Chapter 19
Bacteriocins: Natural Weapons for Control of Food Pathogens

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Abstract Research on antimicrobial peptides is continuously growing because of the possibilities of applications they offer in different domains including food safety, human medicine, and plant biocontrol (phytosanitary).

The present chapter is aiming to shed lights on diversity, function and structure of ribosomally synthesized antimicrobial peptides from Gram positive bacteria usually referred to as bacteriocins. In bacterial systems, competition is often driven by the production of bacteriocins; narrow spectrum proteinaceous toxins that serve to kill closely related species providing the producer better access to limited resources. Despite high levels of bacteriocin diversity, these proteins share many general characteristics. They are generally high molecular weight protein antibiotics that kill

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closely related strains or species. The bacteriocin gains entry into the target cell by recognizing specific cell surface receptors and then kills the cell by forming ion-permeable channels in the cytoplasmic membrane, by nonspecific degradation of cellular DNA, by inhibition of protein synthesis through the specific cleavage of 16s rRNA, or by cell lysis. In this chapter, the limits and performances of production will be presented. Further clear evidences on their aptitudes to master growth of microbes will be discussed as well as the main achievements and perspectives of their applications in food, environment and medical domains.

1 Lactic Acid Bacteria Bacteriocins: Brief Overview

This chapter is focused on the role of lactic acid bacteria (LAB) bacteriocins in the control of food pathogens, which constitute a serious public concern worldwide. LAB-bacteriocins are produced by strains belonging to the genera of *Lactococcus, Lactobacillus, Leuconostoc, Enterococcus, Pediococcus, Carnobacterium* and *Streptococcus*. In 1976, Tagg and coworkers have defined bacteriocins as proteinaceous compounds with inhibition activity against related bacteria. The continuing research on LAB-bacteriocins has shed light on their capacities of antagonism. Remarkably, LAB-bacteriocins were reported to be active against Gram negative bacteria such as *Campylobacter jejuni* (Cole et al. 2006; Stern et al. 2006; Nazef et al. 2008; Messaoudi et al. 2011). LAB bacteriocins should be defined as naturally and ribosomally-synthesized antimicrobial peptides displaying a large antagonism spectrum. The LAB bacteriocins are documented in an online database, named BACTIBASE (Hammami et al. 2010) that is available at http://bactibase.pfba-lab-tun.org. Overall, BACTIBASE provides physicochemical, structural, microbiological, and taxonomic informations about bacteriocins produced by both Gram-positive and Gram-negative bacteria.

LAB bacteriocins have been subjected to different classification schemes due to their biochemical and genetic diversities and their bioactivities. The first classification scheme was provided by Klaenhammer (1993). As new bacteriocin members were identified and being characterized, this classification was amended at different instances (Tagg et al. 1976; Cotter et al. 2005). In 2001, Cintas and collaborators have proposed a classification scheme including four main classes, among which: Class I lantibiotics are post-translationally modified, heat-stable, low molecular mass peptides (<5 kDa) characterized by the presence of unusual amino acids, such as lanthionine or β-methyllanthionine. Class II bacteriocins are small heat-stable, unmodified peptides (<10 kDa) and are subdivided into three subclasses, namely, class IIa (pediocin-like), class IIb (two-peptide), and IIc (other [i.e., non-pediocin-like], one-peptide bacteriocins). Class III bacteriocins are large (>30 kDa) and heat-labile proteins. Lastly, class IV bacteriocins include cyclic peptides with covalently linked N- and C-termini. Recently, an updated classification was reported by Rea et al. (2011). This novel classification is briefly described below.

1.1 Class Ia (Lantibiotics)

Bacteriocins of this class are <5 kDa and 28 amino acids in length. Lantibiotics undergo post-translational modifications leading to unusual aminoacids such as lanthionine (Lan), and/or B-methyllanthioonine (meLan) and dehydroalanine (Dha). The linear or type A lantibiotics comprise bacteriocins such as nisin, subtilin or epidermin. The type A lantibiotics are known to be elongated, cationic and amphiphilic and could contain until 34 amino acids in length. They act by pore forming leading to the death of the target cell upon a cascade of damages like the dissipation of membrane potential and efflux of small molecules. The globular lantibiotics or type B lantibiotics such as merscaidin, mutacin and lacticin 481 are structurally more compact, they are small peptides less than 19 aminoacids. Their mode of action is based on the inhibition of lipid II, which is the key precursor of peptidoglycan in the cell wall. Remarkably, nisin, which is a linear lantibiotic (type A lantibiotic) could act by pore forming or lipid II inhibition (Breukink et al. 1999). As this classification has become misleading, the novel classification of lantibiotics contains four subclasses (subclass I, subclass II, subclass III and subclass IV).

1.2 Class Ib (Labyrinthopeptins)

Recently identified (Meindl et al. 2010), these peptide are characterized by their "labyrinthine" structure and the presence of "labionin", which is a carbocyclic, post-translationally modified amino acid.

1.3 Class Ic (Sactibiotics)

Bacteriocins of this class are subtilosin A and Thuricin CD produced by *Bacillus subtilis* and *Bacillus thuringiensis* 6431, respectively. Subtilosin A is a circular peptide, post-translationally modified with cross-linkages between the sulphur and cystein residues. Thuracidin CD is a dipeptide (Trnα, Trnβ) with intramolecular crosslinkages between three cysteine residues in each peptide and the α-carbons.

1.4 Class II: Unmodified Bacteriocins

We find in this class peptides less than 10 kDa with linear or cyclic structures. This class has been committed to intensive investigation and despite its heterogeneous traits, different classifications were suggested. Currently, four subclasses (Class IIa, Class IIb, Class IIc and Class IVd) are proposed and they are briefly described below.

1.4.1 Class IIa (Pediocin-Like Bacteriocins)

Bacteriocins of this subclass are certainly of major interest because of their potential as food preservatives but also as alternatives to current antibiotics. Class IIa bacteriocins display activity against *Listeria* strains and even against other pathogens such as *Clostridium* spp. There are more than 30 bacteriocins in this repertoire with specificities. Class IIa bacteriocins are ranking from 37 to 57 amino acids in length and all of them share a YGNGV box at the N-terminal moitiey. Class IIa bacteriocins are also named cystibiotics because they contain at least two cysteines in the C-terminal part leading to disulphide bond formation. It happens that models of class IIa bacteriocins such as divercin V41 could harbor four cystein residues, in which two residues are located in the C-terminal part and the other two in the N-terminal parts, respectively.

1.4.2 Class IIb (Two Peptide Bacteriocins)

Class IIb bacteriocins consist of two distinct peptides, which are necessary to obtain high antimicrobial activity. The antimicrobial activity requires the presence of both peptides at equal amounts. There are at least 16 bacteriocins nowadays known as class IIb bacteriocins. Studies of the mode of action of class IIb bacteriocins have revealed a leakage in the membrane of the sensitive target bacteria. However, specificities in the mode of action, mainly in the movement of the ions across the membrane, have been reported for plantaricin E/F and plantaricin J/K. All class IIb bacteriocins comprise between 30 and 50 aminoacids, they are cationic, amphiphatic, membrane active and synthesized as pre-peptide cut of and vehiculed outcell by the dedicated ABC transporter. It was also demonstrated that the synthesis of class IIb bacteriocins is regulated in some bacteria by three component regulatory systems.

1.4.3 Class IIc (Circular Bacteriocins)

Structurally, the circular bacteriocins are characterized by the head –to-tail cyclization of their backbone. They are produced by LAB as well as by non-LAB strains. The best characterized are Enterocin AS-48, grassericin, carnocyclin A and lactocyclicin A. They are known to have potent antimicrobial activity, which is thought to be attributed to their circular structure. In this sense, it has been established that the enzymatic hydrolysis of Enterocin AS-48 by thermolysin releases a linear component lacking bioactivity despite its helical structure. Overall, circular bacteriocins (class IIc bacteriocins) display broad spectra including activity against food spoilage pathogens. Enterocin AS-48 and lactocyclicin Q are also active against Gram negative bacteria.

1.4.4 Class IId (Linear and Non-pediocin Like Bacteriocins)

Class IId bacteriocins have no significant similarities to the other class II bacteriocins. Class IId bacteriocins are synthesized by the *sec*-independent double glycine motif and then are transported by ABC transporters. Some of the class IId bacteriocins are synthesized without an N-terminal leader sequence or signal peptide. For this reason, they are named "leaderless bacteriocins".

Enterocin L50, produced by *Enterococcus faecium* L50, consists of two peptides named Enterocin L50A (EntL50A) and Enterocin L50B (EntL50B), which are highly similar (70%).

1.5 Bacteriolysins

They were formerly denominated class III bacteriocins. Overall, they are large, heat labile proteins. In this class, we can find helveticin J from *Lactobacillus helveticus* J and enterolysin from *Enterococcus faecalis*. It should be noted that other class IId bacteriocins from non LAB exist, such as zoocin A, linocin and millericin.

2 Bacteriocins and Control of Food Pathogens

In the last years, bacteriocins have been considered very promising agents for fighting foodborne pathogens (García et al. 2010; Mills et al. 2011). Even though bacteriocins are produced by either Gram-positive or Gram-negative bacteria, the most accepted peptides for food preservation or even clinical applications are those produced by Gram-positive bacteria, especially lactic acid bacteria (LAB). Those bacteriocins are produced by a bacterial group which is generally present in different foodstuffs and even intensively used in foods, moreover, LAB are generally recognized as safe (GRAS status) (Carr et al. 2002; Pedersen et al. 2005) and their Qualified Presumption of Safety (QPS) has been proposed by the EFSA (2007). These peptides were described in detail and many applications have been proposed (Acuña et al. 2010; De Vuyst and Leroy 2007). Although a number of peptides were described in the literature so far, nisin and pediocin PA-1 are better positioned than the other peptides as food preservatives.

This book chapter focuses on the role ascribed to the LAB bacteriocins in the control of foodborne pathogens able to grow in different food matrices. The main bacterial pathogens of concern in food industry are those able to survive and multiply in the raw materials, such as *Listeria monocytogenes*, *Staphylococcus aureus*, *Escherichia coli, Salmonella* spp., *Bacilli* and *Clostridia*.

2.1 *Listeria monocytogenes*

Through the last two decades, many studies have been carried out to search for bacteriocin producing strains able to inhibit *Listeria monocytogenes.* The application of bacteriocins or bacteriocin producing starter cultures in food can provide an additional hurdle to *L. monocytogenes* and can possibly ensure the safety of food products in the future. Among all bacteriocins tested, nisin (in the commercial form Nisaplin) has been tested extensively in foods. In the dairy industry, nisin has found many applications, especially in processed cheeses and cheese products (e.g., hard cheese, soft white cheeses, slices, spreads, sauces, dips) to prevent proliferation of *L. monocytogenes* (Davies and Delves-Broughton 1999; Thomas and Delves-Broughton 2001). In skim milk, whey, or simulated milk ultrafiltrate media, the use of a combination of nisin and pulsed electric fields (PEFs) resulted in a significant inhibition of *L. monocytogenes* (Calderón-Miranda et al. 1999).

Addition of nisin to pasteurized liquid whole egg reduced the viable counts of *L. monocytogenes* and increased the shelf-life of the refrigerated product (Delves-Broughton et al. 1992; Knight et al. 1999; Schuman and Sheldon 2003). Both nisin and pediocin PA-1/Ach acted synergistically with heat treatments against *L. monocytogenes* (Knight et al. 1999; Muriana 1996) in liquid whole egg and in egg white during pasteurization (Boziaris et al. 1998).

Although the application of nisin in meats is limited due to several factors such as its poor solubility, interaction with phospholipids, and inactivation by glutathione (Montville et al. 1995; Rayman et al. 1983; Rose et al. 1999; Stergiou et al. 2006), addition of nisin has shown to extend the lag phase of *L. monocytogenes* inoculated into minced buffalo meat (Pawar et al. 2000). In meat marketing, prime cuts are often vacuum-packaged in order to extend their shelf-life during distribution before preparation of retail cuts. As a result of these practices, meat can become contaminated with *L. monocytogenes* and spoilage bacteria that may shorten the shelf-life of retail meats. Under modified atmosphere packaging, nisin was able to completely inhibit the growth of *L. monocytogenes* in pork (Fang and Lin 1994a, b). In sausages and other fermented meat products, addition of nisin induced a significant inhibition of *L. monocytogenes*. The lower pH of sausages compared to fresh meats may increase the solubility of nisin, and probably the antimicrobial activity as well. Addition of nisin alone was effective in inhibiting *L. monocytogenes* in sucuk, a Turkish fermented sausage (Hampikyan and Ugur 2007).

The effectiveness of nisin in sausages increases in combination with other antimicrobials. The combination of nisin and a grape seed extract showed an enhanced antibacterial activity in refrigerated turkey frankfurters with reduction of *L. monocytogenes* populations to undetectable levels (Sivarooban et al. 2007). In ham and/or bologna sausages, a mixture of nisin-lysozyme-EDTA inhibited the growth of *Leuconostoc mesenteroides* and *L. monocytogenes* (Gill and Holley 2000a, b). Activity of nisin against *L. monocytogenes* in minced beef was potentiated with thyme essential oil, decreasing the impact of the oil on the meat organoleptic properties (Solomakos et al. 2008).

Although effective, the addition of bacteriocin as food ingredients may be limited by the degradation of the active compound by different bacterial proteases especially in fermented foods or by the interaction of the bacteriocin with several food compounds such as fat. The use of bacteriocin-producing starter or adjunct cultures in foods represents therefore an efficient alternative to overcome these problems. It may also significantly reduce costs associated with nisin production, purification and processing. Nisin-producing strains have been reported to inhibit *L. monocytogenes* in several types of cheeses, such as cheddar cheese (Benech et al. 2003), cottage cheese (Benkerroum and Sandine 1988) or Camembert (Maisnier-Patin et al. 1992; Sulzer and Busse 1991). In Manchego cheese made from raw ewe's milk, *Lactococcus lactis* subsp. *lactis* ESI 515 reduced viable counts of *L. innocua* by 4.08 log units after 60 days of ripening, and the produced nisin was detected in cheese through the ripening period.

In vegetables, *L. monocytogenes* can proliferate rapidly and several listeriosis outbreaks have been associated with fresh produce, such as raw celery, tomatoes, and lettuce (Beuchat 1996). Leverentz et al. (2003) showed that nisin reduced *L. monocytogenes* populations on honeydew melon slices and apple slices. The listericidal effect was enhanced by application of nisin in combination with a phage mixture (Leverentz et al. 2003). Exposure of *L. monocytogenes* Scott A to nisin in tofu resulted in an initial reduction of viable counts followed by regrowth of survivors to nisin during further incubation (Schillinger et al. 2001). Nisin was tested alone or in combination with sodium lactate, potassium sorbate, phytic acid, and citric acid as possible sanitizer treatments for reducing the population of *L. monocytogenes* on cabbage, broccoli, and mung bean sprouts (Bari et al. 2005). After a 1-min wash, a significant reduction of *L. monocytogenes* was observed on cabbage and broccoli, with nisin-phytic acid combination (Bari et al. 2005).

Lacticin 3147 produced by *L. lactis* subsp. *lactis* DPC3147 is another bacteriocin with a high potential for application in the preservation of foods (Ross et al. 1999). Lacticin 3147 powder was shown to rapidly inactivate *L. monocytogenes* Scott A in an infant milk formulation (Morgan et al. 1999). In natural yogurt and in cottage cheese supplemented with lacticin 3147 powder, viable cell numbers of *L. monocytogenes* were reduced by 99 and by 85%, respectively, within 2 h (Morgan et al. 2001). An increased bactericidal effect was reported for the combined treatment of lacticin 3147 concentrates and HHP against *L. monocytogenes* in milk and whey (Morgan et al. 2000). The lactocin 705 is another bacteriocin produced by *Lactobacillus casei* CRL 705 (Vignolo et al. 1996) which was highly effective against *L. monocytogenes* in beef slurry (Vignolo et al. 1998) and also in a meat system when used in combination with enterocin CRL35 produced by *E. faecium* CRL35 (Farías et al. 1994) and nisin (Vignolo et al. 2000).

Application of enterococcal bacteriocins on foods to inhibit the growth of *L. monocytogenes* has been the focus of many investigations (reviewed by Foulquié Moreno et al. 2006; Giraffa 1995). An early report indicated that bacteriocin from *E. faecium* DPC1146 had a rapid bactericidal effect on *L. monocytogenes* in milk (Parente and Hill 1992). A decrease of viable *L. monocytogenes* was also reported in enterocin-added yogurt and in Saint-Paulin cheese (Lauková et al. 2001).

However, after 6 weeks and at the end of the experiment, the difference in surviving listeria was only 1 or 0.7 log units compared to the control cheese (Lauková et al. 2001). In "bryndza" (a traditional Slovak dairy product from sheep milk), the addition of enterocin CCM 4231 has reduced the levels of *L. monocytogenes* Li1 during a 7-day ripening period (Lauková and Czikková 2001). In contrast, when concentrated enterocin CRL35 was added to goat cheese, the population of *L. monocytogenes* diminished by 9 log units by the end of the ripening period without affecting the cheese quality (Farías et al. 1999). Similarly, cultured broths obtained from raw ewe's milk containing enterocin 4 (enterocin AS-48) significantly reduced viable counts of *L. monocytogenes* (Rodríguez et al. 1997), whilst in soy milk the enterocin CCM 4231 has completely eliminated *L. monocytogenes*. The enterococcal *faecal* CCM4231 was able to grow and produce enterocin in soy milk (Lauková and Czikková 1999). In fermented meat, enterocins can inhibit *Listeria*, as shown for enterocin CCM 4231 when incorporated in dry fermented Hornád salami (Lauková et al. 1999c), and enterocins A and B in espetect (traditional Spanish sausages; Aymerich et al. 2000). In a meat sausage model system, added enterocin AS-48 inhibited the growth of *L. monocytogenes* (Ananou et al. 2005a, b).

Bacteriocinogenic enterococci could be used as cocultures for preservation of meat products (e.g., fermented sausages and sliced vacuum-packed cooked meat products) and for the control of emergent pathogenic and spoilage bacteria (Foulquié Moreno et al. 2006; Hugas et al. 2003). When used as starter cultures in sausage fermentation, the bacteriocinogenic strains *E. faecium* CCM 4231 and *E. faecium* RZS C13 were partially competitive and strongly inhibited the growth of *Listeria* spp. (Callewaert et al. 2000). *E. faecium* CTC492 (producer of enterocins A and B) partially prevented ropiness due to *Lactobacillus sakei* CTC746 in sliced vacuum-packaged cooked ham (Aymerich et al. 2002). The strain *E. casseliflavus* IM 416K1 (producer of enterocin 416 K1) was able to eliminate *L. monocytogenes* in artificially inoculated "cacciatore" Italian sausages (Sabia et al. 2003). The cyclic bacteriocin enterocin AS-48 produced *in situ* by an *E. faecalis* strain or a food-grade *E. faecium* transconjugant controlled the growth of *L. monocytogenes* in a meat model system (Ananou et al. 2005a, b).

On the other hand, a limited number of studies have focused on the application of pediocin-producing strains in dairy foods, given the poor adaptation of pediococci to dairy substrates. Early experiments indicated that inhibition of *L. monocytogenes* in milk required a high cell concentration of pediococci (Raccach and Geshell 1993). For this reason, genetically engineered pediocin-producing LAB were developed, such as *L. lactis* subsp. *lactis* or the yogurt starter culture *Streptococcus thermophilus* (Coderre and Somkuti 1999; Somkuti and Steinberg 2003). In cheddar cheese, the pediocin PA-1 producer *L. lactis* subsp. *lactis* MM217 reduced the counts of inoculated *L. monocytogenes* from 10^6 to 10^2 CFU/g within 1 week of ripening, and then to about 10 CFU/g within 3 months (Buyong et al. 1998). It was concluded that pediocin-producing starter cultures have significant potential for protecting cheese against *L. monocytogenes* (Buyong et al. 1998). In a more recent study, the pediocin PA-1-producing derivatives *L. lactis* CL1 and *L. lactis* CL2 also reduced the counts of *L. monocytogenes* during cheese ripening (Rodríguez et al. 2005).

Similarly, heterologous production of pediocin PA-1/AcH in nisin-producing and non nisin-producing *L. lactis* strains previously selected as starters because of their technological properties for cheese making reduced viable counts of *L. monocytogenes* in cheese below 50 or 25 CFU/g at the end of the ripening period (Reviriego et al. 2007).

Pediocin production has also been reported in non-pediococcal LAB from dairy environments. Spraying with a cell suspension of the pediocin AcH producer strain *Lactobacillus plantarum* WHE92 on the surface of Muenster cheese was reported to prevent the growth of *L. monocytogenes* (Ennahar et al. 1998). Because *L. plantarum* WHE 92 exists naturally in Muenster cheese, it did not adversely affect the ripening process (Ennahar et al. 1998). On red smear cheese, an almost complete inhibition of *L. monocytogenes* by pediocin-producing *L. plantarum* was also reported (Loessner et al. 2003). However, pediocin-resistant listeria were readily detected, they were able to proliferate in the cheese, regardless of the produced bacteriocin. It was concluded that the continuous use of pediocin AcH does not appear to be suitable as a primary means of food preservation (Loessner et al. 2003).

Besides the previously mentioned bacteriocins, there are other bacteriocins which have been shown to be very effective against listeriae. Among those bacteriocins, we can mention propionicin PLG-1 (produced by *Propionibacterium thoenii* P127) (Lyon and Glatz 1993) which was shown to kill or inhibit several psychrotrophic spoilage or pathogenic bacteria including *L. monocytogenes, Pseudomonas fluorescens, Vibrio parahaemolyticus, Yersinia enterocolitica*, and *Corynebacterium* sp., suggesting its potential use as an antibacterial food preservative (Lyon et al. 1993). The bacteriocin-producer strain *Streptococcus salivarius* subsp. *thermophilus* B was tested as a thermophilic starter in yogurt to control *L. monocytogenes.* Use of the Bac+ starter was reported to extend the product shelf-life by 5 days (Benkerroum et al. 2002).

2.2 Escherichia coli and Salmonella spp.

Escherichia coli and *Salmonella enterica* are of major concern in a wide variety of foods that have not undergone a germ reducing process. Enteric bacteria are especially tolerant towards adverse environmental conditions such as low pH, high salt concentrations (Small et al. 1994; Cheville et al. 1996; Brown et al. 1997) and have been shown to survive during storage in acidic (or low pH) foods or products with high concentrations of salt or organic acids (Presser et al. 1998; Glass et al. 1992; Leyer et al. 1995; Reitsma and Henning 1996).

Several reports suggest that bacteriocins of LAB may contribute to the inactivation of Gram-negative microorganisms in foods if these are applied in combination with chelating agents (Shefet et al. 1995; Scannell et al. 1997). The architecture of the outer membrane (OM) of Gram-negative organisms prevents penetration of the bacteriocins to their target cells, the cytoplasmic membrane, and therefore confers a high degree of resistance (Stevens et al. 1991; Schved et al. 1994). Chelating agents such as EDTA as well as the application of sublethal stress such as heating or freezing

were shown to disrupt the permeability barrier of the LPS leading to an increased sensitivity of Gram-negative bacteria towards LAB bacteriocins (Stevens et al. 1991; Kalchayanand et al. 1992; Cutter and Siragusa 1995; Murdock et al. 2007).

Nisin was proposed as a hurdle in association with chelating agents for controlling *Salmonella* and *E. coli*. The first report using this approach conclusively showed that at least 20 *Salmonella* serovars were inhibited with simultaneous treatment of 50 µg/ml nisin and 20 mM EDTA. In fact, the population was reduced by up to 5.3 log CFU units after an hour of treatment. Neither EDTA nor nisin alone were able to inhibit the growth of *Salmonella* (Stevens et al. 1991). Later, Cutter and Siragusa (1995) showed a significant inhibition effect by combining 50 µg/ml nisin with different chelators such as 500 mM lactate, 100 mM citrate, 50 mM EDTA or 1% (w/v) sodium hexametaphosphate in buffer. *Salmonella typhimurium* population was reduced up to 5.5 log CFU units. On the other hand, the combination of 1 µM nisin (~3.35 µg/ml) with 0.5–5 mM trisodium phosphate was successfully used in controlling *S. enteritidis*. Cell counts were reduced by 6 log CFU units after only 30 min of treatment (Carneiro de Melo et al. 1998). The main flaw of these reports though, is that experiments were performed under cell starvation conditions, which seem to constitute a different model from food products and hence the conclusions may not be accurate. Cutter and Siragusa (1995) only got 0.4-log units reduction of *Salmonella* upon nisin-lactate treatment when experiments were carried out in beef instead of buffer. In the same trend, Carneiro de Melo et al. (1998) only found over 1 log unit reduction when nisin–trisodium phosphate was applied in chicken skins instead of buffer. Furthermore, although Branen and Davidson (2004) working with trypticase soy broth instead of buffer they still observed a synergistic effect with nisin–EDTA combination on two pathogenic *E. coli* strains, the effect on *S. enteritidis* was not synergistic at all. However, they did observe some bactericidal activity with a minimal bactericidal concentration of 46.9 µg/ml nisin and 1.25 mg/ml EDTA (~3.4 mM). It is important to note that Branen and Davidson (2004) used a low concentration of the chelator, which does not allow direct comparisons between them. Besides, it was shown that *S. typhimurium* OM was stabilized by nisin pre-treatment when cells were suspended in 0.1 mM EDTA. Therefore, nisin should not be used in combination with chelating agents at low concentrations. On the other hand, high concentrations of these agents would be able to completely disrupt the OM and therefore, nisin would reach the inner membrane (IM) and exert its bactericidal effect (Helander and Mattila-Sandholm 2000).

Nisin also showed a positive effect in association with other chemicals. For example in ham and/or bologna sausages, a mixture of nisin-lysozyme-EDTA inhibited the growth of *E. coli* O157:H7 (Gill and Holley 2000a). In fresh pork sausages, a combination of nisin and organic acids reduced the viable counts of *Salmonella* Kentucky and *S. aureus* (Scannell et al. 1997). In apple juice, a combination of nisin and cinnamon accelerated death of *Salmonella Typhimurium* and *E. coli* O157:H7, enhancing the safety of the product (Yuste and Fung 2004). When nisin and lysozyme were tested for inactivation of *Salmonella typhimurium* in orange juice in combination with PEFs, the combination of the two antimicrobials had a more pronounced bactericidal effect than either nisin or lysozyme alone (Liang et al. 2002).

The combined effect of bacteriocins and other hurdles had been shown to be highly effective against Gram-negative bacteria, such as nisin and curvacin A in combination with low pH, 5% NaCl, or propylparabene. This combination also leads to an increased sensitivity of *E. coli* and *S. enterica* towards nisin and curvacin A (Gänzle et al. 1999). These results suggested that bacteriocins may be active against *E. coli* at environmental conditions near the growth limiting factor levels even if a functional outer membrane is present. In another study, an inhibitory synergetic effect was obtained against *Salmonella enteritidis* PT4 in liquid whole egg and in egg white when both nisin or pediocin Pa1/Ach were applied in combination with pasteurization (Boziaris et al. 1998). Sakacin P produced by *L. sakei* strains Lb674 and LHT673 (Holck et al. 1994; Tichaczek et al. 1994) also acted synergistically against *E. coli* when tested in combination with the fish antimicrobial peptide pleurocidin (Lüders et al. 2003).

Recently *in vitro* experiments (in growth media) performed by Smaoui et al. (2010) showed that BacTN635, a peptide produced by *Lactobacillus plantarum* TN635 was able to kill *Salmonella.* The plantaricin-producing strain *L. plantarum* 2.9 (isolated from ben saalga, a traditional pearl millet fermented food from Burkina Faso) produced a strong inhibitory activity in malted millet flour, decreasing the survival of *E. coli* O157:H7, and *S. enterica* (Valenzuela et al. 2008). This strain could be used as a starter culture to improve the safety of ben saalga (Ben Omar et al. 2006). Paracin 1.7, a bacteriocin produced by *Lactobacillus paracasei* HD1.7, was also reported to be effective in inhibiting *Salmonella* (Ge et al. 2009).

Regarding enterocins, enterocin AS-48 has been shown to be active against some Gram-negative bacteria especially when combined with outer-membrane permeabilizing agents (Abriouel et al. 1998). This bacteriocin was evaluated on *S. choleraesuis* LT2 in combination with EDTA and Tris. The cell survival was reduced proportionally to the enterocin concentration. This positive effect could be enhanced either by using acidic (pH 4) or alkaline conditions (pH 9) or mild heat treatment (Abriouel et al. 1998). Both nisin and enterocin AS-48 were successfully used for surface decontamination of fruits and vegetables. In this regard, a positive effect of nisin-chelating agent treatments in foods was reported by Ukuku and Fett (2004). They combined 50 μg/ml nisin with 20 mM EDTA, 3% sodium lactate or 2% potassium sorbate as sanitizer treatments on whole and fresh-cut cantaloupe. All the combinations reduced *Salmonella* by 3 log units/cm^2 at day 0 of treatment and by 2 log units/cm^2 after 3–7 days of treatment. Combined treatment of enterocin AS-48 with each of the following preservatives (lactic, polyphosphoric and peracetic acids, sodium hypochlorite, hexadecylpyridinium chloride and hydrocinnamic acid) significantly reduced (P 0.05) the *S. enterica* counts during storage at 15°C for at least 48 h. This synergistic effect was further explored for other Gram-negative bacteria (*E. coli* O157:H7, *S. sonnei, Shigella flexneri, E. aerogenes*, *Y. enterocolitica, A. hydrophila* and *P. fluorescens*), using a combination treatment of enterocin AS-48 and polyphosphoric acid. The enterocin AS-48 (25 μg/ml) alone did not significantly (P 0.05) reduce the growth of these bacteria during storage. However, the combination of enterocin AS-48 (25 μg/ml) and polyphosphoric acid (0.1–0.2% range) significantly reduced the viable counts of all of the above mentioned Gram-negative

bacteria during storage at 6 and 15°C, as compared to treatment with either AS-48 or polyphosphoric acid alone. These results indicate the potential of combination treatments of AS-48 along with other preservatives to effectively control Gram-negative bacteria in vegetable foods (Molinos et al. 2008).

Another enterocin which has shown best results against Gram-negative bacteria was enterocin E 50–52, a pediocin-like bacteriocin produced by *E. faecium* (NRRL B-30746) that has been shown to be very effective in controlling *S. enteritidis* as well as *E. coli* O157:H7 among others. It should be noted that the anti-*Salmonella* activity was not only demonstrated *in vitro* but also in therapeutic tests in chickens (Svetoch et al. 2008). Kang and Lee (2005) reported that an enterocin P-like bacteriocin produced by *E. faecium* GM-1 had a broad antimicrobial spectrum including *S. typhimurium*. This finding is in sharp contrast to enterocin P itself, which is unable to kill Gram-negative bacteria (Cintas et al. 1997). Another recently reported bacteriocin with broad inhibitory spectrum is the enterocin produced by an *E. faecium* strain isolated from mangrove environment. In particular, it was shown that this enterocin was active against *S. paratyphi* (Annamalai et al. 2009). Ferreira et al. (2007) screened 70 strains of *Enterococcus mundtii* and found that only four of them produced bacteriocins active against *Salmonella Enteritidis*. These bacteriocins were only partially purified and characterized so far (Ferreira et al. 2007). One of the newest bacteriocins from LAB reported to be active against *Salmonella* spp. is lactococcin BZ, which was produced by *L. lactis* subsp. *lactis* BZ. This peptide is relatively heat labile because its activity was abolished after 15 min at 110°C. It is also sensitive to beta mercaptoethanol. The anti-*Salmonella* activity did not seem to be that high, at least as compared to other food pathogens tested (Şahingil et al. 2011). Enterocin 012 and acidophilin 801 are among the few long known bacteriocins able to kill *Salmonella*. On one hand, acidophilin 801, a bacteriocin produced by *L. acidophilus* IBB 801 with a very narrow inhibitory spectrum, surprisingly inhibits *Salmonella Panama* 1467 and *E. coli* Row (Zamfir et al. 1999; Jennes et al. 2000). On the other hand, enterocin 012 is a bacteriocin produced by *Enterococcus gallinarum* 012, a strain isolated from the duodenum of an ostrich. Remarkably, enterocin O12 has a lytic activity to the bactericidal or bacteriostatical activities usually reported for the LAB-bacteriocins (Jennes et al. 2000).

2.3 Endospore-Forming Bacteria

Endospore-forming bacteria represent an important threat to the safety and shelf-life of many foods and foodstuffs, because endospores may survive heat treatments applied to foods. After germination under suitable storage conditions, the resulting vegetative cells may propagate and produce food-poisoning toxins or cause food spoilage. Frequently, the cooking process does not inactivate heat-resistant bacterial spores and, consequently, endospore-forming *Bacillus* spp. and *Clostridum* spp. can be found in the final products, even during storage at low temperature (5°C) (Gould 1995). *Clostridium botulinum* and *Bacillus cereus* belong to these genera that are

reported as the cause of several food-borne outbreaks (Angulo et al. 1998; Doan and Davidson 2000), thus, their inhibition by bacteriocins has a high significance.

In dairy food, nisin has been tested extensively. One of the earliest applications was to prevent gas blowing in cheese caused by *C. tyrobutyricum* (De Vuyst and Vandamme 1994; Hirsch et al. 1951). More recently, a strain of *L. lactis* ssp. *lactis* IPLA 729 isolated from raw milk cheese producing the natural variant nisin Z was reported to reduce the levels of the spoilage strain *C. tyrobutyricum* CECT 4011 in Vidiago cheese (a semihard farmhouse variety manufactured in Asturias, Northern Spain) during ripening. The produced nisin Z activity was stable in the cheese at least until 15 days of ripening. The nisin-producing strain was used in combination with a suitable starter to achieve desired acidification (Rilla et al. 2003).

Nisin has been tested for its useful contribution to control *Bacillus* and *Clostridium* growth in potato-based products by Thomas et al. (2002). Addition of 6.25 μg of nisin per gram of cooked mashed potatoes retarded the growth of *B. cereus* and *B. subtilis*, previously inoculated in the product not vacuum packaged, for at least 27 days at 8°C and the growth of *C. sporogenes* and *Clostridium tyrobutiricum*, added as spores in the product and then vacuum packaged, for at least 58 days at 25°C. Nisin remained at active levels after pasteurization, but the authors highlighted that, in order to be effective against temperature abuse and in extending shelf-life of final products, nisin must be well mixed to the various ingredients.

Incorporation of nisin in canned vegetables can prevent spoilage caused by nonaciduric (*Bacillus stearothermophilus* and *Clostridium thermosaccharolyticum*) and aciduric (*Clostridium pasteurianum, Bacillus macerans* and *Bacillus coagulans*) spore formers (Thomas et al. 2000). Nisin was also an effective preservative in fresh pasteurized "home-made"–type soups (Thomas et al. 2000) and in the control of *Bacillus* and *Clostridium* in cooked potato products (Thomas et al. 2002). In one example, in nisin-added, pasteurized, vacuum-packaged mashed potatoes inoculated with a cocktail of *Clostridium sporogenes* and *C. tyrobutyricum* spores, no bacterial growth was observed and the shelf-life of the mashed potatoes was extended by at least 30 days (Thomas et al. 2002). Similar results were reported in trials involving a cocktail of *B. cereus* and *B. subtilis* strains (Thomas et al. 2002). In heat-treated cream, growth of *Bacillus cereus* during storage was completely inhibited by low concentrations of nisin (Nissen et al. 2001; Pol et al. 2001).

Concerning the effect of nisin on Gram-positive spores like *Bacillus* and *Clostridium* spp., several reports showed that spores were particularly susceptible to nisin, being more sensitive than vegetative cells (Delves-Broughton et al. 1996). Nisin action against spores was caused by binding to sulfhydryl groups of protein residues (Morris et al. 1984). It was observed that spores became more sensitive to nisin the more heat damaged they are, and it is an important factor in the use of nisin as a food preservative in heat processed foods. For example, spores of *Clostridium anaerobe* PA3679 which have survived heat treatment of 3 min at 121.1°C were 10 times more sensitive to nisin than those which had not been heat damaged (Delves-Broughton et al. 1996). Sensitivity of spores to nisin varied, those of species like *Bacillus stearothermophilus* and *Clostridium thermosaccharolyticum* being particularly susceptible, as were all spores which open their coats by mechanical rupture.

Enterocin AS-48 added to a rice-based infant formula dissolved in whole milk completely inactivated *B. cereus* and prevented its growth for at least 15 days at 37°C (Grande et al. 2006). Enterocin AS-48 was also able to suppress *B. coagulans* vegetative cells in tomato paste, syrup from canned peaches, and juice from canned pineapple for at least 15 days of storage at 37°C (Lucas et al. 2006). In a nonfat hard cheese, the strain *E. faecalis* A-48-32 produced enough enterocin AS-48 to inhibit *B. cereus* and reduce the cell counts of bacilli by 5.6 log units after 30 days of ripening (Muñoz et al. 2004). Growth of starter cultures used in cheese making was not affected by the bacteriocin-producing strain. Similarly, the same strain A-48-32 successfully inhibited *B. cereus* in skim milk (Muñoz et al. 2004, 2007).

The enterocin EJ97 produced by *E. faecalis* EJ97 (Gálvez et al. 1998) had a bactericidal effect on *Bacillus macroides*/*Bacillus maroccanus* after several incubation conditions (4 h at 37°C, 24 h at 15°C and 48 h at 4°C); its activity was reduced at pH 5.0 and 9.0 and enhanced by sodium nitrite, sodium benzoate, sodium lactate and sodium tripolyphosphate. The *in situ* efficacy of pure enterocin EJ97 was obtained with a 10-fold higher concentration, whereas no inhibition was detected with the application of *E. faecalis* EJ97 as a developing bacterium in purée, although it was able to produce the bacteriocin *in situ*. Thus, the enterocin EJ97 has a potential to preserve food spoiled by *B. macroides*/*B. maroccanus* if used in concentrated pure form.

Thermophilin from *Streptococcus thermophilus* ST580 is active against *C. tyrobutyricum* (Mathot et al. 2003). Strain ST580 could be used as thermophilic starter for hard cheese making because the bacteriocin is not active against thermophilic lactobacilli. Furthermore, curds made with strain ST580 and inoculated with *C. tyrobutyricum* endospores showed no gas production for up to 20 days (Mathot et al. 2003). The strain *S. macedonicus* ACA-DC 198 isolated from Greek Kasseri cheese produced the food-grade lantibiotic macedocin in skim milk supplemented with nitrogen sources (Georgalaki et al. 2002; Tsakalidou et al. 1998) as well as in cheese (Anastasiou et al. 2007; Van den Berghe et al. 2006). Since macedocin showed inhibitory activity toward *C. tyrobutyricum*, it could be used as a nisin substitute to inhibit gas formation in cheese (Georgalaki et al. 2002). O'Mahony et al. (2001) showed that added variacin, a bacteriocin produced by *Kocuria varians* (in the form of a milk-based ingredient) inhibited the proliferation of *B. cereus* in chilled dairy products, vanilla, and chocolate desserts in a concentration-dependent way.

Alicyclobacillus acidoterrestris is a spore-forming bacterium known to cause problems in fruit juices and fruit juice-based drinks either not heat-treated or pasteurized (Pettipher et al. 1997). Komitopoulou et al. (1999) studied the growth of *A. acidoterrestris* in fruit juice and its sensitivity to heat treatment and nisin. The spores were confirmed to be heat-resistant after 10 min at 80°C, 2 min at 90°C and 1 min at 95°C in orange, grapefruit and apple juice. The resistance was reduced with decrement of pH of juices, although the effect waless marked at higher temperatures. Nisin addition (100 AU/ml) completely prevented *A. acidoterrestris* under all temperature and time of storage conditions. In particular, the presence of nisin during heating decreased the decimal reduction time up to 40% and its minimal inhibition concentration against *A. acidoterrestris* spores was only 5 AU/ml at 25°C.

Control of *A. acidoterrestris* in fruit juice was also approached with enterocin AS-48 (Grande et al. 2005). Vegetative cells of *A. acidoterrestris* DSMZ 2498 were inactivated by 2.5 μg/ml of this bacteriocin in natural orange and apple juices incubated at 37°C. No growth was detected in both juices until the 15th day of observation. Commercial orange, apple, pineapple, peach and grapefruit juices were then added with the same concentration of enterocin AS-48 and inoculated with vegetative cells or endospores of strain DSMZ 2498 and maintained at different incubation temperatures (4, 15 and 37°C) for 3 months. In those cases, no viable cells were observed during the whole incubation, except for apple, peach and grapefruit juices at 37°C containing vegetative cells which, however, were stable for up to 60 days. Treatment with enterocin AS-48, as revealed by electron microscopy, determined cell damage and bacterial lysis and disorganization of endospore structure in all fruit juices object of the study. These findings showed that enterocin AS-48 can be a valid substitute of the intense heat treatments necessary for inactivation of *A. acidoterrestris* endospores without altering the chemical composition of fruit juices.

2.4 Staphylococcus aureus

Staphylococcal food poisoning is among the most common causes of reported food borne diseases (Tirado and Schimdt 2001; WHO 2002; Le Loir et al. 2003; EFSA 2010), requiring hospital attention by up to 19.5% of the affected individuals (EFSA 2010). In many countries, *S. aureus* is the second or third most common pathogen responsible for outbreaks of food poisoning (Veras et al. 2008). *S. aureus* is found in the nostrils as well as on the skin and hair of warm-blooded animals, and up to 30 e 50% of human population are carriers (Le Loir et al. 2003). *S. aureus* has been isolated from several foods including meat and meat products, chicken, milk and dairy products, fermented food items, salads, vegetables, fish products, etc. (Tamarapu et al. 2001; Jørgensen et al. 2005; Seo and Bohach 2007). Most strains were capable of producing one or more heat stable enterotoxins (Balaban and Rasooly 2000; Ortega et al. 2010) which were the cause of the gastrointestinal symptoms observed during intoxications (Tamarapu et al. 2001). One of the approaches proposed for the control of *S. aureus* in foods was the application of bacteriocins either singly or in combination with other antimicrobials (Gálvez et al. 2008).

To control the development of *S. aureus* in foods, in addition to traditional chemical and physical preservatives, several bacteriocins of LAB, either alone or combined with other hurdles, have been used with varying degrees of success. In this sense, many recent studies have shown the effect of nisin against *S. aureus*. In sliced cheese, immobilized nisin in a polyethylene/polyamide packaging was shown to reduce the population of *S. aureus* (Scannell et al. 2000b). In fresh pork sausages, a combination of nisin and organic acids reduced the viable counts of *S. aureus* (Scannell et al. 1997). The combination of sodium citrate or sodium lactate with lacticin 3147 was also reported to be an effective biopreservative (Scannell et al. 2000a).

In skim milk, whey or simulated milk ultrafiltrate media, increased nisin activity in combination with pulsed electric fields (PEFs) has been reported against *S. aureus* (Sobrino-López and Martín Belloso 2006).

Compared to nisin, pediocin has been shown to be more effective against *S. aureus* (Cintas et al. 1998; Eijsink et al. 1998). Moreover, the evaluation of antibacterial efficacy of the bacteriocins, nisin and pediocin AcH revealed that they had better antibacterial property in combination due to synergistic effect than when used singly (Hanlin et al. 1993; Mulet-Powell et al. 1998).

Lacticin 3147 powder was shown to rapidly reduce *S. aureus* viable cell counts in an infant milk formulation (Morgan et al. 1999). Similarly, as was reported with nisin an increased bactericidal effect was shown for the combined treatment of lacticin 3147 concentrates and HHP against *S. aureus* in milk and whey (Morgan et al. 2000).

Regarding enterocins, enterocin CCM 4231 reduced the viable counts of *S. aureus* SA1 in skim milk, Sunar (milk nourishment for suckling babies), and yogurt (Lauková et al. 1999a, b). Enterocin AS-48 may also be an interesting bacteriocin to inhibit the growth of *S. aureus*. Several reports demonstrated the susceptibility of *S. aureus* to AS-48 in BHI broth, a sausage model system, milk and cheese and in vegetable sauces (Ananou et al. 2004; Grande et al. 2007; Muñoz et al. 2007). Muñoz et al. (2007) indicated that bacteriocin AS-48 was effective at controlling *S. aureus* in milk whether added exogenously or produced by a bacteriocinogenic strain. The efficacy of AS-48 was greatly enhanced by combination with a moderate heat treatment, which is of great technological relevance. In unripened cheese, AS-48 was also effective in controlling staphylococci when added as an adjunct culture during the manufacture of cheese.

In vegetable sauces anti-staphylococcal activity of AS-48 was significantly improved when the enterocin was used in combination with different phenolic compounds and even some of the combinations of enterocin AS-48 and phenolic compounds served to completely inactivate *S. aureus* in sauces. Nevertheless the effect depended largely on the type of food, which in turn had a great influence on the activity of AS-48 as well as the phenolic compounds tested individually (Grande et al. 2007). The storage temperature was also an important factor in the inhibition of *S. aureus* by AS-48 in sauces being more effective at high (22 ºC) than at low (10°C) storage temperatures.

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