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REVIEW PAPER

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An overview of lactic acid bacteria

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Abstract

Lactic acid bacteria (LAB) are renowned for the potential of producing antimicrobial compound and other value added products. Undeniable to concern these probiotic has contributed to the importance of human life. Deserving an attention for its capabilities, this paper will discuss on the general description of lactic acid bacteria, genetics, metabolism and its application to the industries.

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Introduction

The term Lactic Acid Bacteria (LAB) was gradually accepted in the beginning of the 20th century (Carol *et. al.*, 2010). Other terms as "milk souring" and "lactic acid producing" bacteria had previously been used for the same bacteria causing a slight confusion. This ended with publication of a monograph about lactic acid bacteria written by Orla-Jensen, 1919, a work that had great impact on the systematic of LAB (Axelsson, 1989). Classification of LAB genera was based on morphology, mode of glucose fermentation, growth at certain temperatures, and range of sugar utilization. Even though the taxonomy has been revised since then, characters used by Orla-Jensen are still very important in current classification of LAB. Lactic acid bacteria constitute a group of bacteria that have morphological, metabolic and physiological similarities, and they are also relatively closely related phylogenetically. The general description of the bacteria within the group is gram-positive, non-sporulating, non-respiring cocci or rods, which do, through fermentation of carbohydrates, produce lactic acid as their major end product. The common agreement is that there is a core group consisting of four genera; *Lactobacillus, Leuconostoc, Pediococcus* and *Streptococcus*. Recent taxonomic revisions have proposed several new genera and the remaining group now comprises the following: *Aerococcus, Alloiococcus, Carnobacterium, Dolosigranulum, Enterococcus, Globicatella, Lactococcus, Oenococcus, Tetragenococcus, Vagococcus, and Weissella. Lactobacilli, Carnobacteria* and some *Weissella* are rods while the remaining genera are cocci (Jin *et al.*, 2009). For identification of LAB, phenotypic methods have been most commonly used (Corsetti *et. al.*, 2001). More recently, genetic techniques, such as 16S rDNA sequencing have been developed which allows a more consistent and accurate identification of individual strains (Buddhiman *et al.*, 2008). Determination of short sequences of 16S rDNA is today used as a simple way for species determination of isolates of lactic acid bacteria (Schleifer & Ludwig, 1995).

The taxonomy of Lactic Acid Bacteria has been based on the gram reaction and the production of lactic acid from various fermentable carbohydrates. The classification of lactic acid bacteria into different genera is largely based on morphology, mode of glucose fermentation, growth at different temperatures, and configuration of the lactic acid produced, ability to grow at high salt concentrations, and acid or alkaline tolerance. For some of the newly described genera (Pilar *et. al.*, 2008), additional characteristics such as fatty acid composition and motility are used in classification. The measurements of true phylogenetic relationship with rRNA sequencing have aided the classification of lactic acid bacteria and clarified the phylogeny of the group. Most genera in the group form phylogenetically distict group, but some, in particular *Lactobacillus* and *Leuconostoc* are very heterogeneous and the phylogenetic cluster do not correlate with the current classification based on phenotypic characters. New tools for classification and identification of lactic acid bacteria are underway (Sascha and Magdalena 2010). The most promising for routine used are nucleic acid probing techniques, partial rRNA gene sequencing using the polymerase chain reaction, and soluble protein patterns. The growth is optimum at pH 5.5-5.8 and the organisms have complex nutritional requirements for amino acids, peptides, nucleotide bases, vitamins, minerals, fatty acids and carbohydrates**.**

Lactic Acid Bacteria are gram-positive usually non-motile, non-spore-forming rods and cocci. They lack the ability to synthesize cytochromes and porphyrins (components of respiratory chains) and therefore cannot generate ATP by creation of a proton gradient. The LAB can only obtain ATP by fermentation, usually of sugars. Since they do not use oxygen in their energy production, lactic acid bacteria happily grow under

anaerobic conditions, but they can also grow in oxygen's presence. They are protected from oxygen byproducts (e.g. H_2O_2) because they have peroxidases. These organisms are aerotolerant anaerobes (Michaela *et al.*, 2009). Two main sugar fermentation pathways can be distinguished among lactic acid bacteria. Glycolysis (Embden-Meyerhof pathway) results in almost exclusively lactic acid as end product under standard conditions, and the metabolism is referred to as homolactic fermentation (Derek *et al.*, 2009). The 6-phosphogluconate/phosphoketolase pathway results in significant amounts of other end products, such as ethanol, acetate, and CO_2 in addition to lactic acid and the metabolism is referred to as heterolactic fermentation. Various growth conditions may significantly alter the end-product formation by some lactic acid bacteria. These changes can be attributed to an altered pyruvate metabolism and/or the use of external electron acceptors such as oxygen or organic compounds.

Physiology and morphology

Orla-Jensen used a few characters as classification basis: morphology (cocci or rods, tetrad formation), mode of glucose fermentation (homo- or heterofermentation), growth at certain "cardinal" temperatures (e.g., 10°C and 45°C), and form of lactic acid produced (D, L, or both) (Kenji *et al.*, 2009). As well be seen, these characters are still very important in current lactic acid bacteria classification. After the work by Orla-Jensen, the view emerged that the core of lactic acid bacteria comprised four genera: *Lactobacillus, Leuconostoc, Pediococcus* and *Streptococcus*. There has always been some controversy on what the boundaries of the group are, but this will not be dealt with here. The classification section of this chapter will concentrate on these four genera, or rather what used to be these genera, since major taxonomic revisions have recently resulted in the description of new genera (Sangoyomi *et al.*, 2010).

Orla-Jensen regarded lactic acid bacteria as a "great natural group," indicating a belief that the bacteria included were phylogenetically related and separated from other groups. At that time, only phenotype characters could be examined and evaluated phylogenetic markers. Today, we have means to examine, in detail, macro-molecules of the cell, believed to be more accurate in defining relationships and phylogenetic positions. These are, of course, the nucleic acids. Fortunately, nature has provided us with different kind of nucleic acids for different kind of taxonomic studies. Close relations (at species and subspecies level) can be determined with DNA-DNA homology studies (Todd 1993). For determining phylogenetic positions of species and genera, ribosomal RNA (rRNA) is more suitable, since the sequence contains both well-conserved and less-conserved regions. It is now possible to determine the sequence of long stretch of rRNA (~1500 bases of 16S rRNA) from bacteria (Huili *et al.*, 2011) comparisons of these sequences are currently the most powerful and accurate technique for determining phylogenetic relationships of microorganisms (Philippe et. al., 2009). With this technique, a clearer picture of phylogeny of lactic acid bacteria is emerging, and the ideas of Orla-Jensen can be examined with some accuracy. In addition, rRNA sequencing is becoming an important aid in the classification of lactic acid bacteria, as exemplified by the descriptions of new genera (De Klerk *et al.*, 1967; Dower *et al.*, 1988).

The physiology of lactic acid bacteria has been of interest ever since it was recognized that these bacteria involved in the acidification of food and feed products. Increased knowledge of lactic acid bacteria physiology, such as metabolism and nutrient utilization has been one way to achieve more controlled processes. Today, modern genetic techniques are considered to be promising in this regard. However, effort in this direction will not be fruitful unless there is a sound understanding of the physiology of these bacteria. The designation Lactic

Acid Bacteria perhaps implies that these bacteria have a somewhat "simple" metabolism (Delphine *et al*., 2011), resulting in one or few fermentation end products. This may also be the case in laboratory environment that we often impose to them. However, it is clear that lactic acid bacteria have a very diverse metabolic capacity, which enables them to adapt to a variety of conditions.

General description

Lactic Acid Bacteria which is gram-positive, nonsporing, catalase-negative, devoid of cytochromes, of nonaerobic habit but aerotolerant, fastidious, acid tolerant and strictly fermentative with lactic acid as the major end product during sugar fermentation. Lactic Acid Bacteria are generally associated with habitats rich in nutrients, such as various food products (milk, meat, vegetables), but some are also members of the flora of the mouth, intestine and vagina of mammals (Whittenbury 1964). Variations of this general theme are common, excluding the gram-positive and nonsporing characters, which cannot be disputed (spore-forming bacteria that resemble lactic acid bacteria, e.g., *Sporalactobacillus*, are more related to bacilli). A key feature of Lactic Acid Bacteria that must emphasized is an ability to synthesize porphyrin groups (e.g., heme) (Alessandro *et al*., 2010). This is the actual physiological background for some of the characteristic mentioned. This makes acid lactic bacteria devoid of a "true" catalase and cytochromes when grown in laboratory growth media, which lack hematin or related compounds. Under these conditions, which are "normal" in most studies of these bacteria, lactic acid bacteria do not possess the mechanism of an electron transport chain and rely on fermentation, i.e., substrate-level of phosphorylation, for generating energy. Since catalase activity, mediated by non-heme "pseudocatalase," can occur in some lactic acid bacteria, the lack of cytochromes may be a more reliable characteristic in preliminary diagnosing than the commonly used catalase test (Klaenhammer 1988). However, it is important to note that the situation may be totally different if hematin (or hemoglobin) is added to the growth medium. A true catalase, and even cytochoromes, may be formed by some lactic acid bacteria, in some cases, resulting in respiration with a functional electron transport chain.

The genera that, in most respects, fit the general description of the typical lactic acid bacteria are (as they appear in the latest edition of *Bergey's Manual* from 1986) *Aerococcus (A.), Lactobacillus (Lb.), Leuconostoc (Ln.), Pediococcus (P.),* and *Streptococcus (S.)*. Major revision of taxonomy of lactic acid bacteria, in particular of streptococci, was anticipated in *Bergey's Manual* of 1986 (Barry 2009) and to some extent already realized by the year of that issue. Thus, the former genus *Streptococcus* was first divided into three: *Enterococcus (E.), Lactococcus (L.),* and *Streptococcus sensu stricto* (Alexander *et al*., 2001; Zongzhi *et. al*., 2008). Later, some motile lactic acid bacteria, otherwise resembling lactococci, were suggested to form separate genus, *Vagococcus (V.)* (Aly *et. al*., 2004). The genera *Lactobacillus, Leuconostoc,* and *Pediococcus* have largely remained unchanged, but some rod-shaped lactic acid bacteria, previously included in *Lactobacills*, are now forming the genus *Carnobacterium (C.)* (Elliot *et al*., 1991), and the former species *Pediococcus halophilus* has been raised to genus level, forming the genus *Tetragenococcus (T.)* (Facklam *et al*., 1998). Revisions after 1986 are supported by extensive chemotaxonomic and genetic data.

Genetics

Currently, more than 19 complete genomes of streptococci are available, covering different strains of five species. A program aimed at extensive sequencing of the genomes of nonpathogenic LAB was announced in 2002 by the Lactic Acid Bacteria Genome Sequencing Consortium (Klaenhammer *et al*., 2002), but the actual breakthrough occurred only in the last 6 years (2005 and 2006). The *Lactobacillales* have

relatively small genomes for nonobligatory bacterial parasites or symbionts (characteristic genome size, ~2 megabases, with ~ 2,000 genes), with the number of genes in different species spanning the range from ~1,600 to ~3,000. This variation in the number of genes suggests that the evolution of LAB involved active processes of gene loss, duplication, and acquisition. The current collection of LAB genomes is a unique data set that includes multiple related genomes with a gradient of divergence in sequences and genome organizations. This set of related genomes is amenable to detailed reconstruction of genome evolution, which is not yet attainable with other groups of bacteria.

Metabolism

Lactic acid bacteria are chemotrophic, they find the energy required for their entire metabolism from the oxidation of chemical compounds. The oxidation of sugars constitutes the principle energy producing pathway. Lactic acid bacteria of the genera *Lactobacillus, Leuconostoc* and *Pediococcus*, the important bacteria to winemaking, assimilate sugars by either a homofermentative or heterofermentative pathway.

Homofermentative metabolism of hexoses

Homofermentative bacteria transform nearly all of the sugars they use, especially glucose into lactic acid. The homofermentative pathway includes a first phase of all the reactions of glycolysis that lead from hexose to pyruvate. The terminal electron acceptor in this pathway is pyruvate which is reduced to lactic acid (See Fig. 1). In fermentation, pyruvate is decarboxylated to ethanal, which is the terminal electron acceptor, being reduced to ethanol.

Heterofermentative metabolism of hexoses

Bacteria using the heterofermentative pathway, which includes *Leuconostoc* (the most important bacterium in enology) use the pentose phosphate pathway. In this pathway, NADPH is generated as glucose is oxidized to ribose 5-phosphate. This five-carbon sugar and its derivatives are components of important biomolecules such as ATP, CoA, NAD+, FAD, RNA and DNA. NADPH is the currency of readily available reducing power in cells (NADH is used in the respiratory chain). This pathway occurs in the cytosol.

After being transported into the cell, a glucokinase phosphorylates the glucose into glucose 6-P (glucose 6-phosphate). Its destination is completely different from the glucose 6-P in the homofermentative pathway. Two oxidation reactions occur: the first leads to gluconate 6-P and the second, accompanied by a decarboxylation, forms ribulose 5-P (See Fig. 2). In each of these reactions a molecule of NADP+ is reduced. Ribulose 5-P can then be epimerized either to ribose 5-P or to xylulose 5-P.

Xylulose 5-P is then cleaved into acetyl-phosphate and glyceraldehydes 3-phosphate (See Fig. 3). The glyceraldehyde 3-phosphate is metabolized into lactic acid by following the same pathway as in the homofermentative pathway. The acetylphosphate has two possible destinations, depending on environmental conditions.

This molecule can be successively reduced into ethanal and ethanol, in which case the molecules of the coenzyme NADPH formed during the two oxidation reactions of glucose at the beginning of the heterofermentative pathway, are reoxidized. This reoxidation is essential for regenerating the coenzymes necessary for this pathway. The final products are then lactate and ethanol.

Or the acetyl-phosphate can produce acetate (acetic acid) through the enzyme acetate kinase. This reaction also yields a molecule of ATP. The final products of this pathway are then lactate and acetate (See Fig. 4). Bacteria of the genus *Leuconostoc* preferentially produce lactate and ethanol in a slightly aerated

environment and lactate and acetate in an aerated environment.

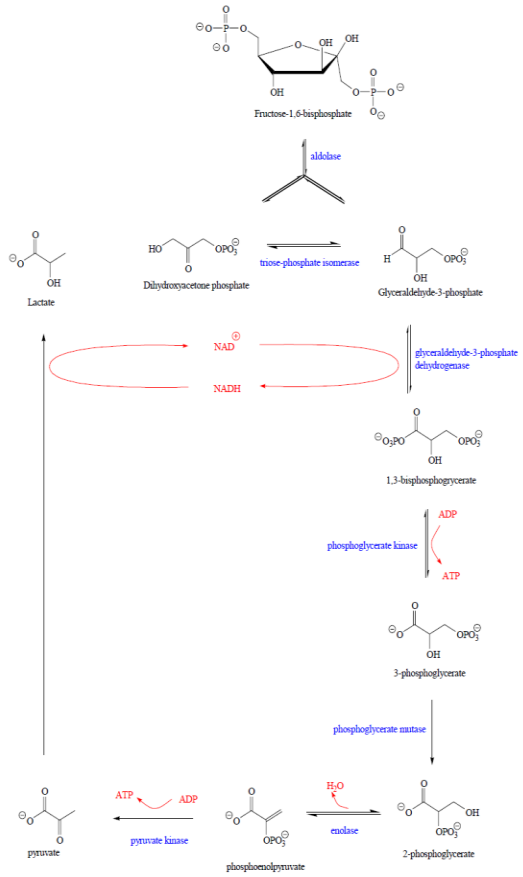

Fig. 1. Homofermentative Metabolism of Fructose 1,6-biphosphate Formation of Lactic Acid.

Significance of antimicrobial compounds

Since the early 1099s there has been a marked worldwide increase in the industrial production of cheeses and fermented milks (Fefer *et al.*, 1995). Process technology has progressed towards increasing mechanization, increase in factory sizes, shortening processing times, and larger quantities of milk processes daily in the factory. Milk can be fermented to more than 1000 products with demands of their own special flavor, texture, and final product quality (Franklin 1998). All this is reflected in enormous demands at the starter cultures, their activity, stable quality, and bacteriophage resistance. The art of making cultured food products by using the former day's whey or fermented product for today's process has been changes to a science with exact knowledge of the factors influencing the specific starter and strains (Fujitoshi *et al.*, 2005).

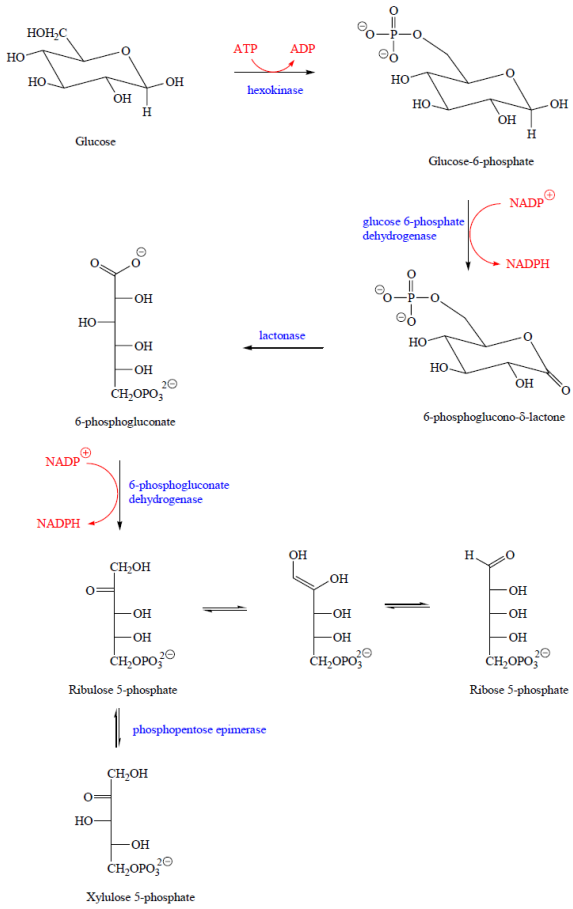

Fig. 2. Heterofermentative Metabolism of Glucose Pentose Phosphate Pathway Glucose to Xylulose.

Broad spectrum compound

John (2002) demonstrated the presence of bacteriocin-like compound, designated lactocidin, produced by *L. acidophilus* in veal-liver agar cultures. It was nonvolatile, insensitive to catalase, activity at neutral pH, and retained within dialysis membranes. The compound reported has broad spectrum activity against gram-positive and gram-negative bacteria. Because the broad spectrum activity, lactocidin was later reported to be due to the combined effect of

organic acids, H_2O_2, and antibiotic type substances (Klaenhammer, 1988). Two other bactericin-type compounds were produced by strains of *L. acidophilus*, acidolin and acidophilin. Reuterin is a low-molecular-weight, nonproteinaceous, soluble, pH-neutral compound produced by heterofermentative *Lactobacillus ruteri* (Kim *et al.*, 2008). It has a broad spectrum of inhibitory activity against species of gram-negative and gram-positive bacteria, yeast, fungi and protozoa. Bacterial species inhibited include *Salmonella, Shigella, Clostridium, Staphylococcus, Listeria, Candida* and *Trypanosoma* (Michael *et al.*, 1988; Yasin *et al.*, 1996)

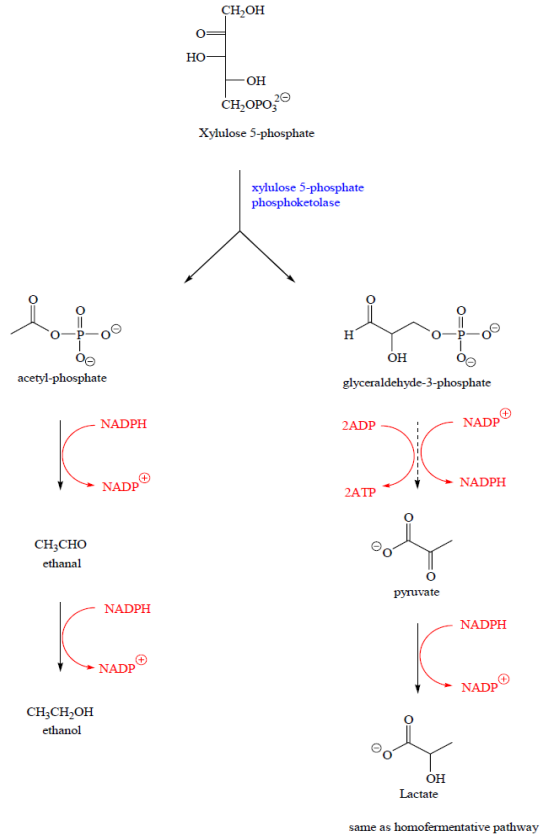

Fig. 3. Heterofermentative Metabolism of Glucose Pentose Phosphate Pathway xylulose to Lactic acid and Ethanol.

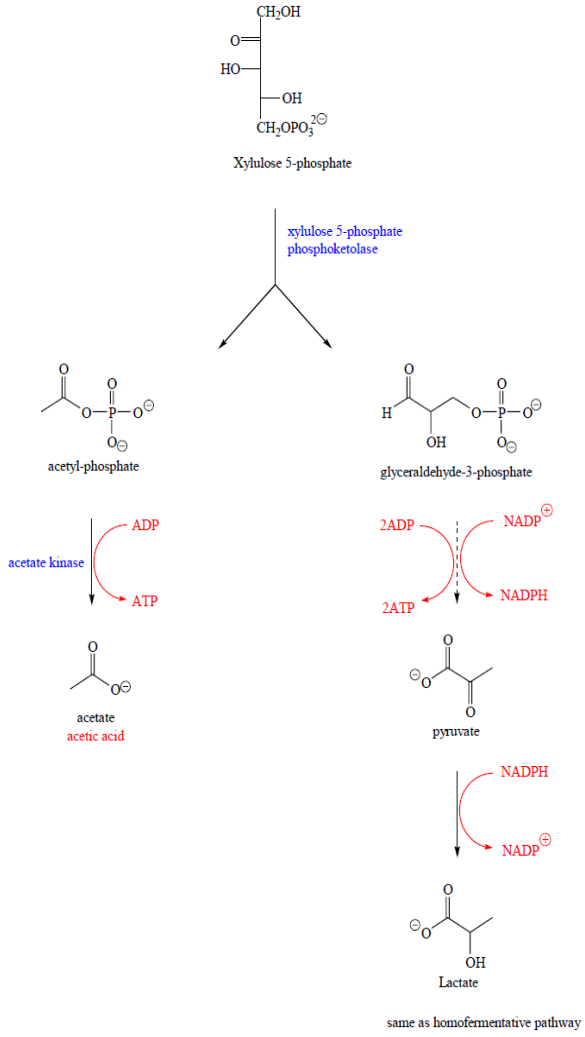

Fig. 4. Heterofermentative Metabolism of Glucose Pentose Phosphate Pathway Xylulose to Lactic acid and Ethanol.

Inhibition could not be totally related to organic acids or H_2O_2. An inhibitor termed "bulgarican" was produced by *Lactobacillus bulgaricus* DDS14, isolated by methanol-acetone extraction and purified by silica gel chromatography. The spectrum of antimicrobial activity of bulgaricans included *Bacillus subtilis, E. coli, Proteus vulgaris, Sarcina lutea, S. aureus, Pseudomonas aeruginosa, P. fluorescens,* and *Serratia marcescens*. No molds were inhibited. The pH for optimum activity was <4.5. *Lactobacillus casei* strain GG isolated from normal human feces

produced an inhibitor with broad spectrum activity. The compound was distinct from organics acids and had molecular weight of <1000. The inhibitor was heat-stable (121° C, 15 min) and resistant to trypsin, proteinase K, bromelin, carboxypeptidase A and *Streptomyces griseus* protease. The substance was inhibitory to strains of *E. coli, Psedomonas, Salmonella, Streptococcus, Bacillus, Clostradium and Bifidobacterium*. It was not inhibitory to Lactobacillus. Inhibition occurred at pH 3-5. Silva *et al*., (1987) (Sylvie 2011).suggested that the inhibitor was not a bacteriocin, but rather closely resembled a microcin (low-molecular-weight peptides produced mostly by *Enterobacteriaceae*). Lactobacillus GG is currently used to produce a fermented whey drink and yogurt-type product which are reported to have numerous health benefits.

Application of LAB

Two key groups of organisms are involved in the production of red, white, and sparkling wine (Nannelli *et al*., 2008). The yeasts, typically strains of *Saccharomyces cerevisiae*, carry out the primary or alcoholic fermentation, in which sugars are converted to ethanol and CO_2. Lactic Acid Bacteria, especially *Oenococcus oeni* (formerly *Leuconostoc oenos*, conduct the secondary or malolactic fermentation (MLF) of wine by decarboxylating L-malic acid to L-lactic acid and CO_2. Apart from these two crucial reactions in grape vinification, a myriad of other changes occur to complete the transformation of grape juice to wine. Compounds that stimulate our visual, olfactory, gustatory, and tactile senses are either released from the various ingredients or are synthesized, degraded, or modified during vinification. Many of these processes involve the action of enzymes (García-Ruiz *et al*., 2008). Such enzymes can be free or cells associated and originate from sources that include enzyme addition, the grapes themselves, the grape microflora (fungi, yeast, or bacteria), the inoculated microbes, or microbes associated with winery equipment and storage vessels to which the wine is exposed during production. Current viticultural practices and vinification processes are essentially protocols for favoring the activities of certain enzymes while discouraging the activities of others. Thus, winemakers can broadly achieve desirable outcomes during fermentation by using a selected wine yeast strain characterized by desirable physiological and hence enzymatic properties. Conversely, adverse reactions, such as the browning associated with polyphenoloxidases, can be minimized by excluding oxygen from the grape juice or through addition of sulfur dioxide (SO_2) to inhibit enzyme activity. A more recent strategy in the history of winemaking is the addition to juice or wine of a microbial culture or enzyme preparation that confers a specific or select group of enzymatic activities (García-Ruiz *et al*., 2011).

These activities can either amplify the effect of indigenous enzymes or be novel. Initially, such additives addressed issues of juice-processing efficiency and wine recovery. Thus, the gelling seen in many fruit juices as a result of pectins has for many decades been reduced or eliminated with pectinase enzymes, most often derived from *Aspergillus* fungi, which increase juice extraction or minimize filter blockage. Enzyme-based solutions that provide a broader range of benefits, such as flavor enhancement or manipulation of colour (Francisco *et al*., 2009), have now become available. In the development of new enzyme treatments, efforts have often been centered on desirable activities identified in the microorganisms used or encountered during vinification, especially the yeast. In part, this approach has been taken because of legal restrictions on the nature of additives that can be added to wine. It is unlikely that the use in winemaking of wine yeast with a novel enzymatic capability would require regulatory approval, whereas the addition of an enzyme extract or purified enzyme preparation may require such approval (Raffaella *et al*., 2009). Despite the appeal of this approach, extensive efforts have

yielded only a small number of technologically important enzymes, and even fewer of these enzymes perform satisfactorily under winemaking conditions, which include a high sugar (glucose and fructose) content, a low pH (pH 3.0 to 4.0), low temperatures (15°C), and the presence of ethanol (up to 15% [vol/vol] or more) or SO_2. Interestingly, the LAB that grow and thrive in grape juice or wine under conditions that interfere with the production and activity of desirable enzymes in yeast or fungi have been poorly studied as a source of enzymes with potential usefulness in vinification. Young wine can be a nutritionally deficient environment that could be expected to lead to the elaboration by lactic acid bacteria.

Bacteriocins produced from LAB can be used as food additives. For instance, nisin is commercially made in a partially purified form (De Vuyst & Vandamme 1994; Schnürer & Magnusson 2005) and a marketed preparation with the pediocin PA-1 (AcH) producer is available (Rodríguez *et al.,* 2002). As an alternative to the addition of bacteriocins to foods, bacteriocins may be produced directly in the food as a result of starter culture or co-culture activity. Several studies have indeed indicated that LAB starter cultures or co-cultures are able to produce their bacteriocins in food matrices, and consequently display inhibitory activity towards sensitive food spoilage or pathogenic bacteria. The latter trait has mainly been documented for fermented sausage, fermented vegetables and olives, and dairy products (Leroy & De Vuyst 2004). For instance, bacteriocin extraction has been demonstrated in the case of Cheddar cheese and fermented sausage and sourdough. Because of the complexity of the food matrix and the difficulty of quantifying bacteriocin activities in foods, in vitro studies can be performed to simulate and study the in situ functionality of bacteriocinogenic starters. In this way, the kinetics of bacteriocin production by LAB strains in foods have been described in detail, amongst others through mathematical modeling and positive predictive microbiology (Leroy *et al*., 2002). Insights in the relationship between the food environment and kinetics of the starter culture have yielded valuable information about the in situ production of bacteriocins and its interactions with the target strains, which will be important if bacteriocins or bacteriocinproducing strains are to be increasingly used in food systems (Leroy *et al*., 2005). In particular, such information is essential when dealing with the potential problem of bacteriocin-resistant target bacteria. Application of bacteriocin-producing starter cultures in sourdough (to increase competitiveness and hence establish a desired microbial population), in fermented sausage (anti-listerial effect to meet the zero-tolerance policy in ready-to eat foods), and in cheese (anti-listerial and anti-clostridial effects), have been studied during in vitro laboratory fermentations as well as on pilot-scale level (Verluyten *et al*., 2003). Results of these studies were highly promising and underline the important role that functional; bacteriocinogenic strains of LAB may play in the food industry as starter cultures, co-cultures, or bioprotective cultures, to improve food quality and safety.

Conclusion

Lactic acid bacteria contribute to the enormous environmental and health benefits. Extensive research should be performed to discover the secret of these bacteria. Thus, the research fund and expertise should be extended and harnessed to achieve the purpose.

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