studied because they are both the most abundant ones and the most prominent candidates for industrial application (Nes et al., 1996). When analyzing the range of antimicrobial action, bacteriocins are divided into three groups: 1) those with a narrow range of antagonist activity, acting against strains within the same species as the producer, or species of the same genus; 2) those with a moderate extent of growth inhibition, possessing activity against other bacterial species, including the pathogenic ones as *L. monocytogenes*, *Staphylococcus aureus*, *Clostridium perfringens* or *Clostridium botulinum*; 3) those exhibiting a broad spectrum of inhibiting activity, including Gram-positive and Gram-negative bacteria, and even fungi (propionicin PLG-1) (Gwiazdowska and Trojanowska, 2005).

Table 1. Classification of bacteriocins produced by LAB (Garneau et al., 2002; Jack et al., 1995; Kaškonienė et al., 2017; Klaenhammer, 1993; Nes et al., 1996; Słońska and Klimuszko, 2010)

Class		Characteristics and subclasses
I.	Lantibiotics	Small heat-stable ribosomally generated peptides (<5 kDa) containing lanthionine and/or β-methyl lanthionine Type A. Linear, positively charged peptides with a molecular weight of 2,164–3,488 Da Type B. Globular peptides negatively charged or uncharged with molecular masses of 1,959–2,041 Da
II.	Non-lantibiotics	Low molecular weight (<10 kDa), relatively heat-stable peptides, generated only from unmodified amino acid, ribosomally synthesized as inactive tripeptides activated by post-translational cleavage of the N-terminal fragment Class IIa. pediocin-like, antilisterial bacteriocins that have a characteristic motif of amino acids Tyr-Gly-Asn-Gly-Val-Xaa-Cys near the N-terminal region Class IIb. two-peptide bacteriocins Class IIc. cyclic bacteriocins Class IId. linear non-pediocin-like one-peptide bacteriocins
III.	Large, heat-labile bacteriocins	Large (>30 kDa) proteins, mostly produced by *Lactobacillus* bacteria
IV.	Complex bacteriocins	Complex proteins whose activity depends on the presence of carbohydrate or lipid moieties

The impact of bacteriocins produced by *Lactobacillus* on sensitive cells causes a rapid reduction in their population, revealing their bactericidal or bacteriostatic properties. The first bacteriocin action mechanism is a disorder of the integrity of the cytoplasmic membrane of bacteria by creating specific channels – pores that would lead to the dissipation of the membrane potential and the passive efflux of small metabolites such as ions (e.g., potassium and phosphate), amino acids, nucleotides (ATP) and other cytoplasmic solutes. This would result in the termination of all biosynthetic processes (synthesis of macromolecules such as DNA, RNA, proteins, and polysaccharides), leading to cell death (Chen and Hoover, 2003; Servin et al., 2004; Sip et al., 2009). This mechanism of action has been found in *L. sakei* subsp. *sakei* 2a, bacteria isolated from Brazilian pork sausage (de Carvalho et al., 2010). Sakacin P − bacteriocin produced by this strain is capable of inhibiting the growth of *L. monocytogenes* by forming pores in the membrane of target cells, dissipating the proton motive force, reducing the intracellular ATP concentration with no detectable increase in extracellular ATP and mediating a concentration-dependent efflux of 5(6)-carboxyfluorescein from liposomes prepared from *L. monocytogenes* lipids. Concerning the secondary mode of action of bacteriocins, it has been reported that since the pores formed in the membrane are not sufficiently large to allow efflux of high molecular weight components, following membrane depolarization by pore formation, there should be an enhanced osmoinduced influx of water through the pores. The resulting increase in osmotic pressure will encourage subsequent cell lysis by osmotic shock (Cintas et al., 2001). Bactericidal activity of bacteriocins may be accompanied by lysis of sensitive cells induced by integrating them with anionic cell surface polymers like teichoic acid, lipoteichoic acid and teichuronic acid in the cell wall of sensitive bacteria, which results in the release, and therefore activation, of autolytic enzymes, which under normal conditions are electrostatically bound to these polymers (Cintas et al., 2001; Gwiazdowska and Trojanowska 2005).

Bacteriocin secreted by the LAB have a wide spectrum of activity against Gram-positive bacteria, but Gram-negative bacteria, which have an additional lipopolysaccharide outer membrane that impedes the penetration of antimicrobial agents, are generally not sensitive to LAB-bacteriocins. They are only inhibited by purified LAB-bacteriocins if the permeability barrier properties of their outer membrane are impaired by chemical agents (e.g., organic acids, EDTA and other chelating agents) or stressing environmental

conditions (e.g., pH, freezing, mild heating or high hydrostatic pressure) (Chen and Hoover, 2003; Cintas et al., 2001; O'Shea et al., 2013; Servin, 2004). Nisin, a bacteriocin produced by many strains of *Lactococcus lactis* subsp. *lactis* and by *L. lactis* BB24 isolated from Spanish-dry fermented sausages, has a broad spectrum of bactericidal activity towards a wide range of Gram-positive bacteria, including *S. aureus* and *L. monocytogenes*. To date, nisin is the most thoroughly studied and characterized LAB bacteriocin, it is commercially produced and is also approved by both the United States FDA and the WHO. This antimicrobial compound has been affirmed as GRAS (Generally Recognized as Safe) and approved for use as a food preservative (E234) in over 50 countries (Chen and Hoover, 2003; Cintas et al., 2001; Gwiazdowska and Trojanowska, 2005). Another commercially available bacteriocin is pediocin PA-1, marketed as Alta® 2341, which inhibits the growth of *L. monocytogenes* in meat products (Settanni and Corsetti, 2008).

The use of bacteriocin-producing LAB as natural antimicrobials agents for food preservation is gaining more and more interest among manufacturers, because it can replace or reduce the addition of chemical preservatives as well as the intensity of heat treatments. It also comes up to the expectations of consumers who are increasingly aware of the negative impact of synthetic preservatives and the advantages of their natural counterparts (Cleveland et al., 2001; Gálvez et al., 2007). In addition, LAB are regarded as safe bacteria with GRAS status (Słońska and Klimuszko, 2010) and bacteriocins of LAB are assumed to be degraded by the digestive proteases (Cleveland et al., 2001; Gálvez et al., 2007; Vandenbergh, 1993), which indicates their neutral effect on the gut microbiota.

THE USE OF BACTERIOCINS PRODUCED BY LAB IN THE MANUFACTURE OF DRY-CURED MEAT PRODUCTS

The quality and safety of dry-cured meats involves the creation of a hostile environment for undesirable microorganisms, but at the same time fosters the growth and metabolic activity of beneficial microflora (Casaburi et al., 2016).

The use of lactic acid bacteria (LAB) as starter cultures is a common practice in the manufacturing of fermented meats, due to their specific enzymatic profile, which impacts on the taste and aroma of meat products (Kołożyn-Krajewska and Dolatowski, 2009; Lücke, 2000). In addition, they are valuable because of the ability to produce antimicrobial compounds (Todorov et al., 2013). LAB strains isolated from dry-cured meat products exhibit antagonistic properties against many bacteria (Table 2).

The growth of LAB in meat products may cause interference with the growth and development of spoilage bacteria and pathogens via several mechanisms of action, including competition for nutrients and living place (adhesion) on the product or the production of a wide variety of substances inhibiting their growth, especially lactic acid and/or acetic acid, acetoin, diacetyl, hydrogen peroxide, and bacteriocins. The production of these antimicrobial substances seems to be a common phenotype among LAB, since numerous bacteriocins have been isolated (Chen and Hoover, 2003; Cintas et al., 2001; Gálvez et al., 2007; Kraszewska et al., 2005). Class IIa bacteriocins (Table 1) constitute the most dominant group of antimicrobial peptides produced by LAB (Barbosa et al., 2015; Drider et al., 2006; Nes et al., 1996). All the class IIa bacteriocins are described as being active against *Listeria*, while only part of the bacteriocins from other classes are antilisterial. Moreover, several class IIa bacteriocins display spectra of activity against other spoilage and foodborne pathogenic microorganisms, such as spoilage LAB, *Brochotrix* spp., *Clostridium* spp., *Bacillus* spp. and *Staphylococcus* spp (Ennahar et al., 2000).

Under certain circumstances bacteriocins with narrower inhibitory spectra may be more desirable than those with broader activity, since they do not eliminate the preferred starter cultures, but are effective in eliminating *Listeria* strains (Chen and Hoover, 2003). For example, sakacin P, which has modest activity against LAB, is nearly as effective against *Listeria* as pediocin PA-1 (a broad-spectrum lactic acid bacteria bacteriocin that shows a particularly strong antilisterial activity), and might find application in LAB fermentation products that are prone to contamination by *Listeria* (Eijsink et al., 1998). Increased antibacterial activity of the non-lanthionine-containing bacteriocins at low pH values, which is typical for fermentation processes, can be explained by the following factors:

Table 2. The extent of antimicrobial activity of selected strains of LAB isolated from dry-cured and fermented meat products in the years 2013–2016, based on data available in the literature

Producer organism/strain	Range of activity	Reference
L. sakei/LS1, LS2, LS3, LS4, LS5, LS6	Active against: *Enterobacteriaceae* (LS1-LS6) *L. monocytogenes* and *Listeria innocua* (LS5)	Amadoro et al., 2015
L. sakei/MBSa1	Active against: *L. monocytogenes* Inactive against: *Salmonella*, *E. coli*, *Enterobacter*, *Bacillus cereus*, *S. aureus*	Barbosa et al., 2014
L. curvatus/MBSa2, MBSa3	Active against: *Listeria ivanovii*, *L. innocua*, *L. monocytogenes* Inactive against: *B. cereus*, *S. aureus*, *Listeria welshimeri* USP, *Listeria seeligeri* USP, *E. coli*, *Enterobacter aerogenes*, *Salmonella typhimurium*, *Enterococcus faecalis*, *L. lactis*, *Pediococcus pentosaceus*	Barbosa et al., 2015
L. lactis subsp. *lactis* 69	Active against: spoilage halotolerant bacteria, *L. monocytogenes*, *S. aureus*	Biscola et al., 2013 Biscola et al., 2014
L. curvatus/54M16	Active against: *L. monocytogenes*, *B. cereus*, *Brochotrix thermosphacta* Inactive against: tested Gram-negative bacteria, some strains of *Lactobacillus*, strains of *S. aureus*	Casaburi et al., 2016
Lactobacillus plantarum/ESB 202	Active against: *L. monocytogenes*, *L. innocua*	Engelhardt et al., 2015
L. sakei/ST22Ch, ST153Ch, ST154Ch	Active against: *Enterococcus* spp., *Listeria* spp., *E. coli*, *Klebsiella* spp., *Pseudomonas* spp.; *Staphylococcus* spp., *Streptococcus* spp.	Todorov et al., 2013
L. plantarum/BM-1	Active against: *E. faecalis* AS 1.2984, *L. monocytogenes* ATCC 54003, *Lactobacillus pentosus* ATCC 8041, *L. plantarum* F1, *S. aureus* ATCC 6535, *E. coli* CDC 85933, *Shigella dysenteriae* CMCC 51105 and *Staphylococcus enteritidis* CMCC 50041	Zhang et al., 2013

(1) aggregation of the hydrophilic peptides is less likely to happen, and therefore more particles would be available for interaction with sensitive cells; (2) more molecules are available for bactericidal action, since fewer molecules remain bound to the wall; (3) hydrophilic bacteriocins may have enhanced ability to pass through the hydrophilic regions of the cell wall of susceptible bacteria; (4) at higher pH values interaction of the non-lanthionine-containing bacteriocins with putative membrane "receptors" appeared to be inhibited (Jack et al., 1995).

Bacteriocin produced by LAB have the potential to be used in fermented foods for the control of microbial populations in order to extend product shelf-life and safety. Bacteriocin-producing LAB can also improve the sensory characteristics of fermented meat products. Bacteriocin-producing *Lactobacillus*, such as *L. sakei* C2 (Gao et al., 2014) or *L. curvatus* 54M16 (Casaburi et al., 2016), has good potential to be used as a starter culture in fermented sausage production, positively affecting taste and overall acceptability. Bacteriocin-producing LAB can also be applied to control adventitious microbiological contamination in fermented meats i.e., non-starter microflora, which can proliferate, leading to unpleasant flavours and the production of noxious compounds (O'Sullivan et al., 2002).

Bacteriocins may be introduced into a food product via *in situ* production in three major approaches including (I) direct inoculation of bacterial starter or adjunct strains in fermented foods, (II) direct application of purified or semi-purified bacteriocins as food preservatives or as an ingredient based on a fermentate of a bacteriocin-producing strain and (III) the use of purified/partially purified bacteriocins in the form of packaging. However, the technological conditions

or components of the food matrix may interfere with or inhibit the action of bacteriocins, which is why assessment of their microbial action requires thorough testing in food systems. In addition, preservation of food via *in situ* production of bacteriocins by bacterial starter requires a better understanding of the relationship between the growth of the producing organism and the production of bacteriocins in particular foods (O'Shea et al., 2013). As an example, production of bacteriocins MBSa2 and MBSa3 by *L. curvatus* begins in the early exponential growth phase (Barbosa et al., 2015). On the other hand, bacteriocins ST22Ch, ST153Ch and ST154Ch produced by *L. sakei* strains from *Salpicao* (a traditional pork product from northwest Portugal) were secreted at higher levels at the stationary phase of fermentation in the presence of 2% (w/v) D-glucose (Todorov et al., 2013).

Fermentation is an important step in the production of fermented meats, during which the greatest changes occur in the raw material, which may affect the activity of the bacteriocins produced by LAB. Engelhardt et al. (2015) confirmed the antilisterial activity of *L. plantarum* ESB 202 under conditions of stress induced by varying the pH and salt concentration (pH 3.5; pH 8.5; 7.5% NaCl). On the other hand, Casaburi et al. (2016) studied *in vitro* the technological properties of the strain *L. curvatus* 54M16, in order to determine its suitability for use as a starter culture for fermented sausages. As the most preferable conditions for the production of bacteriocins, the authors indicated pH 4.5 and the presence of 4% NaCl. Bacteriocins ST22Ch, ST153Ch and ST154Ch produced by *L. sakei* strains isolated from *Salpicao* exhibit thermal stability and remained active in the pH range from 2.0 to 10.0 (Todorov et al., 2013). Thus the bacteriocin-producing meat borne *L. sakei* exhibit great potential to be used as bioprotective cultures, providing an additional hurdle to enhance the control of *L. monocytogenes* in meat products, because the species' metabolism is particularly well adapted to a meat medium (Fontana et al., 2015; Todorov et al., 2013). A strain of *L. lactis* subsp. *lactis* 69 isolated from charqui (a fermented, salted and sun-dried meat product) was able to form a heat-stable bacteriocin. Its activity was not affected by the pH (2.0–10.0), chemical agents: sodium dodecyl sulfate, ethylenediamine tetraacetic acid, tween 80, and urea (1% w/v). The isolate was able to survive and produce the bacteriocins in a culture medium containing up to 20% (w/v) NaCl (Biscola et al., 2013). Understanding the impact of environmental factors associated with the induction of bacteriocin is essential for effective use of the commercial production of bacteriocins by the LAB.

CONCLUSION

LAB strains producing bacteriocins are gaining importance in the production of dry-cured and fermented meat products due to their activity against undesirable microorganisms. Numerous studies have shown that LAB can be used to reduce the population of unfavorable microflora in dry-cured meat products and are likely to have a commercial application in food preservation as natural food preservatives. Due to their antilisteria activity, bacteriocinogenic strains of LAB and their bacteriocins may be beneficial as preservation agents in dry-cured and fermented products, and can be used as technological alternatives to chemical preservatives, meeting the increased demand for foods with few or even no chemical additives.

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