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Review Article

Lactic Acid Bacteria and the Food Industry - A Comprehensive Review

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ABSTRACT

Recently, more people are showing interest in knowing what the packaged food they buy contains, and not just that, they want to also know the different processes those foods went through, at least to a certain extent. This rising interest can be traced to the rising need for special diets and nutritional requests of certain groups of people who wants to either just live a healthier lifestyle or are made to turn to healthy eating due to health challenges occasioned by illnesses. The importance of the lactic acid bacteria to the food industry cannot be over-emphasized and as such, more awareness about it should be created for informational purpose. Although there are numerous literatures on lactic acid bacteria online, mostly dealing with their identification and purification, there is a gap in getting these technical information together in a form that can be understood by anyone who wishes to learn more about lactic acid bacteria. This review article explores the numerous benefits of lactic acid bacteria in the food industry, highlighting its key uses for fermentation and preservation. More so, this review pinpoints the health benefits of certain strains of lactic acid bacteria in form of probiotics in addition to its well-known antimicrobial properties. Lactic acid bacteria confer numerous beneficial characteristics to foods ranging from enhanced taste to provision of healthy probiotics. Lactic acid bacteria may also experience a decrease in viability and functionality when stored while controlling and optimizing their metabolic activity is another major concern in the food industry.

Key words: Lactic acid bacteria, probiotics, fermentation, food preservation, antimicrobial, starter cultures

INTRODUCTION

Lactic acid bacteria (LAB) have been used in food fermentations for more than 4000 years. It is important to acknowledge that the widespread term "lactic acid bacteria" have no official status in taxonomy and is only a general term of convenience used to describe a group of functionally and genetically related bacteria. Lactic acid bacteria consist of bacteria genera within the *Firmicutes* comprised of about 20 genera. The main members of the lactic acid bacteria are genera: *Lactococcus*, *Lactobacillus*, *Streptococcus*, *Leuconostoc*, *Pediococcus*, *Carnobacterium*, *Aerococcus*, *Enterococcus*, *Oenococcus*, *Tetragenococcus*, *Vagococcus* and *Weisella*. *Lactobacillus* is the largest genus of this group, comprising around 80 recognized species. [1,2,3,4,5]

Using lactic acid bacteria in food fermentation is one of the known ancient food preserving techniques. Properties such as nutritional, environmental and adhesional adaptations have provided lactic acid bacteria with the ability to adapt and present in different environments ranging from food matrices such as dairy products, meats, vegetables, sourdough bread, and wine. [6-7] Lactic acid bacteria are known for their fastidious nutritional requirements which may vary among species and even among strains. [8-11] Strains of lactic acid bacteria are also known as fast growing microorganisms that can explore different metabolic activities. Metabolic activities are associated with production of many beneficial compounds such as organic acids and antimicrobial compounds, unique enzymes that can breakdown complex organic compounds into simple functional compounds, among others. [7-10,12]

Thus the fast growing characteristics and diverse metabolic activities are the keys of lactic acid bacteria benefits and applications. Lactic acid bacteria have a long history of application in fermented foods because of their beneficial influence on nutritional, organoleptic, and shelf- life enhancements. [13-14] They cause rapid acidification of the raw material through the production of organic acids, mainly lactic acid. In addition, their production of acetic acid, ethanol, aromatic compounds, bacteriocins, exopolysaccharides, and several enzymes is of high nutritional importance. Whereas a food fermentation process with lactic acid bacteria is traditionally based on spontaneous fermentation or back slopping, industrial food fermentation is performed by the deliberate addition of lactic acid bacteria as starter cultures to the food matrix. This has been a breakthrough in the processing of fermented foods, resulting in a high degree of control over the fermentation process and standardization of the end products. The use of functional starter cultures, a novel generation of starter cultures that offers functionalities beyond acidification, is being explored. [14-16] For instance, lactic acid bacteria are capable of inhibiting various microorganisms in a food environment and display crucial antimicrobial properties with respect to food preservation and safety.

In addition, it has been shown that some strains of lactic acid bacteria possess interesting health promoting properties known as probiotics; one of the characteristics of these probiotics is the potential to combat gastrointestinal pathogenic bacteria such as Helicobacter pylori, Escherichia coli, and Salmonella.

Characteristics of the Genera *Lactobacillus*

Lactobacilli are described as Gram-positive, catalase-negative, non-sporing rods, whose length varies between 1.5 µm and 5 µm. They may also have a slender, curved or bend appearance and frequently are able to form chains. Colony morphology is also variable on agar plates, with some strains producing large round colonies and others producing small or irregular colonies. [17,3] Most of the lactobacilli are mesophilic, but the genus also contains species that are psychrotrophic, thermoduric or thermophilic. Temperature optimum varies from 30 to 45 ºC. Some species show high tolerance to salt, osmotic pressure and low water activity. Acid tolerance is a common feature of lactobacilli and most of the strains are able to grow at pH below 4.4. The optimum pH value for their growth is 5.5-6.5. Some strains are ethanol tolerant and bile tolerant as well. Most of the species are aero tolerant, but some of them require strict anaerobic conditions. [3-4]

Metabolic Activity of Lactic Acid Bacteria

Metabolic activity of lactic acid bacteria has gained much focus in research and industry. The main metabolic activity of lactic acid bacteria is breaking down different carbohydrates and related compounds to obtain energy and carbon molecules. [18-20] Other metabolic activities such as breaking down proteins, lipids, and other compounds are also important for normal growth. Thus, the metabolic activities of lactic acid bacteria can include: carbohydrates metabolism, protein metabolism, lipids metabolism, and other metabolic activity.

Carbohydrates Metabolism

Carbohydrates are the main source of energy for bacterial growth. Lactic acid bacteria metabolize carbohydrates into different useful compounds (mainly lactic acid) through a common process known as fermentation. Fermentation is the metabolism of sugar in which energy is derived from partial oxidation of an organic compound using organic intermediates as electron donors and electron acceptors. [21,7] No outside electron acceptors are involved; no membrane or electron transport system is required; and all ATPs are produced by the substrate level phosphorylation. According to the mode of splitting carbon skeleton thus leading to different sets of end products, three major pathways of hexoses fermentation were described to occur within lactic acid bacteria. [22,7] Based on fermentation pathways, lactic acid bacteria can be divided into two physiological groups: homofermentative (e.g. *Pediococcus*, *Streptococcus*, *Lactococcus lactis*, *Lactobacillus delbrueckii*, and *Lactobacillus casei*) and heterofermentative (e.g., *Lactobacillus amylovorus*, *Lactobacillus reuteri*, and *Lactobacillus manihotivorans*, *Weisella*, *Leuconostoc*). [23,7] Homofermentative lactic acid bacteria metabolize one molecule of hexose sugars such as glucose to two molecules of lactic acid and two molecules of ATP resulting in more than 85% lactic acid from one molecule of glucose. [21,7] Heterofermentative lactic acid bacteria produce only 50% lactic acid fermenting one molecule of glucose to one molecule of lactic acid, one molecule of ethanol/acetate, one molecule of CO2, and only one molecule of ATP. [21] The ratio of acetate/ethanol depends on the oxidation reduction potential of the system. The difference in acid production and change in pH could be used as a basis for differentiation of these two groups of lactic acid bacteria.

Protein Metabolism

Lactic acid bacteria have gained much attention due to their proteolytic activities, which are of special importance in the accelerated maturation and enzyme modification of different food products such as cheese. Proteolysis is the process in which proteins are broken down by proteinases and peptidases into polypeptides, amino acids, and peptides. [24-25] Proteinases and peptidases can be found as extracellular and secreted as free enzymes outside the cell or intracellular inside the cell. The proteolytic systems of lactic acid bacteria are important as a means of making protein, peptide, and amino acids available for bacterial growth, but these systems can also form the rheological and organoleptic properties of fermented foods. [24,26] Proteolysis has been particularly well documented in relation to the growth of lactobacilli and lactococci in milk, where they are largely responsible for flavor development during cheese production foods. [24,26] Proteinase also helps to reduce the allergic properties of milk and milk products for infants which can lead to a severe nutritional problem of protein energy deficiency. [27] Of cheese making lactic acid bacteria strains, *Lactobacillus helveticus* and *Lactococcus lactis* have been studied in greatest detail. [25] Many peptidases (e.g. Aminopeptidase C, Aminopeptidase N, Aminopeptidase A, X-prolyldipeptidyl-aminopeptidase, Prolidase) have been identified and classified. This peptidase has exhibited wide differences among lactic acid bacteria species and even strains. [25] Lactic acid bacteria proteolytic systems are comprised of three components: 1) cell wall bound proteinase that initiates the degradation of extracellular protein into oligopeptides, 2) peptide transporters that take up the peptides into the cell, and 3) intracellular peptidases that degrade peptides into shorter peptides and amino acids. [26] Amino acids can be further converted into various flavor compounds, such as aldehydes, alcohols and esters. [28] The advantage of direct transport of peptides into the cell prior to hydrolysis lies in the reduction of the amount of metabolic energy used for amino acid uptake. Amino acid catabolism by lactic acid bacteria is also believed to have an important role in the ability to obtain energy in nutrient limited environments. In addition, proteinase, oligopeptide transport system, and peptidases were shown to be distributed unevenly among lactic acid bacteria strains, which were probably the result of the presence or absence of plasmids that encode them. [26]

Lipid Metabolism

Lipid metabolism is the breakdown of lipid by lipases into fatty acids and glycerol. Lactic acid bacteria strains have either intracellular or extracellular lipases. [29-30] In addition, lactic acid bacteria strains perform unique fatty acid transformation reactions including is omerization, hydration, dehydration, and saturation. [31] These functions can be used in food industry and probiotics. For example, lipolyses of milk fat by lactic acid bacteria constitute the main biochemical changes in cheese flavor development. [29-30] However, not all lactic acid bacteria strains can metabolize lipids. Meyers and others (1996) screened over 100 different lactic acid bacteria strains for lipase production and identify only 29 lipase producing strains. Lipase activity of lactic acid bacteria has shown to provide different health benefits to the host. Lipases are useful in the preparation of dietetic formulations for infants, geriatrics, and convalescents. [31-32] Evidence from mice, preclinical and clinical trials have revealed that lactobacilli can also break down cholesterol into serum lipids. [32] The hypolipemic effect of Lactobacillus could be due to a lower intestinal absorption of lipids or a higher lipid catabolism. [32] have suggested that the hypocholesterolemic effect of *Lactobacillus reuteri* could be related to the hydrolase activity of bile salts by the cells. In addition, lactic acid bacteria can produce conjugated linoleic acid (CLA) from linoleic acid. [31] Conjugated fatty acids such as CLA have attracted much attention as a novel type of biologically beneficial functional lipid. Castor oil, which is rich in the triacylglycerol form of ricinoleic acid, was also found to act as a substrate for CLA production by lactic acid bacteria with the aid of lipase-catalyzed triacylglycerol hydrolysis. Thus, some isomers of CLA reduce carcinogenesis, atherosclerosis, and body fat.

Other Metabolic Activities

Lactic acid bacteria strains express several other metabolic activities that are major contributors to sensory changes in fermented foods such as flavor, astringency, and color by breaking down different organic compounds in the food matrix. [33] These enzymes also play important roles in the probiotic characteristics of lactic acid bacteria contributing to a variety of health benefits in humans, animals, and plants. [34] Lactic acid bacteria metabolize different simple and complex functional compounds such as terpenoids, carotenoids, sterols, polyphenols, and isoflavones. [18,34-35] In general these complex functional compounds are known for their health benefits but they are unavailable for gut absorption. The metabolic process in food fermentation or in the gut will degrade these compounds to smaller metabolites that can be absorbed and benefit the host organism. [35]

Diacetyl is produced during conversion of citric acid in milk to pyruvate and pyruvate is converted to α-acetolactate and then to the precursor for diacetyl. Most lactic acid bacteria strains can decarboxylate α-acetolactate by α-acetolactate decarboxylase enzyme to the metabolic end product acetoin and aromatic compounds whereas some lactic acid bacteria strains do not contain the responsible enzyme, resulting in accumulation of α-acetolactate and high production of diacetyl in dairy products. [18] Diacetyl is important in the buttery flavor in fermented foods and is used as additives in the food industry.

Acetaldehyde is a major contributor to flavor in dairy products, and it is produced mainly by lactic acid bacteria. In addition, lactic acid bacteria can be used to inhibit the growth of harmful microorganisms by producing different antimicrobial compounds including bacteriocin, hydrogen peroxide, carbon dioxide, and diacetyl in addition to the rapid production of lactic acid. [36] Wine lactic acid bacteria play a prominent role in the production of grape wines where their growth and metabolism may positively or negatively affect wine quality. [37] Lactic acid bacteria may also metabolize diacetyl and acetaldehyde during malolactic fermentation in wine and remove Ochratoxin A from wines. [38] Lactic acid bacteria can be also used for the production of exopolysaccharides (EPS) during fermentation to ensure proper rheology, texture and mouth feel of fermented food. [39] Exopolysaccharides could be an alternative low calories and low cost ingredient that can be used to produce smooth and creamy yogurt instead of fat, protein, sugars, or stabilizer. [39] However the production of exopolysaccharides from lactic acid bacteria can be affected by oxygen, pH, temperature, and medium constituents, such as orotic acid and the carbon source. [40]

Table 1: Fermented Foods and Beverages and Their Associated Lactic Acid Bacteria

Fermented Products	Lactic Acid Bacteria
Fermented meats	
- Fermented sausage (Europe)	*Lactobacillus sakei, Lactobacillus curvatus*
- Fermented sausage (USA)	*Pediococcus acidilactici, Pediococcus pentosaceus*
Fermented vegetables	
-Sauerkraut	*Leuconostoc mesenteroides, Lactobacillus plantarum, Pediococcus acidilactici, Leuconostoc mesenteroides, Pediococcus cerevisiae, Lactobacillus brevis*
-Pickles	*Lactobacillus plantarum, Leuconostoc mesenteroides, Lactobacillus pentosus, Lactobacillus Plantarum*
-Fermented olives	*Pediococcus acidilactici, Pediococcus pentosaceus, Lactobacillus plantarum*
-Fermented vegetables	*Lactobacillus fermentum*
Fermented cereals	
-Sourdough	*Lactobacillus sanfransiscensis, Lactobacillus farciminis, Lactobacillus fermentum, Lactobacillus brevis, Lactobacillus plantarum, Lactobacillus amylovorus, Lactobacillus reuteri, Lactobacillus pontis, Lactobacillus panis, Lactobacillus alimentarius,*
-Fermented fish products	*Weisiella cibaria*
	Lactobacillus alimentarius, Carnobacterium piscicola

Lactic Acid Bacteria as Functional Starter Cultures

A starter culture can be defined as a microbial preparation of large numbers of cells of at least one microorganism to be added to a raw material to produce a fermented food by accelerating and steering its fermentation process. The group of lactic acid bacteria occupies a central role in these processes, and has a long and safe history of application and consumption in the production of fermented foods and beverages. [41] They cause rapid acidification of the raw material through the production of organic acids, mainly lactic acid. They also produce acetic acid, ethanol, aroma compounds, bacteriocins, exopolysaccharides, and several enzymes. In this way, they enhance shelf-life and microbial safety, improve texture, and contribute to the pleasant sensory profile of the end product.

The earliest production of fermented foods was based on spontaneous fermentation due to the development of the microflora naturally present in the raw material. The quality of the end product was dependent on the microbial load and spectrum of the raw material. Spontaneous fermentation was optimized through backslopping, i.e., inoculation of the raw material with a small quantity of a previously performed successful fermentation. Hence, backslopping results in dominance of the best adapted strains. It represents a way, be it unconsciously, of using a selected starter culture to shorten the fermentation process and to reduce the risk of fermentation failure. Backslopping is still in use, for instance in the production of sauerkraut and sourdough, and particularly for products which the microbial ecology and the precise role of successions in microbial population are not well known. [42]

The production of fermented foods and beverages through spontaneous fermentation and backslopping represents a cheap and reliable preservation method in less developed countries, whereas in Western countries the large scale production of fermented foods has become an important branch of the food industry. Moreover, the Western consumer appreciates traditionally fermented products for their outstanding gastronomic qualities. [41] The direct addition of selected starter cultures to raw materials has been a breakthrough in the processing of fermented foods, resulting in a high degree of control over the fermentation process and standardization of the end product. Strains with the proper physiological and metabolic features were isolated from natural habitats or from successfully fermented products. [42]

However, some disadvantages have to be considered. In general, the initial selection of commercial starter cultures did not occur in a rational way, but was based on rapid acidification and phage resistance. These starters are not very flexible with regard to the desired properties and functionality of the end product. Originally, industrial starter cultures were maintained by daily propagation. Later, they became available as frozen concentrates and dried or lyophilized preparations, produced on an industrial scale, some of them allowing direct vat inoculation. [43] Because the original starter cultures were mixtures of several undefined microbes, the daily propagation probably led to shifts of the ecosystem resulting in the disappearance of certain strains. Moreover, some important metabolic traits in lactic acid bacteria are plasmid encoded and there is a risk that they are lost during propagation. It is further likely that loss of genetic material occurred due to adaptation to the food matrix. The biodiversity of commercial starters has therefore become limited. This often leads to a loss of the uniqueness of the original product and the loss of the characteristics that have made the product popular. In contrast, the fermentation of traditional fermented foods is frequently caused by natural, wild type lactic acid bacteria that originated from the raw material, the process apparatus, or the environment, and that initiate the fermentation process in the absence of an added commercial starter. Moreover, many traditional products obtain their flavour intensity from the non-starter lactic acid bacteria (NSLAB), which are not part of the normal starter flora but develop in the product, particularly during maturation, as a secondary flora. [44] Pure cultures isolated from complex ecosystems of traditionally fermented foods exhibit a diversity of metabolic activities that diverge strongly from the ones of comparable strains used as industrial bulk starters. These include differences in growth rate and competitive growth behavior in mixed cultures, adaptation to a particular substrate or raw material, antimicrobial properties, and flavour, aroma, and quality attributes. Wild strains need to withstand the competition of other microorganisms to survive in their hostile natural environment, so that they often produce antimicrobials such as bacteriocins. A trend exists in the isolation of wild type strains from traditional products to be used as starter cultures in food fermentation. [45] The consumer pays a lot of attention to the relation between food and health. As a consequence, the market for foods with health promoting properties, so called functional foods, has shown a remarkable growth over the last few years.

Also, the use of food additives is regarded as unnatural and unsafe. Yet, additives are needed to preserve food products from spoilage and to improve the organoleptic properties. The demand for a reduced use of additives and processing seems contradictory with the market preference for products that are fresh, safe, tasty, low in sugar, fat, and salt, and easy to prepare. In cheese making, for instance, the use of raw milk permits the manufacture of high value traditional artisan varieties but brings about safety risks, e.g. the development of Listeria monocytogenes. On the other hand, pasteurization of the milk results in loss of flavour and gives end products that are perceived by the consumer as “boring”. These market trends put the food industry under pressure to look for alternatives. In food fermentation, one of the key points for intervention seems to be on the level of the starter culture. Unfortunately, industrial starter cultures lack the necessary characteristics for product diversification, and the commercial availability of new interesting starter cultures is limited. The increased understanding of the genomics and metabolic of food microbes opens perspectives for starter improvement. Through molecular biology it is now possible to express desirable and suppress undesirable properties of starter culture. [46]

The use of functional starter cultures in the food fermentation industry is being explored. [47] Functional starter cultures are starters that possess at least one inherent functional property. They can contribute to food safety and/or offer one or more organoleptic, technological, nutritional, or health advantages. The implementation of carefully selected strains as starter cultures or co-cultures in fermentation processes can help to achieve in situ expression of desired property, maintaining a perfectly natural and healthy product. Examples are lactic acid bacteria that are able to produce antimicrobial substances, sugar polymers, sweeteners, aromatic compound, useful enzymes, or nutraceuticals, or lactic acid bacteria with health-promoting properties, so called probiotic strains. This represents a way of replacing chemical additives by natural compounds, at the same time providing the consumer with new, attractive food products. It also leads to a wider application area and higher flexibility of starter cultures.

Table 2: Typical Examples of Functional Starter Cultures or Co-Cultures and Their Advantage for the Food Industry

Advantage	Functionality	Lactic acid bacteria
Food preservation	**Bacteriocin production**	
	– Dairy products	*Lactococcus lactis* Subsp. *lactis, Enterococcus* sp.
	– Fermented meats	*Lactobacillus curvatus, Lactobacillus sakei*
	– Fermented olives	*Lactococcus plantarum*
	– Fermented vegetables	*Lactococcus lactis*
Organoleptic	**Exopolysaccharide production**	Several lactobacilli and streptococci
	Production of amylase Aroma generation Enhanced sweetness	Several lactobacilli Several strains
	– Homoalanine- fermenting starters	*Lactococcus lactis*
	– Galactose- positive/glucose negative starters	*Lactobacillus delbrueckii* subsp. *bulgaricus, Streptococcus thermophilus*
	– Malolactic fermentation	*Oenococcus oeni*
Nutritional	**Production of nutraceuticals**	
	– Low-calories sugars	*Lactobacillus plantarum*
	– Production of oligosaccharides	*Lactococcus lactis*
	– Production of B-group vitamins	*Lactococcus lactis, Streptococcus thermophilus*
	Reduction of toxic and antinutritional compound	
	– Production of L(+)- lactic acid isomer	L(+)-lactic acid-producing strains
	– Removal of lactose and galactose	*Streptococcus* thermophilus
	– Removal of raffinose in soy	Several strains
Technological	**Bacteriophage resistance Prevention of over acidification in yoghurt Autolysing starters**	Several strains Lactose-negative *Lactobacillus delbrueckii* subsp. *bulgaricus*
	– Phage-mediated	*Lactococcus lactis* subsp. *lactis*
	– Bacteriocin-induced	*Lactococcus lactis*

Antimicrobial Compounds Produced By Lactic Acid Bacteria

The preservative action of starter culture in food and beverage systems is attributed to the combined action of a range of antimicrobial metabolites produced during the fermentation process. [41] These include many organic acids such as lactic, acetic and propionic acids produced as end products which provide an acidic environment unfavourable for the growth of many pathogenic and spoilage microorganisms. Acids are generally thought to exert their antimicrobial effect by interfering with the maintenance of cell membrane potential, inhibiting active transport, reducing intracellular pH and inhibiting a variety of metabolic functions.

[48] They have a very broad mode of action and inhibit both gram-positive and gram-negative bacteria as well as yeast and molds. [41] One good example is propionic acid produced by propionic acid bacteria, which has formed the basis for some biopreservative products, given its antimicrobial action against microorganisms including yeast and molds.

Obviously, each antimicrobial compound produced during fermentation provides an additional hurdle for pathogens and spoilage bacteria to overcome before they can survive and/or proliferate in a food or beverage, from time of manufacture to time of consumption. Since any microorganism may produce a number of inhibitory substances, its antimicrobial potential is defined by the collective action of its metabolic products on undesirable bacteria. Secondary metabolites produced by lactic acid bacteria which have antagonistic activity include the compound reuterin and the antibiotic reuterocyclin [49] both of which are produced by strains of *Lactobacillus reuteri*. Reuterin is an equilibrium mixture of monomeric, hydrated monomeric and cyclic dimeric forms of b-hydroxypropionaldehyde. It has broad spectrum of activity and inhibits fungi, protozoa and a wide range of bacteria including both gram-positive and gram-negative bacteria. This compound is produced by stationary phase cultures during anaerobic growth on a mixture of glucose and glycerol or glyceraldehydes. The spectrum of inhibition of the antibiotic is confined to gram-positive bacteria including *Lactobacillus sp*., *Bacillus subtilis, Bacillus cereus, Enterococcus faecalis, Staphylococcus aureus* and *Listeria innocua*.

Bacteriocins are ribosomally synthesized antimicrobial compounds that are produced by many different bacterial species including many members of the lactic acid bacteria. [50] Some bacteriocins produced by lactic acid bacteria, such as nisin, inhibit not only closely related species but are also effective against food-borne pathogens and many other gram-positive spoilage microorganisms. [51] For this reason, bacteriocins have attracted considerable interest for use as natural food preservatives in recent years, which have led to the discovery of ever increasing potential sources of these protein inhibitors. Bacteriocin producing strains can be used as part of or adjuncts to starter cultures for fermented foods in order to improve safety and quality.

Lactic Acid Bacteria: Limitations and Challenge in the Food Industry

Lactic acid bacteria have gained increased attentions in research and industry during the last few decades due to the increased applications of lactic acid bacteria and especially with regard to probiotics. The growth characteristics and metabolic activity of lactic acid bacteria have significant impact on the applications. Lactic acid bacteria have fastidious nutritional requirements which required complex nutritional media for normal growth and metabolic activity. The fastidious characteristics of lactic acid bacteria may impact the study of the nutritional requirements and metabolic capacity. Fastidious nutritional requirements may also limit the ability to optimize and control the metabolic activities of lactic acid bacteria. Limitations and challenges with regard to lactic acid bacteria use and applications may apply to different areas including formation of cultivation media, optimizing and controlling metabolic activities, studying the nutritional requirements, and decrease in viability and functionality during storage.

Formation of Cultivation Media

Several culture media have been developed to serve the growth and metabolic activities of lactic acid bacteria. The composition of the culture media has number of factors claimed to affect the growth and functionality of lactic acid bacteria. However, existing media did not satisfy all purposes especially those related to industrial and health applications. For example, existing media such as MRS (de Man-Rogosa-Sharpe) and M17 are expensive, require specific preparation steps, and need a long incubation time. Cost is considered to be the single most important issue with regard to the industrial use of lactic acid bacteria media. Cost is primarily due to the expensive nitrogen sources such as beef extract, yeast extract, and peptone. [52-55] As a result, several studies were carried out to lower the cost of lactic acid bacteria culturing media using low cost materials such as food by-products, agriculture products, and agriculture wastes. With this aim whey and buttermilk, [56] dilapidated egg yolk and yeast autolysate [53] papain hydrolysed whey, [57] cassava bagasse and sugarcane bagasse, [58] ram horn, [59] and many other low cost ingredients were investigated. Many of these materials were able to show a significant improvement in lactic acid bacteria growth and functionality compared to MRS when enhanced with little nutrients. In the laboratory, sweet potato, an abundant agricultural product in the state of North Carolina, was investigated to replace the expensive nitrogen sources in lactic acid bacteria cultivation media. [60] The results indicated that sweet potato could partially replace the expensive ingredient in lactic acid bacteria media and thus could form an alternative low cost medium. In addition to cost, media composition includes number of factors that might affect the growth and functionality of lactic acid bacteria. These limitations include the availability of certain essential molecules that are required for cell metabolism, the production of organic acids that cause a drop in media pH resulting in antimicrobial effects, lack of nutrients during exponential growth, lack of essential minerals such as Fe2+ and Ca2+ that are required by some lactic acid bacteria strains, and lack of different carbon sources that are required or preferred by some lactic acid bacteria strains. [61-62, 53,56] These limitations are due to the fact that lactic acid bacteria strains have a wide range of variations in their growth requirements and that cause much of complexity forming general growth media for lactic acid bacteria.

The fastidious characteristics of lactic acid bacteria, the ability of lactic acid bacteria strains to produce acid and antimicrobial compounds, and the variations in nutritional requirements among lactic acid bacteria strains have added additional limitations and challenges with regard to developing general growth media. In addition, metabolites that are produced by some lactic acid bacteria strains may inhibit the growth of other strains or even the same strain such as in the case of bacteriocin production. On the other hand, low nutrient concentrations may cause fast depletion in the essential nutrient which may negatively affect growth [61] whereas high nutrient concentration such as salts could also negatively affect growth or could be insoluble in water. [63-66] Therefore, several research studies focused on finding alternative ways to lower the cost of the available media [53-54,56] or focused on minimizing negative characteristics of the available media, [67-68,62] whereas others worked on enhancing lactic acid bacteria functionality by optimizing the media composition. [69-70,66]

Studying the Nutritional Requirements

Complex media cannot be used to study the nutritional requirements or the metabolic engineering and metabolic activity of lactic acid bacteria. [9,65,71] Thus several chemically defined medium (CDM) were developed for different research purposes including investigations of the nutritional requirements, identification of specific characteristics, and isolation of auxotrophic mutants. [10] With this aim, a CDM to support a high cell density of lactococci, enterococci, and streptococci, [72] a minimal CDM for exponential growth of *Streptococcus thermophilus*, [9] a food grade media for culturing *Lactobacillus plantarum*, [73] a minimal CDM medium for the growth of *Lactobacillus plantarum*, [71] a CDM for the growth of *Leuconostoc* *mesenteroides*, [64] a selective medium for isolation of lactobacilli from feces, [74] CDM for wine Oenococcus, Lactobacillus, and Pediococcus, [75] an optimized media for the growth of *Lactobacillus sakei*, [65] and several other CDMs were developed. However, establishing CDM requires extensive knowledge of the nutritional requirements of the corresponding species or strain under the study. [9]

Studying the vitamin requirements for lactic acid bacteria growth are complicated since vitamin requirements of lactic acid bacteria represent many differences among strains and some vitamins can replace each other. In general an individual strain requires from one to four vitamins for normal growth.

The growth of microorganisms including lactic acid bacteria required trace amounts of different minerals. [64,76] Studying the mineral requirements of lactic acid bacteria usually observed in CDM by omitting one metal ion in a time. [64,75] However, comprehensive studies on the mineral requirements for bacteria growth and metabolic activity are also complicated and challenging due to several seasons including that metals can replace each other, some metals adsorb others, some metals interact differently in the presence of others, and many organic substances can combine with metals and render them unavailable for growth. In addition, when omitting individual metals to determine their essential role for growth it is possible that small contaminations from other medium compounds or from the glassware may lead to faulty results. [75,77] Thus comprehensive studies and examination on the essential nutritional requirements of lactic acid bacteria have several limitations including the fastidious nutritional requirements of lactic acid bacteria; some nutrients may replace others; some nutrient could be required only in the present of other nutrients; the ability of lactic acid bacteria to adapt to different nutritional environments; and the wide range of differences in the nutritional requirements among lactic acid bacteria strains.

Controlling and Optimizing the Metabolic Activity

For metabolic investigations of lactic acid bacteria it is desirable to have a CDM that can provide reproducibility of chemical composition; avoid unnecessary nutrients and adjust nutrients levels; meet the experimentally determined nutritional requirements of different strains; and support growth at a reasonable rate. [64] On the other hand, since lactic acid bacteria are not naturally optimized for maximal metabolic activity, the enzymatic activity of lactic acid bacteria need to be optimized and maximized towards the desired level of production and the desired end products. Thus many concerns were given to the selection, enhancement, stability, or optimization of different enzymes produced by lactic acid bacteria towards the desired level of activity. Enzymatic activity of lactic acid bacteria is natural process as a result of normal growth and thus the composition of the growth media could play a critical role in the enzymatic activity of lactic acid bacteria.

Growth and metabolic activity of lactic acid bacteria are crucial for the production and quality of fermented foods and for probiotic functionality. Studies related to the growth and metabolic activity of lactic acid bacteria are usually conducted in laboratory media and laboratory environment while use and applications of lactic acid bacteria are conducted in food, feed, or fertilizers. Growth conditions in the laboratory may differ from those available in the industry. Thus it was suggested to study the growth and metabolism of wine lactic acid bacteria in their natural environment wine. [75,78] However, studies in wine may be most relevant from a practical viewpoint and these studies may suffer from reduced applicability to wines made from different grape varieties, in different regions or vintages. In addition, growth in wine tends to be very slow, mainly because of the combined inhibitory effects of ethanol and organic acids. On the other hand, during industrial fermentation, lactic acid bacteria may lead to the formation of compounds with negative organoleptic properties, such as β-D-glucans [79] and acetic acid, [37] as well as the amino acid degradation products such as citrulline, a precursor of carcinogenic ethyl carbamate [80,77] and biogenic amines. Therefore, lactic acid bacteria are often studied in complex laboratory media not containing these inhibitors, such as MRS and M17, where good growth is obtained [75] while similar growth may not be obtained on the industrial environment. It is also important to mention that cultures in the laboratory are cultivated in small quantity while the industry grow the culture in a bulky starter media [80] Thus, CDM is used to study and optimize the growth and metabolic activity of lactic acid bacteria. Upon optimization of an enzymatic activity with a high control coefficient, modeling system can be used to study the effect of the enzyme in the industrial environment. Therefore, larger increase in the importance of bioengineering has been noticed in the areas of lactic acid bacteria applications. However, there is still a gap between laboratory research and industrial application that need to be given more attention.

Decrease in Viability and Functionality during Storage

Viability and functionality of lactic acid bacteria are a major concern especially when it comes to probiotic applications. While not all lactic acid bacteria strains are probiotics [81] most probiotic strains are belonging to lactic acid bacteria or bifidobacteria. Probiotics have been shown to die in the food products during refrigeration distribution and storage. [82-83] Thus, several studies were carried out to enhance the probiotic viability and functionality during storage. With that aim, raffinose, [84] fructooligosaccharides, mannitol, maltodextrin and pectin, [85] inulin [33] and other ingredients were tested. In another studies, encapsulation or microcapsulation were used to protect the bacterial cells from the damage caused by the external environment and to maintain the viability. [86] In food fermentation, the nature of fermented food such as composition (nutrients and antimicrobials), structure (oxygen permeability and water activity) and pH value may affect the functionality of starter culture. [34] Interactions between different strains of lactic acid bacteria during fermentation process or storage may also influence the viability and functionality of lactic acid bacteria. For example, beverages with low pH values below 4.4, combined with long storage periods could cause damage to lactic acid bacteria. Other limitations and challenges include strain selection, inoculation level, growth and survival during processing. [87]

CONCLUSION

Lactic acid bacteria (LAB) play a critical role in food and agricultural applications. The fast growing characteristics of lactic acid bacteria and their metabolic activity have been the key in most applications including food production, agricultural industry, and probiotics. In fermented foods, lactic acid bacteria (LAB) display numerous antimicrobial activities. This is mainly due to the production of organic acids, but also of other compounds, such as bacteriocins and antifungal peptides. Lactic acid bacteria strains also serve in the food industry as starter cultures, co-cultures, or bioprotective cultures, to improve food quality and safety. In addition, antimicrobial production by probiotic Lactic acid bacteria might play a role during in vivo interactions occurring in the human gastrointestinal tract, hence contributing to gut health.

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