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# Food fermentations: role of microorganisms in food production and preservation

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## Abstract

Preservation of foods by fermentation is a widely practiced and ancient technology. Fermentation ensures not only increased shelf life and microbiological safety of a food but also may also make some foods more digestible and in the case of cassava fermentation reduces toxicity of the substrate. Lactic acid bacteria because of their unique metabolic characteristics are involved in many fermentation processes of milk, meats, cereals and vegetables. Although many fermentations are traditionally dependent on inoculation from a previous batch starter cultures are available for many commercial processes such as cheese manufacture thus ensuring consistency of process and product quality. This review outlines the role of lactic acid bacteria in many such fermentations and the mechanisms of antibiosis with particular reference to bacteriocins and gives a brief description of some important fermented foods from various countries. It is anticipated that the contribution of the advances in lactic acid bacteria research towards improvement of strains for use in food fermentation will benefit both the consumer and the producer. © 1999 Elsevier Science B.V. All rights reserved.

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## 1. Introduction

The production of fermented foods is one of the oldest food processing technologies known to man. Since the dawn of civilisation, methods for the fermentation of milks, meats and vegetables have been described, with earliest records dating back to 6000 BC and the civilisations of the fertile crescent in the Middle East (Fox, 1993). Of course, these

processes were artisanal in nature and obviously there could have been no appreciation of the role of microorganisms. Nevertheless, traditions were established by which the handling and storage of certain raw materials in a specific manner, resulted in the development of foods that not only had keeping qualities that were far superior to those of the original substrate, but that also had desirable and organoleptically pleasing characteristics. In most cases, the methodologies and knowledge associated with manufacturing these products were handed down from generation to generation within local communities, monasteries and feudal estates. These

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groups generally produced relatively small quantities of the product which was distributed in or around the immediate area.

By the middle of the 19th century, two events had occurred which had a very significant impact on the manner in which food fermentations were performed and on our understanding of the process. Firstly, the industrial revolution resulted in the concentration of large masses of populations in towns and cities. This meant that the traditional method of supplying such foods within local communities no longer applied. The ability to service these new markets required products to be made in large quantities necessitating the industrialisation of the manufacturing process. Secondly, the blossoming of microbiology as a science from the 1850s onwards resulted in the biological basis of fermentation being understood for the first time. Thus, the essential role of bacteria, yeasts and moulds in the generation of fermented foods came to be understood and this ultimately resulted in more controlled and efficient fermentations.

The coincidence of scientific advancement and the industrialisation of the manufacture of fermented foods was fortunate. Clearly, the traditional approach of backslopping or even natural fermentation of substrate was not an appropriate foundation upon which to base any large-scale industrial process. The advent of retailing and mass marketing required that products of consistent quality and safety be available. For many fermented foods, but particularly milk-derived products, the characterisation of the microorganisms responsible for the fermentation towards the end of the 19th century led to the isolation of starter cultures which could be produced on a large scale to supply factories involved in the manufacture of these products. This significant development had a major impact on the processes used and contributed to ensuring consistency of product and reliability of fermentation. These developments paralleled significant technological advances in the handling and processing of milk which has resulted in dairy fermentations being among the most sophisticated and best researched of the food fermentations to this day. For example, research on the lactic acid bacteria, which have a dominant role in the production of many fermented foods, particularly those that are milk-based, has continued to advance at a very impressive rate through the 20th century

and our understanding of, and ability to manipulate and control these bacteria is now at a level that would have been unimaginable even 20 years ago. This explains, in part, how it is possible to process millions of litres of milk into cheese in a single day in a controlled method where product of the highest quality can be consistently produced.

Although the developed world can claim to have elevated the production of some fermented foods to a large industrial and technologically sophisticated level, it is still true that even in Europe, there are regions where products are manufactured in a traditional localised 'cottage' or 'farmhouse' manner. The concept of using backslopping is still practised for some products including a range of cheeses and fermented meats and vegetables. In fact, many of these products are now considered to be of a premium type because they retain flavour and aroma characteristics that many would claim have all but disappeared in the 'factory' manufactured products. However, it appears to be inevitable and even ironical that as such products become more popular and as demand grows, the only way in which the expanding market can be satisfied is to upscale the manufacturing process where the use of starter cultures becomes almost essential. This often has the consequence of diminishing the uniqueness of the original product and the loss of those very characteristics that originally made the product popular. One of the challenges facing scientists and technologists in the future will undoubtedly be to allow the large-scale production of fermented foods without losing the unique flavour and other traits associated with the traditional products from which they are derived.

The original and primary purpose of fermenting food substrates was to achieve a preservation effect. However, with the development of the many effective alternative preservation technologies which are now commonly available, particularly in the Western World, this is no longer the most pressing requirement and many of these foods are manufactured because their unique flavour, aroma and texture attributes are much appreciated by the consumer. However, even in these situations, the conditions generated by the fermentation are essential in ensuring the shelf-life and microbiological safety of the products. Nevertheless, there are many parts of the world where the preservation role is still the essential

one and where the fermentation process is still performed on an artisanal rather than industrial basis. In many cases these fermentations have only come under scientific scrutiny in the relatively recent past and thus are still only moderately or poorly understood.

In this review, the role of the fermentation process in mediating antibiosis in fermented foods will be examined. This will focus almost entirely on the lactic acid bacteria whose activity in fermented foods and whose biochemical and metabolic properties are well characterised. In addition, the range of different types of fermented products that are produced in different parts of the world will be briefly surveyed. The reader is directed to the excellent overviews in the text edited by Wood (1998) as a source of more detailed information on this topic. Fermented beverages are not within the scope of this review.

## 2. Essential elements of food fermentation

Preservation of foods by fermentation depends on the principle of oxidation of carbohydrates and related derivatives to generate end-products which are generally acids, alcohol and carbon dioxide. These end-products control the growth of food spoilage microorganisms and because the oxidation is only partial, the food retains sufficient energy potential to be of nutritional benefit to the consumer.

Using its most rigorous, chemical definition the term 'fermentation' is applied to describe a strictly anaerobic process; however, the general understanding of the term now encompasses both aerobic and anaerobic carbohydrate breakdown processes.

Most fermented foods, including the major products that are common in the western world, as well as many of those from other sources that are less well characterised, are dependent on lactic acid bacteria to mediate the fermentation process. The end-products of carbohydrate catabolism by these bacteria contribute not only to preservation but also to the flavour, aroma and texture, thereby helping to determine unique product characteristics. Being able to control the specific microorganisms or the succession of microorganisms that dominate the microflora of foods (which is the basis of development of starter cultures) is therefore very desirable. Fermentation may also increase the nutritional quality of food by

increasing digestibility as in the fermentation of milk to cheese. In addition, the contribution of functional attributes to a food through fermentation is likely to be one of the major research themes of the next decade and beyond. This not only includes traditional activities such as the delivery of probiotic bacteria in products such as fermented milks, but will most probably be extended to the generation of functional components like vitamins, antioxidants and other compounds in a variety of different fermented foods (Steinkraus, 1998). Toxicity of foods may also be reduced by fermentation as occurs in the production of gari. A range of fermented foods, their country of origin and the microorganisms which dominate the fermentation, is shown in Table 1.

## 3. Metabolic activity of lactic acid bacteria

Lactic acid bacteria are generally mesophilic but can grow at temperatures as low as 5°C or as high as 45°C. Similarly, while the majority of strains grow at pH 4.0–4.5, some are active at pH 9.6 and others at pH 3.2. Strains are generally weakly proteolytic and lipolytic and require preformed amino acids, purine and pyrimidine bases and B vitamins for growth (Stamer, 1976; Cogan and Hill, 1993; Jay, 1996). An overview of the lactic acid bacteria is presented in the texts edited by Wood and Holzapfel (1996) and Salminen and von Wright (1998) and the reader is directed to these sources for information relating to aspects such as taxonomy, biochemistry, physiology, ecology and applications.

All lactic acid bacteria produce lactic acid from hexoses and since they lack functional heme linked electron transport chains and a functional Krebs cycle, they obtain energy via substrate level phosphorylation. The lactic acid produced may be L (+) or, less frequently, D (–) or a mixture of both. It should be noted that D (–) lactic acid is not metabolised by humans and is not recommended for infants and young children (WHO, 1974), a fact exploited by the marketers of a strain of *Lb. bavaricus* in Germany for use in the production of speciality L (+) sauerkraut (Lucke et al., 1990).

The pathways by which hexoses are metabolised divides lactic acid bacteria into two groups, homofermentative and heterofermentative (Fig. 1). For a detailed description of these pathways the reader is

Table 1  
Examples of fermented foods<sup>a</sup>

Product	Country	Microorganism(s)	Substrate
Bread	International	<i>Saccharomyces cerevisiae</i> , other yeasts, lactic acid bacteria	Wheat, rye, other grains
Bongkrek	Indonesia	<i>Rhizopus oligosporus</i>	Coconut press cake
Gari	West Africa	<i>Corynebacterium manihot</i> , other yeasts, lactic acid bacteria ( <i>Lb. plantarum</i> , <i>Streptococcus</i> spp.)	Cassava root
Idli	Southern India	Lactic bacteria ( <i>Ln. mesenteroides</i> , <i>E. faecalis</i> ) <i>Torulopsis</i> , <i>Candida</i> , <i>Trichosporon pullulans</i>	Rice and black gram dhal
Kenkey	Ghana	Unknown	Maize
Kimchi	Korea	Lactic acid bacteria	Cabbage, vegetables, sometimes seafood, nuts
Mahewu	South Africa	Lactic acid bacteria	Maize
Ogi	Nigeria, West Africa	Lactic bacteria <i>Cephalosporium</i> , <i>Fusarium</i> , <i>Aspergillus</i> , <i>Penicillium</i> spp., <i>Saccharomyces cerevisiae</i> , <i>Candida mycoderma</i> , <i>C. valida</i> , or <i>C. vini</i>	Maize
Oncom	Indonesia	<i>Neurospora intermedia</i> , or <i>Rhizopus oligosporus</i>	Peanut press cake
Soy sauce	The Orient (Japan, China, Philippines)	<i>Aspergillus oryzae</i> or <i>A. soyae</i> , <i>Lactobacillus</i> , <i>Zygosaccharomyces rouxii</i>	Soybeans and wheat
Tempeh	Indonesia Surinam	<i>Rhizopus oligosporus</i>	Soybeans
Nan	India	<i>Saccharomyces cerevisiae</i> Lactic acid bacteria	White wheat flour
Cheese	International	Lactic acid bacteria, ( <i>L. lactis</i> , <i>S. thermophilus</i> , <i>Lb. shermanii</i> ) <i>bulgaricus</i> , <i>Propionibacterium shermanii</i> ) sometimes moulds, ( <i>Penicillium</i> spp.)	Milk
Yoghurt	International	<i>S. thermophilus</i> , <i>Lb. bulgaricus</i>	Milk, milk solids
Fermented sausages	Southern and Central Europe, U.S.A.	Lactic acid bacteria (lactobacilli, pediococci), Catalase positive cocci ( <i>S. carnosus</i> ), <i>S. xylosum</i> , <i>M. varians</i> ) sometimes yeasts and/or moulds	Mammalian meat, generally pork and/or beef, less often poultry
Sauerkraut	International	Lactic acid bacteria <i>Ln. mesenteroides</i> , <i>Lb. brevis</i> , <i>Lb. plantarum</i> , <i>Lb. curvatus</i> , <i>Lb. sake</i>	Cabbage
Pickles	International	<i>P. cerevisiae</i> , <i>Lb. plantarum</i>	Cucumber
Olives	Mediterranean	<i>Ln. mesenteroides</i> , <i>Lb. plantarum</i>	Green olives

<sup>a</sup> Compiled from Jay (1996), Beuchat (1997), Knorr (1998) and Lücke (1998).

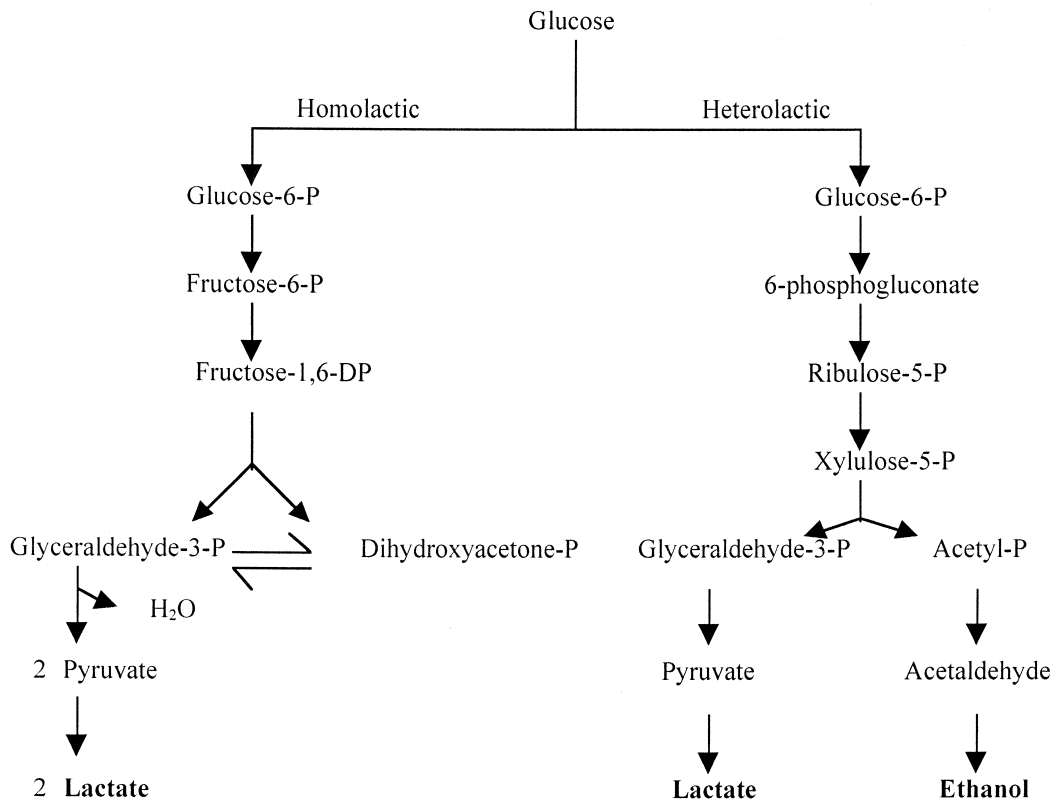


Fig. 1. Generalized scheme for the fermentation of glucose in lactic acid bacteria.

referred to Axelsson (1998). Briefly, homofermenters such as *Pediococcus*, *Streptococcus*, *Lactococcus* and some lactobacilli produce lactic acid as the major or sole end-product of glucose fermentation. However, under altered growth conditions and when the initial substrate is a pentose this may change (London, 1990; Kandler, 1983). Homofermenters use the Embden–Meyerhof–Parnas pathway to generate two moles of lactate per mole of glucose and derive approximately twice as much energy per mole of glucose as heterofermenters. Heterofermenters such as *Weisella* and *Leuconostoc* and some lactobacilli produce equimolar amounts of lactate, CO<sub>2</sub> and ethanol from glucose via the hexose monophosphate or pentose pathway.

The metabolism of the disaccharide lactose is of primary importance in those lactic acid bacteria used in dairy fermentations and is reviewed in Fox et al. (1990) and Axelsson (1998). Lactose may enter the cell using either a lactose carrier, lactose permease, followed by cleavage to glucose and galactose or via

a phosphoenolpyruvate-dependent phosphotransferase (PTS) followed by cleavage to glucose and galactose-6-phosphate. Glucose is metabolised via the glycolytic pathway, galactose via the Leloir pathway and galactose-6-phosphate via the tagatose-6-phosphate pathway. Most *L. lactis* strains used as starters for dairy fermentations use the lactose PTS, the genes for which are plasmid located. Among some thermophilic LAB only the glucose moiety of the sugar is metabolised and galactose is excreted into the medium, although mutants of *S. thermophilus* have been described which metabolise galactose via the Leloir pathway (Thomas and Crow, 1984; Hutkins and Morris, 1987; Cogan and Hill, 1993).

Citrate metabolism is important among *L. lactis* subsp. *lactis* (biovar *diacetylactis*) and *Lc. mesenteroides* subsp. *cremoris* strains used in the dairy industry, as it results in excess pyruvate in the cell. The pyruvate may be converted via  $\alpha$ -acetolactate to diacetyl, an important flavour and aroma component

of butter and some other fermented milk products (Cogan and Hill, 1993) (Fig. 2). Strategies designed to increase the carbon metabolic flux towards diacetyl production have resulted in mutants which produce large amounts of this compound (Hugenholtz, 1993; de Vos, 1996; Swindell et al., 1996).

The proteolytic system of *Lactococcus* has been investigated in detail due to its pivotal role in allowing growth in milk and the development of flavour and texture in cheese. For a recent comprehensive review the reader is directed to Kunji et al. (1996). In summary, casein is degraded by a membrane-anchored serine proteinase (PrtP) with many of the resulting oligopeptides being sufficiently

small to allow them to be transported into the cell via an oligopeptide transport system (Opp), where they are further processed by a variety of intracellular peptidases. Amino acid, and di- and tri-peptide transport systems also exist but there is only poor growth in milk when mutants are deficient in PrtP (Kunji et al., 1995). Commercial culture adjuncts (mesophilic and thermophilic starter cultures) are available to promote proteolysis in cheese and can aid in the development of a consistent cheese flavour (Fox et al., 1996; Beresford and Cogan, 1997). It is notable that over-expression of a lactococcal proteinase did not result in an acceleration of cheese ripening or in an enhancement of flavour (Law et al., 1993). Mutants lacking combinations of up to five

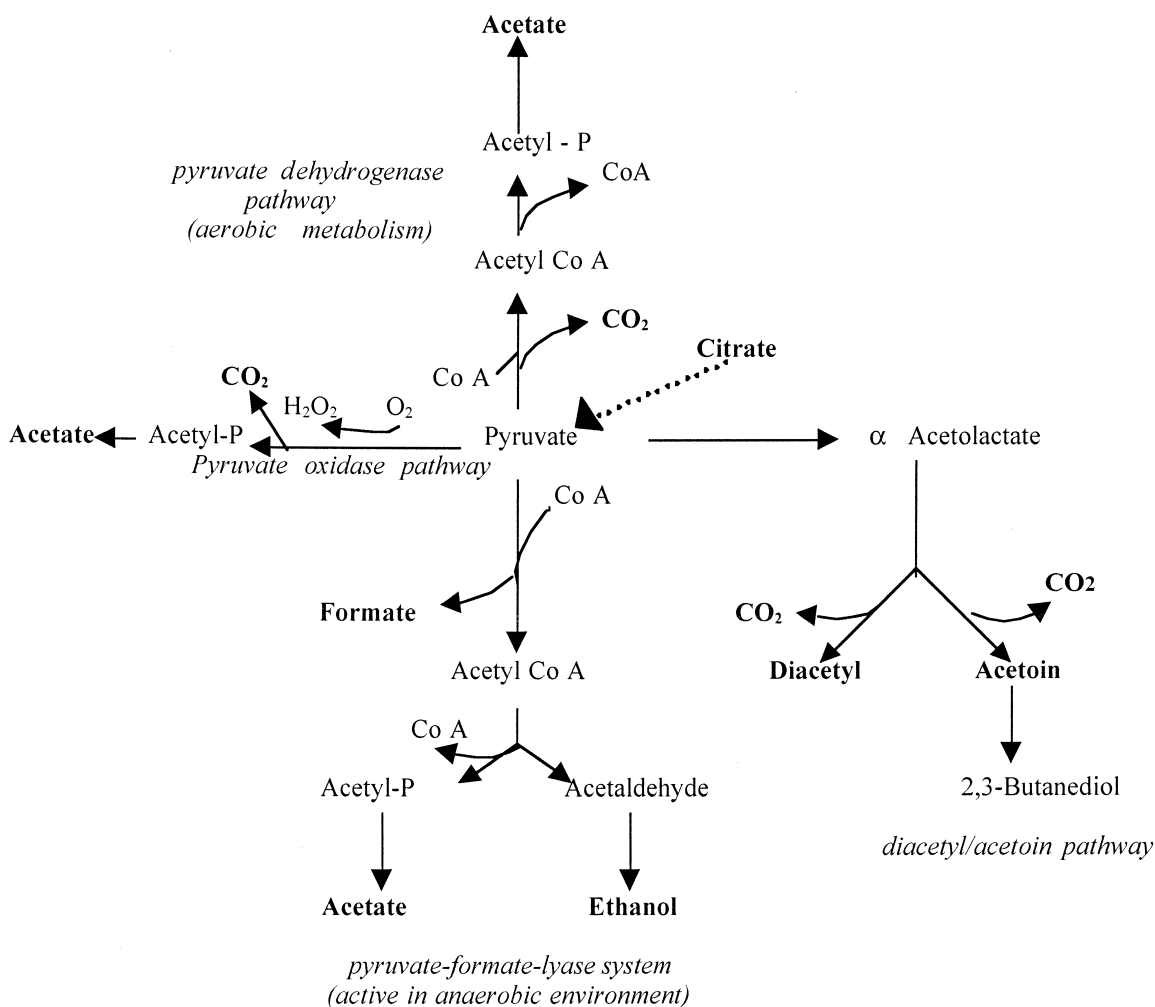


Fig. 2. Generalized scheme for the formation of important metabolic products from pyruvate in lactic acid bacteria.

peptidases have been isolated by Mierau et al. (1996) and these are currently being used to examine the contribution of these enzymes to the flavour and ripening of cheese (Daly et al., 1998).

Lysis of starter cultures during cheese ripening leads to increased proteolytic activity in cheese and thus theoretically results in accelerated ripening and/or a better cheese flavour. A good example of this is found in Swiss cheese where autolytic propionibacteria increase the amount of free proline in the cheese aiding flavour development (Lemee et al., 1994; Dupuis et al., 1995; Østlie et al., 1995). Morgan et al. (1997) have used bacteriocin-induced lysis of a starter to produce cheese with a higher concentration of free amino acids and decreased bitterness levels.

#### 4. Microbial interference

General microbial interference is an effective non-specific control mechanism common to all populations and environments including foods. It represents the inhibition of the growth of certain microorganisms by other members of a habitat and was first used to describe the suppression of virulent staphylococci by avirulent strains (Shinefield et al., 1971). In order to operate efficiently the interfering flora, generally the normal background flora of the habitat, needs to outnumber the target host many times. The mechanisms involved include nutrient competition, generation of an unfavourable environment, competition for attachment/adhesion sites and are common to all genera.

#### 5. Mechanisms of antibiosis mediated by lactic acid bacteria

The specific antimicrobial mechanisms of lactic acid bacteria exploited in the biopreservation of foods include the production of organic acids, hydrogen peroxide, carbon dioxide, diacetyl, broad-spectrum antimicrobials such as reuterin and the production of bacteriocins (De Vuyst and Vandamme, 1994). Many of these factors are thought to play a role in the inhibitory effect of Microguard<sup>R</sup> (Al-Zoreky et al., 1991; Lyon et al., 1993). It is produced by the fermentation of skimmed milk by *Prop-*

*ionibacterium freudenreichii* subsp. *shermanii*, which is subsequently pasteurised and added as a Generally Recognised as Safe (GRAS) food preservative to much of the cottage cheese production in the U.S. to prevent the growth of gram-negative bacteria and moulds.

##### 5.1. Organic acids, acetaldehyde and ethanol

The direct antimicrobial effects of organic acids including lactic, acetic (Fig. 2) and propionic which may be produced by lactic acid bacterial fermentation of foods, are well known (Davidson, 1997). The antagonism is believed to result from the action of the acids on the bacterial cytoplasmic membrane which interferes with the maintenance of membrane potential and inhibits active transport (Sheu et al., 1972; Eklund, 1989; De Vuyst and Vandamme, 1994a), and may be mediated both by dissociated and undissociated acid (Cherrington et al., 1991). The antimicrobial activity of each of the acids at a given molar concentration is not equal. Acetic acid is more inhibitory than lactic acid and can inhibit yeasts, moulds and bacteria (Blom and Mortvedt, 1991). Propionic acid inhibits fungi and bacteria and is present in Microguard<sup>R</sup> as described above and also in another commercial product, Bioprofit<sup>R</sup> where the use of a *Propionibacterium freudenreichii* strain along with *Lactobacillus rhamnosus* increases inhibitory activity against fungi and some gram positive bacteria (Måyrå-Måkinen and Suomalainen, 1995). The contribution of acetaldehyde to biopreservation is minor since the flavour threshold is much lower than the levels that are considered necessary to achieve inhibition of microorganisms (Kulshrestha and Marth, 1974). Similarly, although ethanol may be produced by lactic cultures, again the levels produced in food systems are so low that the contribution to antibiosis is minimal.

##### 5.2. Hydrogen peroxide

Lactic acid bacteria lack true catalase to break down the hydrogen peroxide generated in the presence of oxygen. It is argued that the H<sub>2</sub>O<sub>2</sub> can accumulate and be inhibitory to some microorganisms (Condon, 1987). Inhibition is mediated through the strong oxidising effect on membrane lipids and cell proteins (Morris, 1976; Lindgren and

Dobrogosz, 1990). Hydrogen peroxide may also activate the lactoperoxidase system of fresh milk with the formation of hypothiocyanate and other antimicrobials (Reiter and Harnulv, 1984; Pruitt et al., 1986; Condon, 1987; De Vuyst and Vandamme, 1994a). However, because of the ability of other enzyme systems such as flavoproteins and peroxidases to breakdown  $H_2O_2$  it is not clear what, if any, the in vivo contribution of  $H_2O_2$  is to antibacterial activity (Nagy et al., 1991; Fontaine et al., 1996).

### 5.3. Carbon dioxide

Carbon dioxide, formed from heterolactic fermentation, can directly create an anaerobic environment and is toxic to some aerobic food microorganisms through its action on cell membranes and its ability to reduce internal and external pH (Eklund, 1984; De Vuyst and Vandamme, 1994a). At low concentration, it may be stimulatory to the growth of some bacteria (Lindgren and Dobrogosz, 1990). Production of  $CO_2$  resulting from the use of lactate by propionibacteria in Swiss cheese manufacture is responsible for the characteristic “eyes” of the finished product.

### 5.4. Diacetyl

Diacetyl is a product of citrate metabolism (Lindgren and Dobrogosz, 1990; Cogan and Hill, 1993) and is responsible for the aroma and flavour of butter and some other fermented milk products. Many lactic acid bacteria including strains of *Leuconostoc*, *Lactococcus*, *Pediococcus* and *Lactobacillus* may produce diacetyl although production is repressed by the fermentation of hexoses (Jay, 1982; Cogan, 1986). Gram-negative bacteria, yeasts and moulds are more sensitive to diacetyl than gram-positive bacteria and its mode of action is believed to be due to interference with the utilisation of arginine (Jay, 1986; Motlagh et al., 1991; De Vuyst and Vandamme, 1994a). Diacetyl is rarely present in food fermentations at sufficient levels to make a major contribution to antibacterial activity.

### 5.5. Reuterin

Reuterin is produced during stationary phase by the anaerobic growth of *Lactobacillus reuteri* on a mixture of glucose and glycerol or glyceraldehyde. It

has a general antimicrobial spectrum affecting viruses, fungi and protozoa as well as bacteria (Axelsson et al., 1989; Chung et al., 1989). Its activity is thought to be due to inhibition of ribonucleotide reductase (Dobrogosz et al., 1989).

### 5.6. Bacteriocins

A recent definition of bacteriocins produced by lactic acid bacteria suggests that they should be regarded as extracellularly released primary or modified products of bacterial ribosomal synthesis, which can have a relatively narrow spectrum of bactericidal activity. They should include at least some strains of the same species as the producer bacterium and against which the producer strain has some mechanism(s) of specific self protection (Jack et al., 1995; see also text edited by De Vuyst and Vandamme, 1994). The possibility of exploiting bacteriocins in food fermentations arises where the inhibitory spectrum includes food spoilage and/or pathogenic microorganisms or gives the producing strain a competitive advantage in the food milieu. The target of bacteriocins is the cytoplasmic membrane and because of the protective barrier provided by the LPS of the outer membrane of gram-negative bacteria, they are generally only active against gram-positive cells (Ray, 1993; Abee et al., 1995; Sahl et al., 1995; Venema et al., 1995). In the context of fermentation, important targets include spoilers such as species of *Clostridium* and heterofermentative lactobacilli and foodborne pathogens including *Listeria monocytogenes*, *Staphylococcus* spp., *Clostridium*, *Enterococcus* and *Bacillus* spp. The permeability of gram-negative bacteria can be increased by sublethal injury including that which can occur when using ultrahigh hydrostatic pressure (UHP) and pulsed electric field (PEF) as nonthermal methods of preservation (Kalchayanand et al., 1994). In addition, disruption of the integrity of the outer membrane (Kordel and Sahl, 1986; Kalchayanand et al., 1992) through the use of food grade chelating agents such as EDTA and citrate which bind magnesium ions in the LPS layer can increase the effectiveness of bacteriocins against gram-negative bacteria (Stevens et al., 1992). Many bacteriocins are most active at low pH (Mortvedt-Abildgaard et al., 1995; Garcia-Garcera et al., 1993) and there is evidence that bacteriocinogenic strains can be readily isolated from fresh and fermented



foods (Schillinger and Lucke, 1989; Vaughan et al., 1994; Cintas et al., 1997; Kimura et al., 1997; Kelly et al., 1998; Choi et al., 1999). Strains may naturally produce more than one bacteriocin (van Belkum et al., 1992; Dodd and Gasson, 1994; Quadri et al., 1994; Worobo et al., 1994) and heterologous expression of bacteriocins has been demonstrated in constructed strains (Allison et al., 1995). Protein engineering has led to the development of nisin derivatives with altered antimicrobial activities or greater solubility at pH 6 than the wild-type nisin (Kuipers et al., 1992; Rauch et al., 1994). An advantage of bacteriocins over classical antibiotics is that digestive enzymes destroy them. Bacteriocin producing strains can be used as part of, or adjuncts to starter cultures for fermented foods in order to improve safety and quality.

Bacteriocins of lactic acid bacteria, according to the classification procedure proposed by Klaenhammer (1993) and modified by Nes et al. (1996), are divided into four major subclasses, Table 2. The majority of those produced by bacteria associated with food belong to classes I and II.

### 5.6.1. Class I

Bacteriocins of this class contain post-translationally modified amino acids and are also termed lantibiotics. The most extensively characterised of these is nisin which has GRAS status for use as a direct human food ingredient (Federal Register, 1988). It is produced by strains of *L. lactis* subsp. *lactis* and has a broad inhibitory spectrum against gram-positive bacteria, including many pathogens and can prevent outgrowth of *Bacillus* and *Clostridium* spores (Daeschel, 1989). It sensitises spores

of *Clostridium* to heat allowing a reduction in thermal processing (Hurst, 1981).

Nisin is approved for use, to varying degrees, as a component of the preservation procedure for processed and fresh cheese, canned foods, processed vegetables and baby foods, in up to 50 countries (Hurst, 1981; Delves-Broughton, 1990; De Vuyst and Vandamme, 1994b). Typical levels that are used in foods range between 2.5 and 100 ppm. It is most stable in high-acid foods.

The addition of a nisin-producing strain of *L. lactis* to the starter culture used in the manufacture of nitrate-free Gouda cheese has been demonstrated to result in the prevention of the outgrowth of *C. tyrobutyricum* spores (Hugenholtz and de Veer, 1991) and it has also been shown to inhibit the growth of *L. monocytogenes* in cottage and Camembert cheese (Benkerroum and Sandine, 1988; Maisnier-Patin et al., 1992). Harris et al. (1992) demonstrated the inhibition of nisin-sensitive *Lb. plantarum* and the growth to maximum densities of nisin-resistant *Lc. mesenteroides* in cabbage juice using two nisin-producing strains of *L. lactis* subsp. *lactis* isolated from sauerkraut. Pure nisin and mutants of *Lc. mesenteroides* resistant to high concentrations of nisin were used to achieve an extension of the heterolactic fermentation and a delay in the initiation of the homolactic fermentation of sauerkraut (Breidt et al., 1993). Choi et al. (1990) reduced the rate of acid production in a naturally occurring Korean kimchi fermentation using low levels of nisin. In meats, nisin is not as successful a preservative, but it may allow a reduction in the levels of nitrite used in cured meat products (Rayman et al., 1983; Shahidi, 1991).

Hugenholtz et al. (1995) conjugatively transferred

Table 2  
Classes of bacteriocins produced by lactic acid bacteria<sup>a</sup>

Class	Subclass	Description
I		Lantibiotics—small, heat stable, containing unusual amino acids
II	IIa	Small (30–100 amino acids), heat stable, non-lantibiotic Pediocin-like bacteriocins, with anti-listerial effects Two peptide bacteriocins Sec-dependent secretion of bacteriocins
	IIb	
	IIc	
III		Large (> 30 kDa) heat-labile proteins
IV		Complex bacteriocins with glyco- and/or lipid moieties

<sup>a</sup> Reproduced from Daly et al. (1998) with permission.

the determinants for nisin production and immunity to two components of a starter culture for Gouda cheese manufacture. Both production and immunity were transferred to the citrate-utilising component, *L. lactis* subsp. *lactis* (biovar. *diacetylactis*) and immunity only to *L. lactis* subsp. *cremoris*. Cheese made with these starters showed increased protection against the development of *C. tyrobutyricum* and *Staphylococcus aureus* throughout ripening.

Lacticin 3147, produced by a lactococcal isolate from Irish Kefir grains used in the manufacture of buttermilk, is effective against a wide spectrum of gram-positive bacteria (McAuliffe et al., 1998; Ryan et al., 1998; McAuliffe et al., 1999). Unlike nisin, lacticin 3147 is effective at neutral pH. The genetic determinants of the lacticin are located on a conjugative plasmid and have recently been transferred to strains used in the manufacture of Cheddar cheese (Ryan et al., 1996). The resulting cheeses were of normal composition except that they contained no non-starter lactic acid bacteria (NSLAB). This application of lacticin 3147 will prove very useful in studying the role of these latter bacteria in developing flavour and other characteristics in cheeses.

### 5.6.2. Class II

This class is divided into three sub-groups of which the Class IIa is the most common (Table 2). This group is composed of the pediocin-like bacteriocins with anti-listerial activity. Pediocins are produced by *Pediococcus* spp. and while they are not very effective against spores they are more effective than nisin in some food systems such as meat. Pediococci are the main starter culture used in the manufacture of American-style fermented meats and they are also important in the fermentation of many vegetables. Pediocin PA-1/AcH (Gonzalez and Kunka, 1987; Bhunia et al., 1988) is the prototype bacteriocin of this class and pediocin-producing cultures are readily isolated from fermented foods (Kimura et al., 1997). Many studies report the inhibition of *L. monocytogenes* by pediocins or pediocin-producing cultures in fermented sausages (Berry et al., 1990; Foegeding et al., 1992; Luchansky et al., 1992) and in Italian salami (Campanini et al., 1993).

Sakacin 674 produced by a *Lb. sake* isolated from meat and very similar to pediocin PA-1 (Holck et al., 1994) has been shown to delay or inhibit growth of

*L. monocytogenes* in vacuum-packed, sliced Bologna type sausage whether added in purified form or in the form of a bacteriocin producing culture (Abee et al., 1995).

### 5.6.3. Other bacteriocins

In Europe the principal starters used in the manufacture of dry fermented sausage are *Lb. sake*, *Lb. curvatus* and *Lb. plantarum*. Inhibition of *Listeria* by a bacteriocinogenic *Lb. sake* strain isolated from a naturally fermented sausage has been demonstrated and it was suggested that *Lb. sake* CTC494 be employed as a bioprotective culture in fermented meat products (Hugas et al., 1995).

## 6. Aspects to be considered in the use of bacteriocins/bacteriocinogenic cultures in fermented foods

Sensitivity to bacteriocins is strain dependent and resistance among sensitive cells has been reported with resistance to nisin cited as occurring at a frequency of  $10^{-6}$  (Harris et al., 1992; Ming and Daeschel, 1993; Mazotta et al., 1995). Whether that frequency would be valid in the complex background of a food is unknown. The use of more than one bacteriocin or bacteriocin-producing strain in a specific food system must be carefully controlled so that mutants resistant to one antimicrobial will not be cross-resistant to the others (Rekhif et al., 1994). The implications of resistance arising from general mechanisms such as the alteration of membrane fluidity have to be studied in relation to resistance to other antimicrobial agents (Juenja and Davidson, 1993; Montville and Winkowski, 1997). Nisin is the only bacteriocin with GRAS status for use in specific foods and this was awarded as a result of a history of 25 years of safe use in many European countries and was further supported by the accumulated data indicating its nontoxic, nonallergenic nature (Federal Register, 1988). Other bacteriocins without GRAS status (which can be based on documented use prior to 1958) will require premarket approval. Therefore bacteriocinogenic starters, particularly if used in natural fermentations, will most likely afford the best opportunities for the application of bacteriocins in the near future.

## 7. Fermented foods

Fermented foods are now regarded as part of our staple diet. The main substrates used in the commercial production of the most familiar fermented products are milk, meat, cucumber and cabbage. These yield over 400 varieties of cheese of 20 distinct types (Jay, 1996) and a very extensive range of yoghurt and fermented milk drinks, fermented sausages and salamis, pickles and sauerkraut.

### 7.1. Milk products

The lactic fermentation of milk is required for cheese production. While some cheeses are still made from non-pasteurised milk and may even depend on the natural lactic flora for the fermentation, most are produced on a commercial scale using the appropriate starter culture. These can contain mesophilic *L. lactis* subsp. *lactis* and *L. lactis* subsp. *cremoris* or thermophilic *S. thermophilus*, *Lb. helveticus*, and *Lb. delbrueckii* subsp. *bulgaricus*, depending on the specific application (Cogan and Hill, 1993; see text edited by Cogan and Accolas, 1996). Thermophilic strains are generally used in cheeses with a high cooking temperature such as Swiss and Italian types. Secondary microflora are added in some processes to affect texture (e.g., the production of CO<sub>2</sub> by *Propionibacterium* in Swiss cheese) and flavour (e.g., by the production of diacetyl). Moulds, yeasts and bacteria other than lactic acid bacteria are used as secondary microflora in some varieties of cheese (e.g., *Penicillium roqueforti* in blue-veined cheeses). Starter culture improvement with respect to carbohydrate fermentation, proteolysis, production of flavour compounds and protection from the scourge of phage attack have been the subject of much research and some excellent recent reviews include those of Klaenhammer and Fitzgerald (1994), Dinsmore and Klaenhammer (1995), Garvey et al. (1995), Daly et al. (1996), de Vos (1996), Josephsen and Neve (1998) and Daly and Davis (1998).

The starter used in yoghurt production is a mixed culture of *S. thermophilus* and *Lb. bulgaricus* in a 1:1 ratio. The *Streptococcus*, which is inhibited at pH 4.2–4.4, grows first and the *Lactobacillus*, which adds aroma and flavour (acetaldehyde), can tolerate values as low as pH 3.5–3.8.

Kefir is a fermented milk drink with an alcohol

content of up to 1%. The starter consists of characteristic 'Kefir grains' which contain the acid producing *L. lactis* and *Lb. delbrueckii* subsp. *bulgaricus* and an alcohol-producing *Torula* spp. Kumiss which is produced in Russia is similar to kefir but uses mares milk. Fermentation can result in an alcohol content of up to 2%.

*Lb. acidophilus* and *Lb. delbrueckii* subsp. *bulgaricus* are used in the production of acidophilus milk and Bulgarian buttermilk where the inoculated sterile milk is held at 37°C until a smooth curd develops (Jay, 1996).

The popularity of fermented milk drinks is increasing, not only because of their attractive taste but also because of the many health benefits reportedly associated with them. The topic of probiotic bacteria is one which has been damaged by research of debatable quality over the years, but in the recent past this situation has improved significantly and these developments are reviewed in a number of recent references (Lee and Salminen, 1995; Casas et al., 1998; Charteris et al., 1998; Isolauri et al., 1998; Lichtenstein and Goldin, 1998) as well as in accompanying reviews in this volume.

### 7.2. Meat products

Fermented sausages are produced as a result of the lactic fermentation of a mixture of comminuted meat mixed with fat, salt, curing agents (nitrate/nitrite), sugar and spices and these represent traditional foods of central and southern Europe. Lucke (1998) estimates that the European Union produced 750 000 tonnes of sausage in 1995. These sausages are generally classified as dry or semi-dry. Dry sausages have a water activity ( $a_w$ ) of less than 0.90, are not usually smoked or heat processed and are eaten without cooking. The  $a_w$  of semi-dry sausages is in the range 0.90–0.95 and they generally receive a heat treatment of 140–154°F (60–68°C) during smoking. Fermentation temperatures vary according to the individual product but they are generally less than 72°F (22°C) for dry and mould-ripened sausages and 72–79°F (22–26°C) for semi-dry varieties (Lucke, 1998). Sausages produced without added starter have a final pH of 4.6–5.0, while those produced using starter generally have a final pH of 4.0–4.5. The predominant species during lactic fermentation of sausages are psychrotrophic *Lb. sake*

and *Lb. curvatus*, Hugas et al., 1993; Smalelis et al., 1994. According to Lucke et al. (1990), most European fermented sausages formulated with nitrite are produced with added starter culture, generally consisting of lactic acid bacteria (lactobacilli and pediococci) and catalase-positive cocci (*S. carnosus*, *Micrococcus varians*). Yeasts and moulds that are available as starters include *Debaryomyces hansenii*, *Candida famata* and *Penicillium nalgiovense* and *P. chrysogenum*, respectively. The use of starter cultures ensures a good quality, standardised, safe product. For a review of the criteria used to select good meat starters see Jessen (1995). Lactic acid bacteria producing bacteriocins have been demonstrated to reduce the count of *L. monocytogenes* by one log early in meat fermentation and this is one particular application where the use of bacteriocinogenic cultures appears to have potential value as an additional inhibitory hurdle (Foegeding et al., 1992; Hugas et al., 1995).

### 7.3. Vegetable products

While there are 21 different commercial vegetable fermentations in Europe along with a large number of fermented vegetable juices and blends, the most economically relevant of these are the fermentations of olives, cucumbers (pickles), and cabbage (sauerkraut, Korean kimchi) (Bückerhuskes, 1997). As raw vegetables have a high microbial load and cannot be pasteurised without compromising product quality, most vegetable fermentations occur as a consequence of providing growth conditions (such as added salt) that favour the lactic acid bacteria. These bacteria are present on fresh vegetables in very low numbers, accounting for only 0.15–1.5% of the total population (Bückerhuskes, 1997). The starting material for fermented juice is pasteurised mash or juice and starters of lactobacilli (including *Lb. plantarum*, *Lb. casei*, *Lb. acidophilus*), *L. lactis* and *Lc. mesenteroides*.

## 8. Traditional fermented foods

Some examples of non-Western fermented foods are presented in Table 1. Any attempt to provide an in-depth coverage of such a subject would require a far greater forum than is afforded in this paper.

Interested readers are directed to the reference material of Wood (1998) and Dirar (1993). We have attempted in Table 1 to present various aspects of some of the better known traditional fermented foods arranged where possible by continent/country of origin.

### 8.1. Africa

Pottery linked to wine brewing in Africa has been discovered on excavation sites dating from as early as 690 BC to 560 AD (Odunfa and Oyewole, 1998). Many of the foods with the longest recorded pedigree are sour milks and alcoholic beverages. These foods are of particular importance in ensuring adequate intake of proteins and/or calories to consumers living in a climate which favours the rapid deterioration of food. Differing processes with products of different organoleptic properties also extend the attractiveness of what would otherwise be a limited and somewhat monotonous diet. Some fermentations (e.g., cassava) make otherwise inedible foods edible.

Breads are also among some of the oldest fermented foods and approx. 60% of the world population eats flat breads and gruels made from grains (Beuchat, 1997). Sourdough breads are made with starters containing yeasts such as *Saccharomyces* spp. and *Torulopsis* and homofermentative and heterofermentative lactic acid bacteria. Heterofermentative strains such as *Lb. sanfrancisco*, *Lb. brevis* and *Lb. fermentum* are responsible for the characteristic sensory qualities of such breads.

'Gari', based on the fermentation of cassava which is one of the most abundant food crops in the tropics, has a long shelf life of about 6 months and is the staple diet of much of the population of West Africa. As a fermented food, it is an example of the rendering safe for human consumption of a food which would otherwise be toxic due to high inherent levels of cyanogenic glucosides. During the fermentation there is a reduction of pH, linamarase activity and total cyanide levels (Ikediobi and Onyike, 1982) while acid (predominantly lactic acid) levels increase. Lactic acid bacteria associated with the fermentation include *Lb. plantarum* (Oyewole and Odunfa, 1990) and the fermentation also involves other microorganisms including yeasts (Ofuya and Nnajifor, 1989).

'Ogi' is a fine paste-like sour gruel eaten in Nigeria resulting from the submerged fermentation of cereals. It is consumed as a breakfast cereal by adults and is an important traditional weaning food of infants. Similar foods in other African regions are 'Koko' or 'Kenkey' in Ghana and 'Mahewu' in South Africa. The fermentation is dominated by a variety of lactic acid bacteria, particularly *Lb. plantarum*, while other bacteria such as *Corynebacterium* hydrolyse the corn starch, and yeasts of the *Saccharomyces* and *Candida* species also contribute to flavour development. Mahewu is produced on a large-scale industrial basis and some attempts to develop starter cultures have been made (Schweigart and Fellingham, 1963; van Noort and Spence, 1976). A starter culture has been used to produce an improved version of ogi called DogiK. The starter strains are lactobacilli isolated from local fermented foods with strong antibacterial activity (Olukoya et al., 1994).

### 8.2. India

'Idli' is fermented steamed cake of rice and dehulled blackgram dhal produced in India. Lactic acid bacteria such as *Lc. mesenteroides*, *Lb. delbrueckii*, *P. cerevisiae*, *E. faecalis* and *L. lactis* are responsible for pH reduction and may increase the thiamin and riboflavin content (Lewis and Johar, 1953; Mukherjee et al., 1965; Rajalakshmi and Vanaja, 1967). Yeasts also contribute to the fermentation. 'Nan' is leavened flat sourdough bread with a central pocket now prepared worldwide. Organisms involved in the fermentation include *Saccharomyces* yeasts and lactic acid bacteria, particularly *Lactobacillus* species.

### 8.3. Indonesia

Tempe kedele developed in Indonesia is a soybean fermentation. Soybeans are first soaked in water, generally overnight at ambient temperature, and they are then dehulled, partially cooked and inoculated with moulds of the genus *Rhizopus*. Tempeh, which contains over 40% protein, is a meat substitute and is used in soups or sliced, salted and deep fat fried in coconut oil. Lactic acid bacteria including *Lb. casei* and *Lactococcus* species dominate the fermentation, which may be initiated by the addition of a commer-

cial culture or a small amount of a previous batch. Following fermentation, beans are bound together with the mycelia of *Rhizopus oligosporus* to form a compact 'cake'. Tempe is being advocated as a protein-rich source of vitamin B12 in the Western vegetarian's diet. The vitamin is thought to be produced by *Klebsiella pneumoniae* and *Citrobacter freundii* (Steinkraus, 1998) and is one of the most frequently cited examples of 'bio-enrichment'. Tempeh bongkrek is a coconut press cake, which has led to deaths in its native central Indonesia. Toxicity is due to the production of toxoflavin and bongkrekic acid by the bacterium *Burkholderia cocovenenans* which can grow in the first few days of fermentation if *Rhizopus* growth is not favoured.

Oncom (Ontjom) is a fermented peanut press cake. *R. oligosporus* is less frequently used in this product than *Neurospora intermedia*. It is reported that the phytic acid content of peanut presscake is reduced by fermentation (Fardiaz and Markakis, 1981).

### 8.4. The Orient

The characteristic aroma and flavour of soy sauce is due to the enzymatic activities of yeasts, *Tetragenococcus halophilus* and some *Lactobacillus* species. Soy sauce (or shoyu) is a condiment widely used in the cooking and seasoning of Japanese food. There are five main types of soy sauce in Japan, each with its own distinctive colour, flavour and use (Fukushima, 1979). In general, the pH of the sauce is within the range pH 4.6–4.8 and the characteristically high salt concentration is 17–19%. Concentrations of salt less than 16% can result in the development of putrefactive species during fermentation and ageing and levels greater than 19% interfere with the growth of halophilic bacteria such as *P. halophilus* and osmophilic yeast such as *Zygosaccharomyces rouxii* (Beuchat, 1997).

Because soybeans contain high levels of protein and oligosaccharides such as stachyose, raffinose, melibiose and sucrose but no significant level of simple sugars, fermentation by lactic acid bacteria and yeast requires the exogenous saccharifying enzymes supplied by the 'koji'. As a result, the first step in soy sauce fermentation is the production of koji whereby soybeans or a mixture of beans and wheat are inoculated with *Aspergillus oryzae* or *A. soyae* and allowed to stand for 3 days at 25–35°C

and 27–37% moisture. This stage is analogous to malting in the brewing process. In the mash stage, called moromi, koji is added to brine to give a salt concentration of 17–19% and fermented at room temperature for 12–14 months (home preparation) or at 35–40°C for 2–4 months (commercial preparation). The bacteria and yeast involved in the fermentation include *P. halophilus*, *Lb. delbrueckii*, *Z. rouxii* and *Torulopsis* species (Yong and Wood, 1976). The liquid (sauce) is removed from the mash and pasteurised at 70–80°C before bottling.

## 9. Developments in food fermentations

Throughout the world there are many different types of fermented foods in which a range of different substrates are metabolised by a variety of microorganisms to yield products with unique and appealing characteristics. In many of these foods, the biological and microbiological bases of the fermentation processes are poorly understood. What little information is available often deals with the identification and perhaps preliminary characterisation of the primary microflora in the finished product. In some instances, there will undoubtedly be a need in the future to produce these foods in circumstances where quality and safety can be guaranteed. This in turn will necessitate a more thorough understanding of the microorganisms involved, in terms of the types and their specific activities, so that the fermentation process can be made more reliable and predictable. It is likely that basic microbiological analyses in conjunction with the appropriate technological developments will, in the first instance at least, be sufficient to achieve these objectives.

For those fermentations where there already exists a considerable body of knowledge regarding the role and activity of the relevant microflora, the challenges facing the scientists and technologists are somewhat different. Fermentations involved in the production of many cheeses, yoghurts and some fermented meats in particular, are already quite sophisticated, are generally reliable and predictable and can deliver products of excellent quality. Here, the goals are to further improve reliability and product quality through optimisation of starter culture performance and to eliminate those factors that impede the fermentation process. In this regard, it is to be

anticipated that the considerable resources that have been devoted to the 'biotechnology of lactic acid bacteria' over the past number of years will deliver results with respect to these objectives. This is already evident in the case of the protection of cheese starter cultures of *L. lactis* against bacteriophage infection. This provides an excellent case study as to how a deliberate, programmed research effort, designed to provide a more complete understanding of phage-host interactions, has ultimately yielded strategies for the development of non-recombinant phage resistant strains for use in industrial fermentations (Allison and Klaenhammer, 1998).

The development of the correct flavour characteristics is a critical factor in the production of a range of fermented foods. However, the specific mechanisms by which flavour is generated is not fully understood, although the principal components contributing to flavour, such as protease, peptidase and lipase activities may be known. This is well exemplified in a product such as Cheddar cheese where the fine and subtle flavour attributes of the mature product is an essential element in determining the quality of the cheese. There now exists the ability to manipulate the proteolytic system of certain lactic acid bacteria, albeit in a crude way (McGarry et al., 1994; Mierau et al. 1996). Other recent advances related to an understanding of the pathways of amino acid metabolism and the role of cell lysis during product maturation will not only illuminate the biological basis for flavour development but will also allow this characteristic to be controlled and modified according to the needs of the market.

There are many other areas where additional functionality can be developed in lactic acid bacteria and in most cases the potential to achieve this is a direct consequence of the fundamental knowledge that has been generated regarding the genetic make-up of these hosts. The prospect of metabolic engineering of strains of lactic acid bacteria to generate derivatives with new attributes is now a real one. It will soon be possible to produce strains that secrete high levels of polysaccharides for use as food-grade texturisers, or to elaborate elevated levels of flavour compounds such as diacetyl, acetaldehyde or acetate (de Vos, 1996). The manipulation of the metabolic flux of these hosts may also yield derivatives that produce health-enhancing compounds such as antioxidants and vitamins. The application of lactic acid

bacteria to deliver vaccines is one that is already being intensively investigated and represents a very attractive exploitation of these hosts (Wells et al., 1996)

The very impressive scientific and technological developments that have been made with lactic acid bacteria over the past number of years are likely to relieve many of the bottlenecks encountered with their full and efficient application in food fermentations in the near future. The availability of information regarding the genetic blueprint of these bacteria (the genome sequence of a strain of *Lactococcus* has already been determined and those of several other lactic acid bacteria will be available in the near future) will also provide new applications that are likely to benefit both the producer and consumer. However, the scientific community and the industrial user need to be aware of consumer concerns regarding recombinant DNA technology, particularly in Europe, and especially when it involves food products. Thus, there is a need to ensure that there will be clear consumer benefits arising from the manipulation of these bacteria and also that the traditional positive attitude associated with fermented foods is not compromised by the exciting biotechnological developments in lactic acid bacteria.

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