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Review

A review on proteolytic fermentation of dietary protein using lactic acid bacteria for the development of novel proteolytically fermented foods

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Summary Bioactive peptides generated from food proteins have gained much interest as functional foods. Recently, the application of lactic acid fermentation has developed rapidly thanks to the discovery of probiotic functions in lactic acid bacteria (LAB). Aside from converting a fermentable carbohydrate into lactic acid, many strains of LAB were found to possess proteolytic activity, which is essential for many fermentation processes. The protease enzymes produced from the proteolytic fermentation breakdown proteins in food and generate a variety of high-value products which are discussed in this review. These substances give rise to the production of functional food that exerts diverse health benefits including antioxidant, antihypertension, antihyperglycaemic, antiinflammation, antimicrobial, and anticancer effects. The effects of proteolytic fermentation on the physicochemical and functional properties, biological activities, and sensory attributes of foods are elaborated in this review article. The application of proteolytic fermentation in various food industries, mainly the dairy industry, meat industry, bakery industry, and brewing industry, improved the technological, nutritional, biological, and sensory characteristics, as well as increased the shelf life of food. Ultimately, this review summarises in-depth knowledge of proteolytic fermentation by LAB and generates additional interest in the development of novel proteolytically fermented products.

Keywords Bioactivity, functional food, lactic acid bacteria, microbial protease, proteolytic fermentation.

Introduction

Fermentation has a long history and great importance in food production and preservation, which involved modifying food through controlled microbial growth, for the production of healthier food with extended shelf life (Ağagündüz *et al.*, 2022). Fermented foods are gaining popularity worldwide due to the growing consumer awareness of the high nutritional profile and proven beneficial health effects of fermented food (Ibrahim *et al.*, 2023). In ancient times, food was fermented for preservation purposes, for instance for consumption of kefir when away from their home region. Today, fermented foods and beverages including yogurt, cheese, kombucha, wine, sourdough bread, kimchi, miso, salami, tempeh, and sauerkraut have become an integral part of human's daily diet. Currently, fermented foods are at the junction of two strong trends, which are the rising demand for clean-label foods and immunity-boosting superfoods. In 2022, the global fermented food and beverages market reached USD 575.6 billion and is projected to grow at a compound annual growth rate of 5.6% from 2022 to 2023, totaling around USD 989.2 billion by 2032

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(Future Market Insights, 2022). Thus, fermented foods are believed to be a candidate for the “next big thing” with a promising future in the food industry.

Food fermentation can be categorised into three major categories, namely lactic acid fermentation, alcoholic fermentation, and acetic acid fermentation. Nowadays, lactic acid fermentations are of great popularity because of their ability to impart value-add functional properties and bioactivities to foods as well as the probiotic properties of many lactic acid bacteria (Wang *et al*., 2022). In general, lactic acid fermentations involve three metabolic pathways, which are glycolysis (breakdown of sugar), proteolysis (breakdown of proteins), and lipolysis (breakdown of lipids) (Grujović *et al*., 2022). Whilst the metabolism of sugars converts monosaccharides such as glucose into pyruvate and lipolysis converts triacylglycerols into free fatty acids and glycerol, the pathway that is discussed in this review is proteolysis. In proteolytic fermentation, proteolytic microbes, mainly lactic acid bacteria (LAB) are used to hydrolyse the large proteins into smaller peptides or amino acids with increased digestibility and enhanced bioactivities (García-cano *et al*., 2019). This paper comprehensively summarises the scientific literature on proteolytic fermentation using LAB. In this review, comprehensive knowledge of the proteolytic activity by proteolytic bacteria, products synthesised by LAB during proteolytic fermentation, and the effect of proteolytic fermentation on fermented foods were summarised. Moreover, the application of proteolytic fermentation in various food industries were reviewed.

Proteolytic activity by proteolytic bacteria

In proteolytic fermentation, protease is required to hydrolyse the peptide bonds of proteins. Proteolytic bacteria are a type of bacteria that can breakdown proteins into peptides and amino acids, due to their capability to produce protease during fermentation that hydrolyse protein. Proteolytic enzymes are synthesised inside the bacteria cell and are secreted outside the cell into the external environment, or attached to the surface of the cell (Kieliszek *et al*., 2021). A wide variety of proteolytic microbes such as bacteria, archaea, certain types of algae, and some viruses produce proteases, but most application selects LAB as the candidate. This is because LAB are generally recognised as safe for consumption and provide several positive impacts on human health.

Characteristics of lactic acid bacteria

Lactic acid bacteria (LAB) are Gram-positive, catalase-negative, and non-spore-forming bacteria that are widely used to produce fermented food (Zapaśnik *et al*., 2022). LAB are classified as acid-tolerant and aero-tolerant and can adapt to different food matrices (Emkani *et al*., 2022). Morphologically, they are present in elongated or short non-motile rods or spherical cocci that are often observed in chains, as shown in Table 1. Although proteolytic strains of LAB are present in great quantities, however, it should be noted that not all LAB strains exhibit proteolytic activity.

Among the 60 genera of LAB, *Lactobacillus*, *Lactococcus*, *Leuconostoc*, *Pediococcus*, *Streptococcus*, *Enterococcus*, and *Weissella* are often involved in food fermentation (Wang *et al*., 2021).Currently, *Lactobacillus* is one of the most economically interesting LAB extensively used in fields related to food, feed, pharmaceuticals, and biotechnology due to its probiotic attributes. The *Lactobacillu*s spp. is the largest genus among LAB consisting of 261 species (at March 2020), many of which demonstrate high extracellular proteolytic activity (Lim *et al*., 2019). The taxonomy of *Lactobacillu*s has been reviewed recently by Zheng *et al.* (2020) and the genus has now been reclassified into 25 genera due to the genetic diversity of the genus.

Lactobacillus are categorised as nutrient-fastidious bacteria with complex nutritional requirements because they have limited capability to synthesise essential amino acids, nucleotides, and vitamins (Hossain, 2022). Energy for growth is obtained from carbohydrate metabolism, but many cellular constituents including amino acids, sugar, fatty acids, and minerals need to be harvested from the nutrient medium (Kieliszek *et al*., 2021). Therefore, a nutrient-rich medium is required for their cultivation, where the de Man, Rogosa, and Sharpe (MRS) broth is commonly used as a cultivation medium for laboratory scale. Besides cultivation media composition, the culture conditions such as temperature, pH, oxygen concentration, and water activity also influence the growth rate and lag phase time of *Lactobacillus*. The ideal conditions for *lactobacillus* growth are at 30 °C–40 °C with a pH of 5.5–6.2, although they can survive at temperatures between 2 °C and 53 °C and pH ranging from 4.5 to 6.5 (Śliżewska & Chlebicz-Wójcik, 2020).

Proteolytic system of LAB

The proteolytic activity of LAB has garnered a lot of interest due to its ability to enhance many desirable qualities of foods. The proteolytic systems of most LAB consist of three main components, which are cell-envelope proteinase which degrades proteins into oligopeptides, transport system which is responsible for transferring these peptides across the cell, and intracellular peptidases which generate individual amino acids, as shown in Fig. 1. The proteolytic system of LAB are subject to substantial variations between species- and strain-specific, leading to diverse functionality in protein

Table 1 Proteolytic enzyme producing lactic acid bacteria

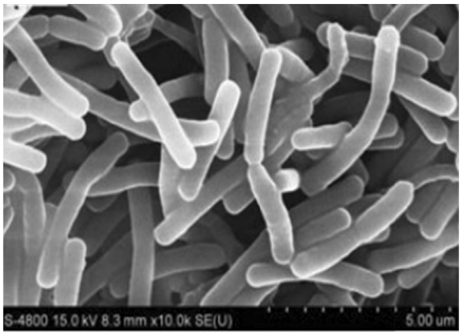
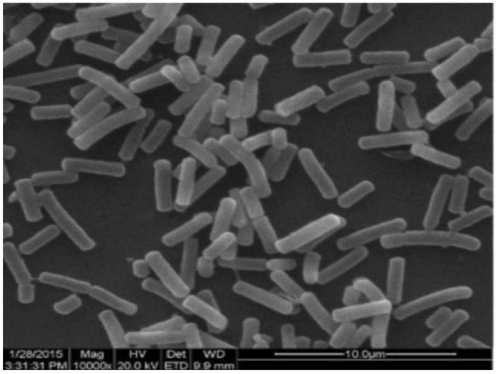
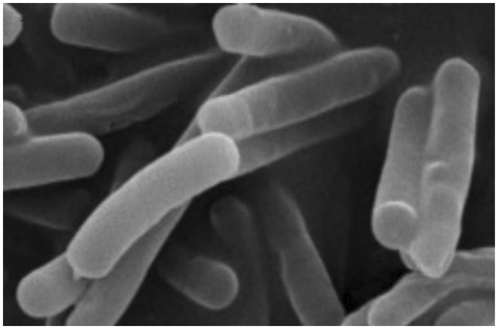
Proteolytic LAB	Morphology of LAB in Scanning Electron Microscopy	Proteolytic products	Applications in food
Lactobacillus helveticus	 Source: Paradeshi *et al.* (2018) Shape: Rod-shaped Arrangement: Occurs singly but tends to form pairs or short chains especially in the later logarithmic phase of fermentation Cell size: 0.7–0.9 μm in width and 4–6 μm in length Optimum pH: 5.5–5.8 Optimum temperature: 42 °C–45 °C	Peptides (antioxidant peptides, antihypertensive peptides, antihyperglycemic peptides, immunostimulating peptides, antimicrobial peptides, opioid peptides, and mineral binding peptides); organic acids (lactic acids, acetic acids, and benzoic acids); bacteriocins; exopolysaccharides; flavour compounds (ketones, esters, alcohols, and aldehydes)	Fermented milk; yogurt; fermented soy protein; fermented whey protein
Lactobacillus acidophilus	 Source: Shao *et al.* (2017) Shape: Rods with rounded ends Arrangement: Occurs singly, in pairs, and in short chains Cell size: 0.6–0.9 μm in width and 1.5–6 μm in length Optimum pH: 5.5–6.0 Optimum temperature: 37 °C	Peptides (antihypertensive peptides and antimicrobial peptides); bacteriocins (acidocin B); organic acids (lactic acids, formic acids, citric acids, acetic acids, and propionic acids); vitamins (nicotinamides (B3), pyridoxines (B6), folates (B9)); flavour compounds (ketones, aldehydes, and alcohols)	Fermented milk; yogurt; fermented soy protein; fermented meat; fermented sausage
Lactobacillus delbrueckii spp. *bulgaricus*	 Source: Gong *et al.* (2020) Shape: Rods with rounded ends Arrangement: Occurs singly or in short chains	Peptides (antioxidative peptides, antihypertensive peptides, and antimicrobial peptides); organic acids (lactic acids, acetic acids, caproic acids, butanoic acids, and formic acids); flavour compounds (diacetyl, acetaldehyde, 2,3-butanedione, and δ-decalactone); vitamins (folates (B9))	Fermented milk; yogurt; cheese

Table 1 (*Continued*)

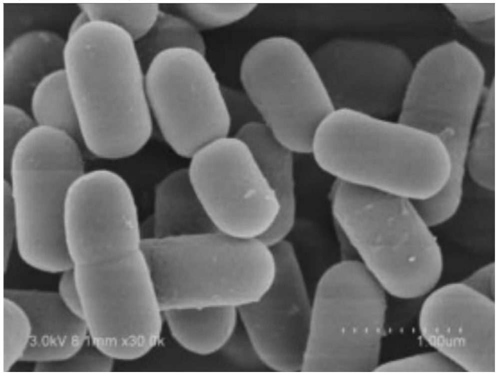
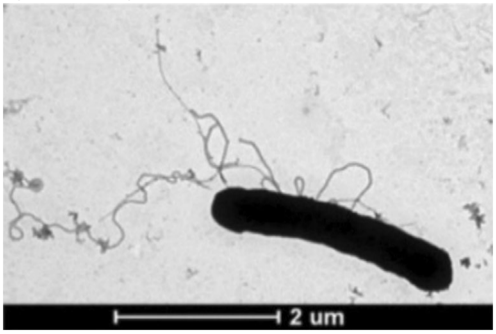
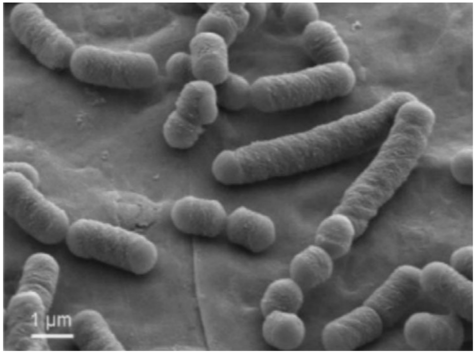
Proteolytic LAB	Morphology of LAB in Scanning Electron Microscopy	Proteolytic products	Applications in food
	Cell size: 0.5–0.8 μm in width and 2–9 μm in length Optimum pH: 5.5–6.0 Optimum temperature: 43 °C–46 °C		
Lactiplantibacillus plantarum	 Source: Wei *et al.* (2016) Shape: Rods with rounded ends Arrangement: Occurs singly or in pairs Cell size: 0.9–1.2 μm in width and 3–8 μm in length Optimum pH: 6.0–6.8 Optimum temperature: 37 °C	Peptides (antioxidative peptides, antihypertensive peptides, anti-inflammatory peptides, and antimicrobial peptides); bacteriocins (plantaricin); exopolysaccharides; organic acids (lactic acids, acetic acids, tartaric acids, malic acids, and citric acids); vitamins (folates (B9) and riboflavins (B2)); flavour compounds (3-methylbutanal, hexanal, (E)-2-octenal, nonanal, 2-heptanone, 2-nonanone, and acetoin)	Fermented milk; cheeses; fermented sausages; fermented fish; sauerkraut; sourdough
Latilactobacillus curvatus	 Source: Cousin *et al.* (2015) Shape: Rod-shaped with a slight moon-shaped curve Arrangement: Arranged in pairs or short chains Cell size: 0.7–0.9 μm in width and 1–2 μm in length Optimum pH: 5.5–6.5 Optimum temperature: 30 °C–37 °C, although some strains may grow at 2 °C–4 °C	Peptides (antimicrobial peptides and antihypertensive peptides); Bacteriocins (curvacin A and sakacin P); exopolysaccharides (dextran); organic acids (lactic acids, acetic acids, citrate acids; butyric acids, and succinic acids)	Fermented meat; fermented sausage; sourdough; cheese
Latilactobacillus sakei	 Source: Chiaramonte *et al.* (2009) Shape: Rod-shaped with rounded ends	Peptides (antihypertensive peptides, antilisterial peptides, and antimicrobial peptides); bacteriocins (sakacin P); vitamins (riboflavins (B2), nicotinamides (B3), pyridoxines (B6), folates (B9)); exopolysaccharides (dextrans); organic acids (lactic acids and acetic acids)	Fermented sausage; yak jerky; fermented wheat germ

Table 1 (*Continued*)

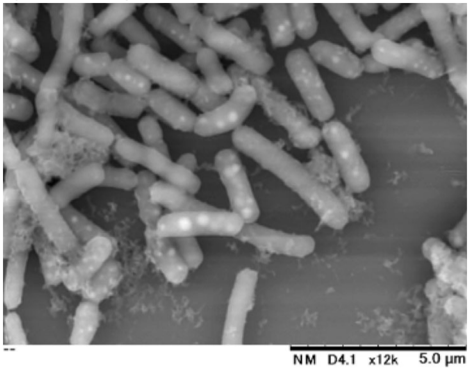
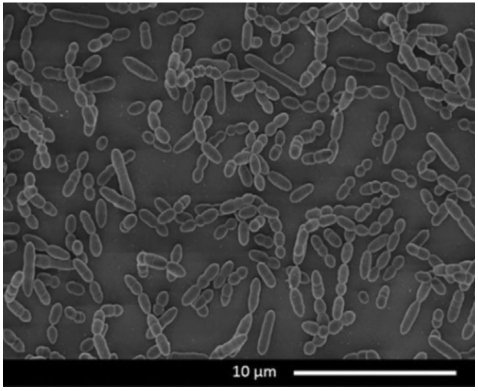
Proteolytic LAB	Morphology of LAB in Scanning Electron Microscopy	Proteolytic products	Applications in food
	Arrangement: Occurs singly or in short chains and frequently slightly curved and irregular, especially during the stationary growth phase Cell size: 0.6–0.8 μm in width and 2–3 μm in length Optimum pH: 5.5–7.5 Optimum temperature: Around 30 °C		
Lacticaseibacillus paracasei	 Source: Noda *et al.* (2019) Shape: Rod-shaped Arrangement: Occurs singly or in chains Cell size: 0.8–1.0 μm in width and 2–4 μm in length Optimum pH: 3.2–3.7 Optimum temperature: 10 °C–37 °C and no grow at 40 °C. Survives heating at 72 °C for 40 s	Peptides (antimicrobial peptides, antihypertensive peptides, antioxidant peptides, immunomodulatory peptides, and anti-inflammatory peptides); organic acids (lactic acids, acetic acids, propionic acids, butyric acids, and succinic acids); polyphenols (isoflavones); exopolysaccharides; vitamins (niacins (B3), pyridoxines (B6), folates (B9), and cholecalciferols (D3))	Yogurt; fermented soybean; fermented daily drinking dessert; fermented spicy rabbit meat
Lactococcus lactis	 Source: Liu *et al.* (2022) Shape: Spherical or ovoid-shaped Arrangement: Arranged in pairs or short chains Cell size: 0.5–1.2 μm in width and 0.5–1.5 μm in length Optimum pH: 5.5–5.8 Optimum temperature: 30 °C–40 °C, and can grow in temperature of 5 °C–53 °C	Peptides (antihypertensive peptides, antimicrobial peptides, calcium and iron binding peptides); Bacteriocins (lactococcin Q); organic acids (lactic acids, acetic acids, succinic acids, propionic acids, and butyric acids); vitamins (menaquinone (K2)); flavour compounds (diacetyl, 2-methylpropanal, and 3-methylbutanal)	Fermented milk; cheese; fermented gluten

Table 1 (*Continued*)

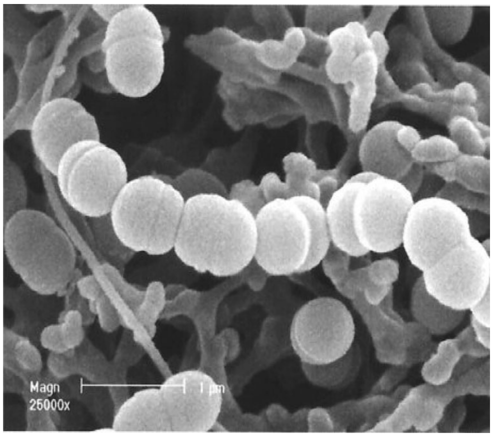
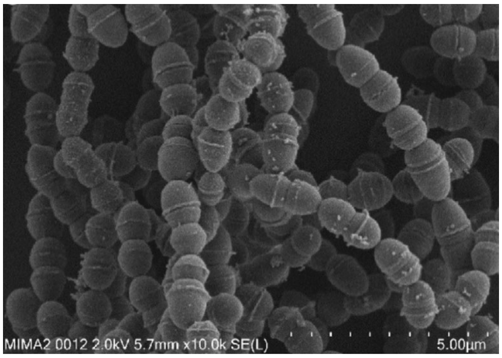
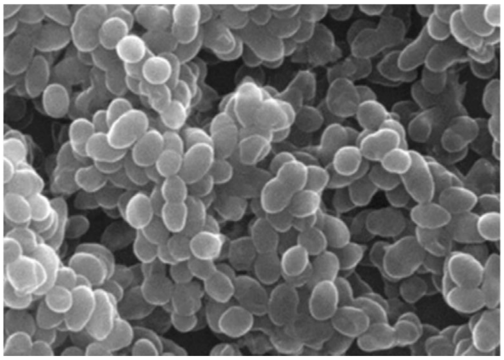
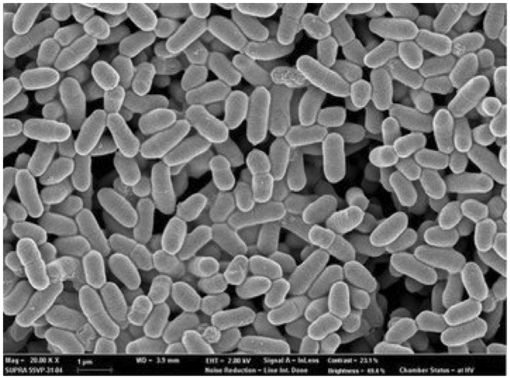
Proteolytic LAB	Morphology of LAB in Scanning Electron Microscopy	Proteolytic products	Applications in food
Leuconostoc mesenteroides	 Source: Kaletunç *et al.* (2004) Shape: Coccus-shaped Arrangement: Arranged in long chains or pairs Cell size: 0.5–0.7 µm in diameter Optimum pH: 5.5, and can grow in pH of 4.5–7.0. Optimum temperature: 30 °C and can grow in temperature of 10 °C–30 °C	Peptides (antifungal peptides and antimicrobial peptides); bacteriocins (mesentericin Y105); exopolysaccharide; organic acids (lactic acids, acetic acids, and linoleic acids); flavour compounds (scetaldehydes)	Fermented milk; fermented soybean; sauerkraut; kimchi; ginseng
Pediococcus acidilactici	 Source: Herdian *et al.* (2018) Shape: Sphere-shaped Arrangement: Arranged in pairs or tetrads Cell size: 1.0–2.5 µm in diameter Optimum pH: 6.0–6.5 Optimum temperature: 25 °C–40 °C, and can grow at 50 °C	Peptides (antimicrobial peptides, antibacterial peptides, and antihypertensive peptides), bacteriocins (pediocin PA-1), exopolysaccharides, organic acids (lactic acids, malic acids, citric acids, propionic acids, and acetic acids); flavour compounds (esters, terpenes, ethyl acetates, ethyl octanoates, and ethyl decanoates)	Fermented milk; Fermented mussel; fermented mutton sausages; fermented wheat dough
Streptococcus thermophilus		Peptides (antimicrobial peptides, antihypertensive peptides, and anti-inflammatory peptides); bacteriocins; exopolysaccharides; organic acids (lactic acids and acetic acids); flavour compounds (aldehydes, ketones, alcohols, esters, and hydrocarbons); vitamins (folates (B9))	Fermented milk; fermented soymilk; fermented whey protein

Table 1 (*Continued*)

Proteolytic LAB	Morphology of LAB in Scanning Electron Microscopy	Proteolytic products	Applications in food
	Source: Boulay *et al.* (2021) Shape: Sphere or ovoid-shaped Arrangement: Arranged in pairs or chains Cell size: 0.7–0.9 μm in diameter Optimum pH: Around 6.5 Optimum temperature: 40 °C–45 °C, with a minimum of 20 °C–25 °C, and a maximum of 47 °C–50 °C		
Enterococcus faecalis	 Source: Zakaria *et al.* (2023) Shape: Sphere or ovoid-shaped Arrangement: Arranged in pairs or chains Cell size: 0.5–1 μm in diameter Optimum pH: 6.0–8.0, and can grow in the pH range of 4.6–9.9 Optimum temperature: 35 °C–37 °C, and can grow in the temperature range of 10 °C–45 °C and survive at temperatures of 60 °C for 30 min	Peptides (antimicrobial peptides and antihypertensive peptides), bacteriocins; exopolysaccharides; organic acids (lactic acids, acetic acids, and formic acids); vitamins (cobalamins (B12)); flavour compounds (diacetyl, acetoin, and 2,3-butanediol)	Fermented milk; fermented soybean; fermented wheat bran
Weissella confusa	 Source: Jin *et al.* (2019) Shape: Coccoid or rod-shaped Arrangement: Occurs singly or in pairs Cell size: 0.4–0.6 μm in diameter Optimum pH: 7.0–7.5 Optimum temperature: 30 °C–37 °C	Peptides (antimicrobial peptides), bacteriocins, exopolysaccharides (galactans and dextrans); organic acids (lactic acids and acetic acids); vitamins (folates (B9))	Fermented milk; fermented sausage; sourdough bread

De Man Rogosa Sharpe (MRS) medium was used for LAB cultivation.

hydrolysis (García-cano *et al.*, 2019). When compared to other *Lactobacillus* species, which typically only contain one cell-envelope proteinase, the presence of several cell-envelope proteinases in *Lactobacillus helveticus* makes it one of the most proteolytic LAB and unquestionably the most effective in synthesising a variety of bioactive peptides (Raveschot *et al.*, 2018). Most of the *Lactobacillus* originating from sourdoughs, including

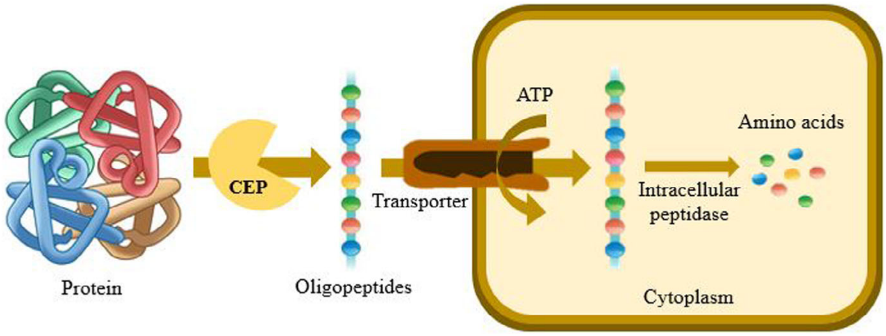


Figure 1 Schematic diagram for proteolytic system of LAB. The proteins are break down into oligopeptides by CEP, which are then transported across cell membranes by transporter systems and synthesised into individual amino acids by intracellular peptidases. ATP, adenosine triphosphate; CEP, cell-envelope proteinase.

Fructilactobacillus sanfranciscensis, lack a cell-envelope proteinase, but their proteolytic system contains cereal-associated protease (Gänzle & Gobbetti, 2013). This explained the ability of *Fructilactobacillus sanfranciscensis* to improve proteolysis of gliadins instead of other proteins since their dipeptidase and aminopeptidase exhibited a significant affinity for the hydrophobic peptides produced by gliadins. To date, the specificities of the proteolytic system of most LAB are still unknown and despite *Lactobacillus helveticus* being the LAB with the most recognised proteolytic activity, no comprehensive comparative genomic analysis of its many strains has been done. Therefore, there is a need for extensive research on the proteolytic system from different LAB species and strains, especially on the characterisation of cell-envelope proteinase.

Metabolite pathway for the proteolysis and metabolism of amino acids

The breakdown of macromolecular proteins during food processing is a crucial step that influences the quality, safety, and nutrition of food. Proteolysis in LAB is classified into protein degradation, peptide transport, peptide degradation, and amino acid catabolism. Fig. 2 demonstrates the metabolic pathway of LAB to breakdown protein using casein in milk as an example (Fig. 2 (1–3)) and the metabolism of amino acids (Fig. 2 (4–16)).

Proteolysis in LAB is started by cell envelope proteinase, where proteins are degraded into oligopeptides (Fig. 2 (1)) (Christensen *et al*., 1999). The dipeptides, tripeptides, and oligopeptides are transferred into cells by oligopeptide, dipeptide, and tripeptide transport systems (Fig. 2 (2)) that have been discovered in LAB. Following uptake, the peptides are broken down intracellularly into amino acids by several peptidases, such as endopeptidases, aminopeptidases, dipeptidases, tripeptidases, and proline-specific peptidases (Fig. 2 (3)). The degradation of proteins can improve the digestibility of raw material by reducing the content of food allergens as some allergenic peptides are converted into inert fragments and bioactive peptides. Previous studies reported that proteolytic activities of LAB reduced the antigenic response to cow's milk, wheat, soy, peanut, egg, fish, and shellfish.

The metabolism of amino acids involves deamination and decarboxylation, where the amine group is removed and converted into ammonia and the carboxyl group is removed to release carbon dioxide, respectively. In the cell, most amino acids can be metabolised at first to their respective α-keto acids by aminotransferases (Fig. 2 (4)) (Mu *et al*., 2021). There is no other type of deaminating enzyme known to exist in LAB. α-Keto acids are central intermediates and can be converted to hydroxy acids by dehydrogenases (Fig. 2 (5)), aldehydes by decarboxylase (Fig. 2 (6)), and CoA-esters by a dehydrogenase complex (Fig. 2 (10)). The resulting aldehydes can be dehydrogenated to alcohols (Fig. 2 (7)) or hydrogenated to organic acids (Fig. 2 (8)), which act as the substrates for esterases and acyltransferases respectively, producing esters (Fig. 2 (9)). The existence of two routes (Fig. 2 (6&8) and Fig. 2 (10)) for the production of carboxylic acid from α-keto acids indicates that one may be redundant, without having any negative effects on the development or survival of LAB. As the dehydrogenase enzyme complex conducts the oxidative decarboxylation of α-keto acids, organic acids are produced without transitory synthesis of aldehyde. This can explain why many LAB lack decarboxylating activity.

Another significant conversion pathway of amino acids is started by lyases, including cystathionine β-lyase and cystathionine γ-lyase, which can convert methionine to methanethiol (Fig. 2 (12)) (Dias & Weimer, 1998). However, these enzymes can only be found in some LAB, including *Lactococcus lactis*, *Limosilactobacillus fermentum*, *Lactiplantibacillus plantarum*,

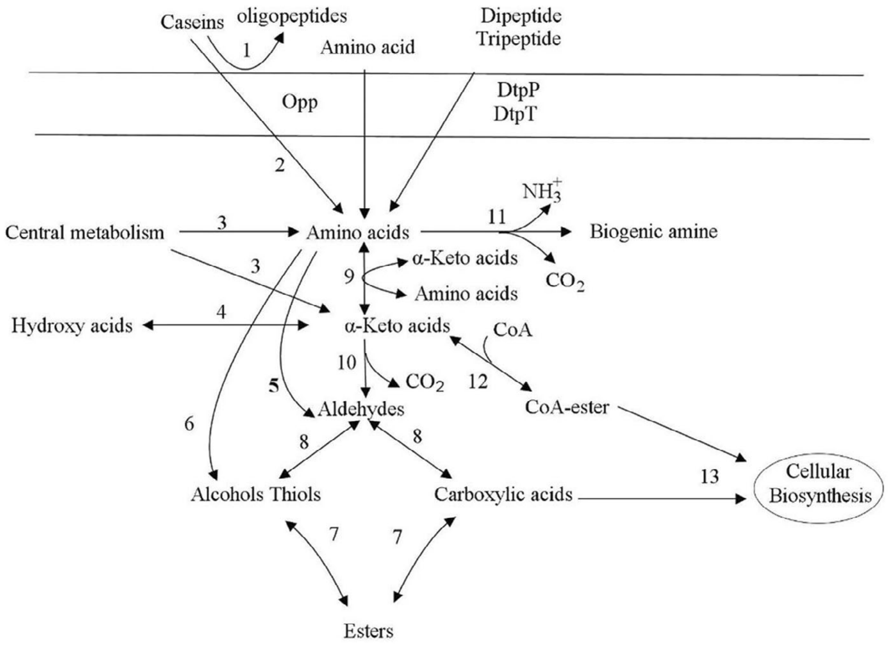


Figure 2 Overview of conversion pathway for the degradation of protein and metabolism of amino acid. Proteolysis in LAB is initiated by cell envelope proteinase (CEP), where proteins are broken down into oligopeptides. The dipeptides, tripeptides, and oligopeptides are transferred into cells by oligopeptide (Opp), dipeptide (DtpP), and tripeptide (DtpT) transport systems. Following uptake, numerous peptidases, including endopeptidases, aminopeptidases, dipeptidases, tripeptidases, and proline-specific peptidases, break down the peptides intracellularly into amino acids. The metabolism of amino acids includes deamination and decarboxylation. A significant number of amino acids are metabolised to α-keto acids by aminotransferases, where α-Keto acids are central intermediates and can be converted to hydroxy acids, aldehydes, and CoA-esters. The resulting aldehydes can be dehydrogenated to alcohols or hydrogenated to organic acids, which act as the substrates for esterases and acyltransferases respectively, producing esters. 1 = cell envelope proteinase, 2 & 3 = peptidases, 4 = aminotransferases, 5, 7 & 8 = dehydrogenase, 6 = decarboxylase, 9 = acyltransferases esterases, 10 = dehydrogenase complex, 11 = aldolases, 12 = lyases, 13 = deiminases decarboxylase, 14 & 15 = biosynthetic enzymes. Adapted from Wang *et al.* (2021).

Brevibacterium linens, and *Bacillus cereus*. Another enzyme that belongs to the family of lyases called threonine aldolase can convert threonine directly into acetaldehyde (Fig. 2 (11)). This enzymatic reaction is highly specific, and threonine does not appear to be degraded by other enzymes. Nevertheless, threonine aldolase is found in almost all LAB and this enables the lyase pathway to contribute mainly to the acetaldehyde pool.

The decarboxylation of amino acids into various biogenic amines (Fig. 2 (13)) is another important conversion route for amino acids. The conversion of these biogenic amines is undesirable as they are responsible for adverse effects involved in several pathogenic syndromes such as headache, oedemas, nausea, diarrhoea, allergy, and respiratory disorders (Tabanelli, 2020). Yet, it is unavoidable that proteolytic fermented foods contain trace amounts of these compounds. For instance, decarboxylation of arginine, tryptophan, tyrosine, histidine, and ornithine results in the production of agmatine, cadaverine, tyramine, histamine, and putrescine respectively. In dairy products, the most extensive biogenic amines are tyramine, histamine, putrescine, and 2-phenylethylamine, while tyramine, cadaverine, putrescine, and histamine are frequently present in fermented meats (Barbieri *et al.*, 2019).

Regulated proteolysis is important to ensure proper quality control, cell cycle progression, and physiological transitions. The regulation of proteolysis at the transcriptional level and the enzyme level has been studied by Marugg *et al.* (1995) and Meijer *et al.* (1996) respectively. The results showed that the regulation of proteolysis was strain and medium-dependent. However, the precise regulatory mechanism of the proteolytic system of *Lactobacilli* spp. is poorly studied. To date, no other regulation mechanisms have been reported other than gene expression (*i.e.* prt genes and prtM gene) and enzyme activity. Hence, future studies should focus on exploring the regulating mechanism of proteolytic fermentation.

Enzymatic activities of microbial proteases

The proteolytic enzymes fall into two classifications, which are exopeptidases and endopeptidases. Exopeptidases are enzymes that catalyse the cleaving of a peptide bond from the terminus of the polypeptide chain while endopeptidases catalyse the cleaving of peptide bonds far away from the terminus of the substrate. Exopeptidases that attack peptides from the N-terminus are aminopeptidases (single amino acid), dipeptidyl peptidases (dipeptide), and tripeptidyl peptidases (tripeptide), whereas peptidases attacking the C-terminus are carboxypeptidases (single amino acid) and peptidyl dipeptidases (dipeptide), as illustrated in Fig. 3. Dipeptidases are exopeptidase which hydrolyse the peptide bond in the dipeptides while omega peptidases eliminated terminal residues with either a free α-amino or α-carboxyl group. The enzymatic activity of proteases can be affected by a variety of factors, such as temperature, pH, concentration of enzyme, and concentration of substrate, which are tabulated in Table 2. These ultimately affect the rate of an enzyme's action as enzymes work best within specific temperatures, pH, concentration of enzyme, and concentration of substrate ranges.

Products synthesised by LAB during proteolytic fermentation

LAB generate a multitude of valuable products while hydrolysing proteins in the foods to fulfil their growth requirement. These substances produced during proteolytic fermentation include peptides and amino acids, organic acids, bacteriocin, vitamins, exopolysaccharides, and flavour substances (Mora-Villalobos *et al.*, 2020). Table 1 shows the products synthesised by some of the most notable proteolytic LAB. The production of these products depends on the microbial strain and culture conditions. As a result, numerous research have been conducted to optimise the culture conditions of fermentation to obtain maximum product, which are detailed in Table 3. These products encourage the application of proteolytic fermentation using LAB for the production of functional food due to their health-promoting properties (Abdul Hakim *et al.*, 2023).

Peptides and amino acids

The proteolytic activity of LAB produces a variety of peptides endowed with biological properties, known as bioactive peptides, in addition to the peptides and free amino acids that are required for the bacteria. These bioactive peptides boost the therapeutic and functional value of fermented foods that exert various health benefits including antioxidant, antihypertensive, antidiabetic, antimicrobial, anticancer, and immunomodulatory activities (Ajayeoba & Ijabadeniyi, 2023). The bioactivities of bioactive peptides are influenced by their specific structural properties, such as amino acid composition, sequence, chain length, hydrophobicity, and net charge (Ahmed *et al.*, 2022).

The bioactivities of the peptides and amino acids produced by proteolytic fermentation have been extensively explored, mainly on antioxidative and antihypertensive activity, where these sequences of peptides are the areas of interest that are increasingly being studied. Kong *et al.* (2020) concluded that the antioxidant and antihypertensive activities were related to the existence of hydrophobic amino acids in the peptide sequences, including

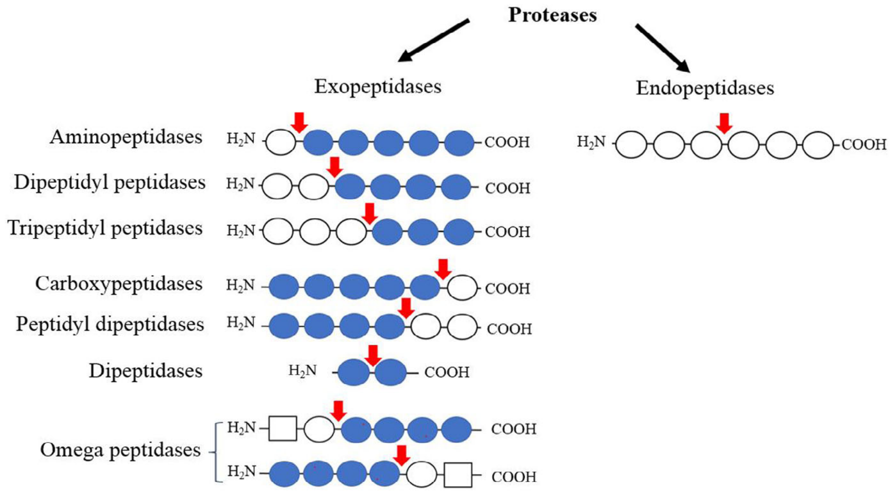


Figure 3 Classification of the activity of protease. Exopeptidases include aminopeptidases (single amino acid), dipeptidyl peptidases (dipeptide), and tripeptidyl peptidases (tripeptide) that attack peptides from the N-terminus, carboxypeptidases (single amino acid) and peptidyl dipeptidases (dipeptide) attack peptides from the C-terminus, and omega peptidases that eliminate terminal residues with either a free α-amino or α-carboxyl group. Endopeptidases catalyse the cleaving of peptide bonds in the middle of the peptide chain. white dot = amino acid residues in the polypeptide chain, blue dot = terminal amino acid in the polypeptide chain, square = blocked ends of the polypeptide chain, arrow = site of action of the enzyme.

Table 2 Factors that affect the protease activity

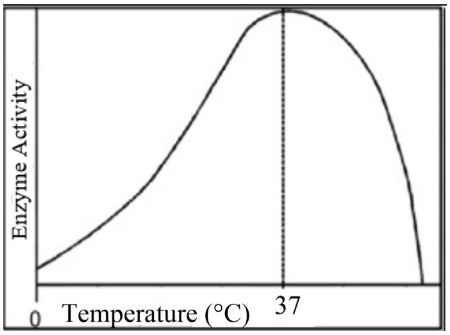
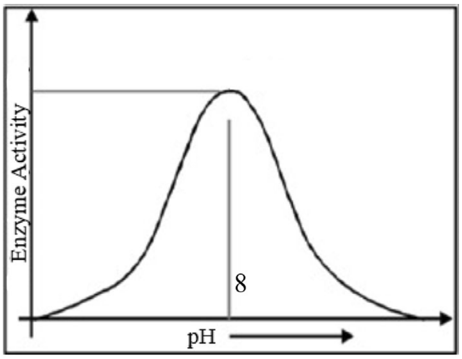
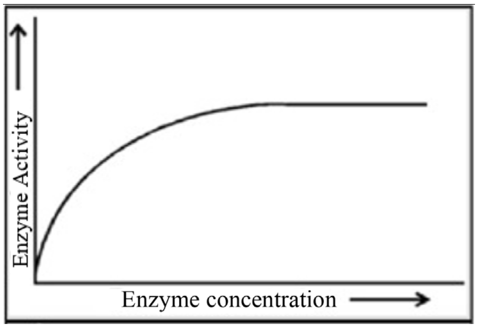
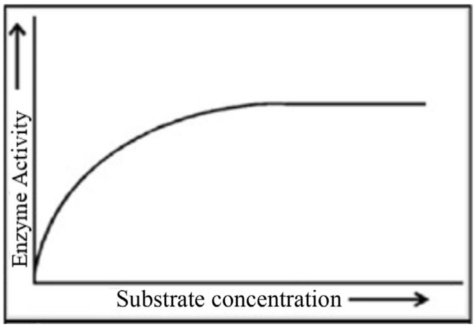
Factors	Graph	Protease activity
Temperature		• Optimum temperature at 37 °C • Little activity at low temperature • Activity decrease up to 75% when incubation at 60 °C • Only 3% activity remained after incubation at 70 °C as denaturation occurs
pH		• Optimum pH at 8 • At pH range of 5–9, the protease activity is around 75% • At pH levels of 3 and 10, the protease activity are 30% and 22% respectively as tertiary structure is disrupted
Enzyme concentration		• Protease activity is proportional to the enzyme concentration • However, up a certain point, extra enzymes cannot bind to any substrate, and the protease activity becomes constant
Substrate concentration		• Protease activity is proportional to the substrate concentration • However, up a certain point, all the active sites of enzymes are engaged, and the protease activity becomes constant

Table 3 Optimised culture conditions that can maximised the products synthesised from proteolytic fermentation

Products	Experimental designs	Optimised conditions	Outcomes	Reference
Peptides and amino acids	Different strains of LAB (*L. acidophilus LA-5*, *B. lactis BB-12*, and their mixed culture) were incubated at different temperatures (34, 38, and 42 °C), time (12, 36, and 60 h), and yeast extract concentrations (2, 4, and 6%), where the production of antimicrobial peptides was optimised using the D-optimal design in response surface methodology	Strain: *L. acidophilus LA-5* Temperature: 38.71 °C Fermentation time: 26.15 h Yeast extract concentrations: 4.45%	14.03 ± 0.68 mm inhibition activities of antimicrobial peptides against *L. monocytogenes*	Amiri *et al.* (2022)
	Different process variables including the incubation temperatures (37 and 42 °C), incubation times (12, 24, 36, 48, 60, 72 h), and inoculation levels (1, 2, 3% v/v) were studied to investigate the maximum peptide production from milk proteins fermented by *Lactobacillus delbrueckii* NCDC 09	Temperature: 37 °C Fermentation time: 24–36 h Inoculum size: 1% v/v	Peptides content at optimum temperature (5.20 mg mL^{-1}), fermentation time (5.19 mg mL^{-1}), and inoculum size (3.50 mg mL^{-1})	Seema & Rajesh (2015)
Organic acids	Various fermentation parameters, such as pH (4.0, 5.0, 6.0, 6.5, and 8.0, 9.0), temperatures (0, 25, 30, 37, 45, and 50 °C), inoculum size (1–5%, v/v), fermentation time: (4, 48, 72, 96, 120, 144, and 168 h), and rotation speed (50–200 rpm) were optimised to maximise the lactic acid production from whey by *Lactobacillus* spp. isolated from the curd sample	pH: 6.5 Temperature: 37 °C Inoculum size: 4%, v/v Fermentation time: 120 h Rotation speed: 150 rpm	Lactic acid content at optimum pH (42.8 mg L^{-1}), temperature (43.6 mg L^{-1}), inoculum size (43.4 mg L^{-1}), fermentation time (41.7 mg L^{-1}), and rotation speed (44.7 mg L^{-1})	Sarkar & Paul (2019)
Bacteriocins	The culture conditions, including LAB strains (*L. fermentum M1*, *L. acidophilus M2*, *L. acidophilus CH1*, and *L. pentousus CH2*) isolated from some dairy products, mediums (MRS media, corn steep liquor-Lactose medium, corn steep liquor medium, and glycerol-molasses-liquid medium), temperatures (30, 60, 90, and 121 °C), pH (pH 2–10), surfactants (SDS, CTAB, EDTA, and Tween 80), organic solvents (Acetone, butanol, chloroform, ethanol, methanol, and propanol), and metal ion (AgNO3, CuSO4, FeSO, MgSO4, MnCl$_2$, and ZnSO) were optimised for maximising bacteriocin production	Strain: *L. acidophilus CH1* Medium: Corn steep liquor medium Temperature: 30 °C pH: 6 Surfactant: Tween 80 Organic solvent: Isopropanol Metal ion: FeSO4	20 ± 0.01 nm inhibition-zone for *B. subtili* and 18 ± 0.01 nm for *E. coli*	Mahrous *et al.* (2013)
	Various culture conditions, such as medium (*viz*, MRS, TGE, TGE + buffer, TGE + Tween 80, and TGE + Tween 80 + buffer), temperatures (20, 28, and 37 °C), and pH (pH 2–12) were optimised for bacteriocin production by *Pediococcus acidilactici* LAB 5	Medium: TGE + Tween 80 + buffer medium Temperature: 37 °C pH: 6	2400 AU mL^{-1} bacteriocins produced at optimum conditions	Mandal *et al.* (2008)
Vitamins	Five different parameters, carbon sources (Glucose, galactose, maltose, sucrose, and lactose), nitrogen sources (Yeast extract, ammonium chloride, tryptone, ammonium sulphate, and glycine), temperatures (20–60 °C), pH (3–7), and	Carbon source: Glucose Nitrogen sources: Yeast extract Temperature: 40 °C pH: 6 Inoculum size: 3%	12.33 mg L^{-1} riboflavin produces at optimum conditions	Hemalatha & Subathra Devi (2022)

Table 3 (*Continued*)

Products	Experimental designs	Optimised conditions	Outcomes	Reference
	inoculum sizes (0.5–3%) were optimised using central composite design in response surface methodology to enhance the production of riboflavin in *L. plantarum–HDS27*			
Exopolysaccharides (EPS)	The LAB strains (*Lactobacillus rhamnosus* ŁOCK 0943, *L. rhamnosus* ŁOCK 0935, and *L. rhamnosus* OM-1), carbohydrate sources (Glucose, maltose, galactose, sucrose, fructose, and lactose), and nitrogen sources (Yeast extract, meat extract, and peptone K) were optimised using a triangular-based mixture design to maximise EPS production	Strain: *Lactobacillus rhamnosus* ŁOCK 0943 Carbohydrate source: Glucose, Nitrogen source: Yeast extract	The optimised culture conditions led to a more than 13-fold increase in EPS yield, which is from 85 to 1138.2 mg L^{-1}	Oleksy-Sobczak & Klewicka (2020)
Flavour substances	The glutamate production from *Lactobacillus plantarum* originating from Minangkabau fermented food was optimised by determining the optimum pH (3, 3.5, 4, 4.5, 5, 5.5, 6, 6.5, and 7), temperatures (30, 33, 36, 39, 42, and 45 °C), fermentation times (12, 24, 36, 48, 60, 72, 96, and 108 h), carbon sources (Glucose, sucrose, maltose, and lactose), concentration of carbon sources (1, 3, 5, 7, 9, 11, 13, and 15%), nitrogen sources (peptone, yeast extract, skim milk, NH_4NO_3, and KNO_2), and concentration of nitrogen sources (0.1, 0.3, 0.5, 0.7, 0.9, 1, 1.1, 1.3, and 1.5%)	pH: 5.5 Temperature: 36 °C Fermentation time: 36 h Carbon source: Glucose Concentration of carbon source: 11% Nitrogen source: peptone Concentration of nitrogen source: 0.5%	Glutamate content at optimum pH (161.519 mg L^{-1}), incubation time (260.551 mg L^{-1}), temperature (350.001 mg L^{-1}), 11% glucose (566 535 mg L^{-1}) and 0.5% peptone (680.525 mg L^{-1})	Maslami *et al.* (2018)
	The fermentation conditions for *Lactobacillus plantarum* MNZ, including glucose concentrations (0%–12% w/v), ammonium nitrate concentrations (0.1–1.3% w/v), pH (2.5–6.5), and temperatures (27–47 °C) were optimised using Response surface methodology to enhance glutamic acid production	Glucose concentration: 12% w/v Ammonium nitrate concentration: 0.7% w/v pH: 4.5 Temperature: 37 °C	Glutamic acid increased up to 3-fold (3.35 mM) at optimum conditions	Zareian *et al.* (2013)

VKWRN, FAGDDAPR, and PPPAEVHEVH, in the sausages fermented with proteolytic *L. plantarum* CD101 and *Staphylococcus simulans* NJ201. Chourasia *et al.* (2022) found that soymilk fermented with proteolytic *Lactobacillus delbrueckii* WS4 strains isolated from traditional chhurpi was linked to the hydrolysis of globulin proteins, where the glycinin-derived peptide, SVIKPPTDE was found to contribute to the antioxidant properties and angiotensin-converting enzyme inhibitory activity. Amorim *et al.* (2019) demonstrated that the fermentation of milk using kefir probiotic strains generated around 35 peptides, where the β-CN-derived peptide YQEPVLGPVRGPFPIIV showed antihypertensive activity.

The liberation of functional low-molecular-weight peptides in fermented fish are claimed to promote health benefit among consumers. In Zhi *et al.* (2022) study, *Bacillus subtilis* CICC 20076, *Bacillus licheniformis* CICC 20033, and *Bacillus amyloliquefaciens* CICC 20029 were used to ferment the protein hydrolysates of scallop (*Argopecten irradians*) mantle, where novel antioxidative with low-molecular-weight peptides (ALLEEWEK and KLADMLNPER) were reported. These identified bioactive peptides have the potential to be utilised as a synthetic peptide substitute to be used as a constituent for developing natural nutraceuticals and food additives because of their insignificant downsides for the application with a high value in the industries.

Nevertheless, more research related to the identification, quantification, organoleptic characteristics, and bioavailability of peptides is needed to resolve some challenges prior to the incorporation of these bioactive peptides into food products and nutraceuticals.

Organic acid

In the metabolism of LAB, various types of organic acids are liberated during the proteolytic fermentation such as lactic acid, acetic acid, formic acid, succinic acid, citric acid, pyroglutamate acid, azelaic acid, caproic acid, linoleic acid, and lipoteichoic acid (Mora-Villalobos *et al*., 2020). A number of LAB strains including *L. lactis*, *L. plantarum*, *Levilactobacillus brevis*, and *Leuconostoc mesenteroides* are capable of producing 2-ketoisocaproic acid from leucine through transamination, which can be reduced to 2-hydroxyisocaproic acid. Organic acids can enhance flavour, preserve nutritional value, increase the storage stability of the food, and exert various health benefits. Propionic acid and benzoic acid can act as a preservative to prevent food deterioration and extend the shelf life of food; citric acid, malic acid, fumaric acid, and tartaric acid can use as acidity regulators to adjust or maintain the pH of food; and ascorbic acid is a popular antioxidant that can increase the food stability by delaying the oxidative decomposition of fats and oils or food components (Shi *et al*., 2022). Besides, these organic acids produced during proteolytic fermentation have been demonstrated for anti-inflammatory properties, antibacterial, immune potentiating, anti-obesity, inflammation regulation, and growth promoters. Mashitoa *et al*. (2023) study reported that the organic acid present in sweet potato smoothies fermented by *L. plantarum* includes tartaric acid, malic, gluconic, ribonic, isocitric, lactic, and acetic acids, which contribute to flavour and taste attributes of the fermented smoothies. Kanjan & Sakpetch (2023) found that the organic acid in cell-free supernatants of *L. plantarum* 124, which are lactic acid (49.57%) and acetic acid (25.85%), could extend the shelf life of Thai curry (Kaeng-Tai-Pla-Haeng) from 7 days to 21 days without any commercial preservatives. However, despite all of these advantages, microbial organic acid production encounters difficulties since microbes are often not tolerant to extreme acidic conditions and acid stress. Thus, is crucial to develop strategies to enhance the robustness of microbes toward extremely low pH conditions, high concentrations of organic acids, and stress from lignocellulosic inhibitors.

Bacteriocin

Bacteriocins are antimicrobial peptides produced by bacteria ribosomes, with bacteriostatic effects against pathogens (Simons *et al*., 2020). Gram-positive and Gram-negative bacteria may both synthesise bacteriocins, but LAB are one of the most used bacteria to produce them (Aljohani *et al*., 2023). Although LAB produced various types of bacteriocins, only three types of bacteriocins are commercial-grade bacteriocins that are approved by The Food and Drug Administration, namely Nisin, Micocin B17, and Pediocin PA-1 (Naskar & Kim, 2021). These bacteriocins are commonly used as food additives in the dairy industry. Bacteriocin has antimicrobial and antibacterial properties that can hinder the growth and reproduction of various foodborne pathogens including *Staphylococcus aureus*, *Pseudomonas fluorescens*, *P. aeruginosa*, *Salmonella typhi*, *Shigella flexneri*, *Listeria monocytogenes*, *Escherichia coli* O157:H7, and *Clostridium botulinum* (Mohamad *et al*., 2022). For example, Colaklar *et al*. (2018) study found that the *Staphylococcus aureus* inhibitory effect of *L. plantarum* bacteriocin derived from a Tulum cheese was observed during the production and maturation of white-brined cheeses. Moreover, Raja *et al*. (2022) study reported that bacteriocins showed good antibacterial activity against ESKAPE pathogens with more than an 11 mm zone of inhibition on selective agar media.

Bacteriocins have a wide application due to their colourless and odourless properties, at the same time high stability as a result of resistance to heat, acidic environments, and salt concentrations (Negash & Tsehai, 2020). Bacteriocins offer many advantages as food preservatives such as improving the shelf life of food, reducing the transmission of risky foodborne pathogens, and maintaining the nutrient values of food products by applying milder treatment to food during processing. Despite these advantages, bacteriocins are often adsorbed into food matrices and easily degraded, which results in a loss of antibacterial properties. As a result, the current trend in food packaging is to incorporate bacteriocins into coatings or films to achieve high stability in complex food systems. To date, bacteriocins show great potential for use as antibiotic alternatives with negligible undesirable effects. Yaacob *et al*. (2022) suggested the potential of bacteriocins as an alternative antibiotic for *Staphylococcus aureus* infection. However, the future research area of bacteriocin could be on the methods that allow LAB to synthesise bacteriocins in controlled doses efficiently and play a role in antibacterial, food preservation, and promoting healthy intestinal in food in a stable manner.

Vitamins

Vitamins are vital micronutrients that are necessary in tiny quantities for normal cell function, growth, and development. Some strains of the LAB can synthesise vitamin K and most of the water-soluble B vitamins, including B2 (riboflavin), B6 (pyridoxine), and B9 (folic acid) during the proteolytic fermentation (Wang *et al.*, 2021). These vitamins have a significant role in many aspects of cellular metabolism and must be obtained from dietary or microbial sources because mammals cannot synthesise them in the body. There is a large volume of published studies that have investigated the synthesised of vitamins through proteolytic fermentation in various foods, where the findings of these studies indicate promising applications at the commercial level. Oguro *et al.* (2017) study found *Latilactobacillus sakei* UONUMA isolated from snow caverns significantly increased the amount of vitamins B2 (riboflavin), B3 (niacin), and B6 (pyridoxine) in koji amazake, a Japanese fermented sweet drink. The study of Hamzehlou *et al.* (2018) revealed that 11 types of *Lactobacillus* species isolated from yogurt can produce vitamins B3 (niacin), B6 (pyridoxine), and B9 (cobalamin), where the largest amounts of vitamin B6 (1566.17 g mL^{-1}) and B9 (1279.72 g mL^{-1}) were generated by *Lacticaseibacillus paracasei* subsp. *tolerance* JCM 1171, *Lactobacillus acidophilus* strain KU revealed the highest level of vitamin B3 (522.7 µg mL^{-1}), and *L. fermentum* generated the greatest quantity of vitamin B2. Liu *et al.* (2019) study suggests that *L. lactis* subsp. *cremoris* MG1363 can synthesise vitamin K2 by using fructose or trehalose as a carbon source. In another study by Bøe & Holo (2020), *L. lactis* ssp. *cremoris* MG1363 is found to boost the amount of vitamin K2 by threefold in fermented milk compared to the wild type. These vitamins synthesised during the proteolytic fermentation of LAB are considered nutritional fortification in the food industry. This provides a safe and economical option to the present vitamin fortification method and widens the application of LAB for the biofortification of food to substitute the controversial synthetic vitamins. The choice of LAB strain is important to maximise the concentration and bioavailability of vitamins in fermented foods for industrial use since previous research has revealed that different LAB strains produced varying vitamin concentrations.

Exopolysaccharides

Exopolysaccharides produced by LAB and fungi are mainly composed of carbohydrates with proteins, deoxyribonucleic acid (DNA), and phospholipids (Angelin & Kavitha, 2020). The most notable LAB capable of producing exopolysaccharides are *Lactobacillus*, *Lactococcus*, *Bifidobacterium*, *Leuconostoc*, *Pediococcus*, *Streptococcus*, *Enterococcus*, and *Weissella* sp. (Sanalibaba & Cakmak, 2016). A variety of exopolysaccharides, including dextran, mutan, insulin, alternan, and levan, are produced by *Lactobacillus*. In recent years, microbial exopolysaccharides have gained increasing popularity in food, cosmetic, and pharmaceutical industries as a result of their interesting and attractive functions including antioxidant, anti-hyperglycaemic, antibacterial, anti-cancer, anti-ulcer, immunomodulatory, anti-inflammatory, and cholesterol-lowering activities that can improve human health.

In the food industry, exopolysaccharides are utilised as additives, especially in fermented dairy products like yogurt and cheese due to their ability as a thickening and structuring agent on rheology, texture, and organoleptic characteristics. Recently, exopolysaccharides have been widely employed as drug carriers due to their biocompatibility, capacity to encapsulate the drug molecules in their interspaces, and capacity to induce a controlled release of the cargo drug molecules, leading to enhanced drug pharmacokinetics. As exopolysaccharides naturally occur in complex, it is necessary to isolate exopolysaccharides effectively and precisely to prevent co-extraction and contamination with pollutants. The significant variation of exopolysaccharides in nature poses an additional challenge to the extraction and purification of exopolysaccharides. Therefore, it is crucial to examine the structure–activity relationship of exopolysaccharides to expand the utilisation of polysaccharides in the food and pharmaceutical industry.

Flavour substances

Aroma and flavour are the primary elements that enhance the organoleptic properties of food and increase overall consumer acceptance. The proteolytic fermentation of LAB enriches the pool of taste-active peptides and amino acids that contribute to the formation of organoleptic characteristics of fermented products. However, further conversion of amino acids to various alcohols, aldehydes, acids, esters, and sulphur compounds are necessary for specific flavour development. The conversion pathway of amino acids to alcohols, aldehydes, acids, and esters compounds has been discussed and shown in Fig. 2, whereas the conversion to sulphur compounds in the lyase pathway is displayed in Fig. 4. Since the type of the substrates in lyase pathway are spliced, these routes are usually shorter, leads directly to smaller and volatile compounds, including sulphury diaryompounds. The metabolism of sulphur-containing amino acids like methionine and cysteine contributes to the formation of methanethiol, sulphides, thioesters, and other volatile sulphur compounds that contribute to the juicy and fresh aroma of tropical fruits (Cannon & Ho, 2018).

In general, the amino acids can be distinguished into three main groups based on their taste, which are umami (aspartic and glutamic acid), sweet (alanine, serine, glycine, threonine, proline, and asparagine), and bitter (valine, histidine, arginine, phenylalanine, and leucine) (Zhao *et al.*, 2016). Ruan *et al.* (2022) found that alanine, phenylalanine, aspartate, glutamate, and

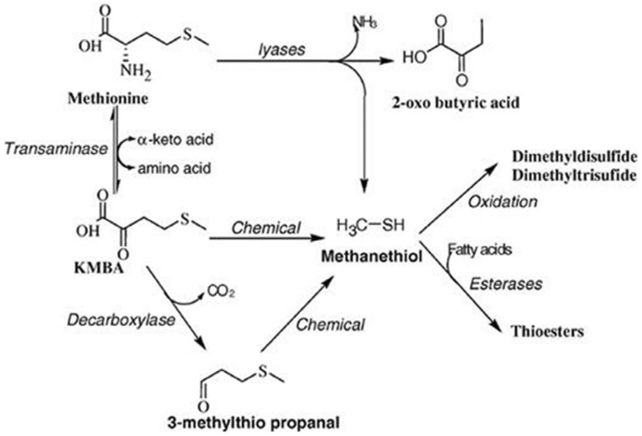


Figure 4 Conversion of methionine to volatile sulphur compounds in lyase pathway. Cystathionine β-lyase produced by LAB can degrade methionine into methanethiol and involved in the conversion of sulphur containing amino acids for the production of sulphury flavour compounds. Adapted from Smit *et al.* (2005).

glycine were the amino acids that contribute to the umami and sweet taste in fermented seafood soy sauce. Apart from the taste properties, the amino acids are capable of acting as substrates for the synthesis of aroma-active compounds in food. Ketones are carbonyl molecules that provide a variety of natural flavours and smells, where many saturated as well as unsaturated aromatic, aliphatic, and cyclic ketones have been documented to contribute to the aroma of cheese (Caron *et al*., 2021). Notably, the study on the metabolic pathways that convert peptides or amino acids into taste-active derivatives is in the early stages. The development of innovative fermentation strategies to enhance the flavour of food products will thus be made possible by having a deeper knowledge of metabolic pathways and the interactions between taste-active compounds.

Effect of proteolytic fermentation on the fermented food

Proteolytic fermentation modifies and enhances the physicochemical properties including solubility, water and oil retention capacity, emulsifying, foaming, and gelling properties; biological activity including antioxidant, antihypertensive, and antihyperglycaemic activity, and sensory attributes in the food industry. This results in the production of a variety of value-added food products with desirable properties.

Effect on physicochemical and functional properties

In terms of physicochemical and functional properties, protein solubility is a very critical property as it defines most of their other characteristics, including emulsifying, foaming, and gelling properties. Proteolysis and acid-induced hydrolysis enhance the solubility of proteins by breaking down the proteins into amino acids with a simpler structure, which facilitates the solubility of proteins in food and increase their extractability. Arteaga *et al.* (2021) study found that the protein solubility of pea seed (*Pisum sativum L.*) fermented with *L. plantarum* DSM 20174, *Schleiferilactobacillus perolens* DSM 12744, *L. fermentum* DSM 20391, *Lacticaseibacillus casei* DSM 20011, *Leuconostoc mesenteroides* subsp. *cremoris* DSM 20200, and *Pediococcus pentosaceus* DSM20336 are pH-dependent, where enhanced solubility of globulins was observed at low pH due to proteolysis, while declined protein solubility at high pH might be due to the hydrophobic groups being exposed on the protein surface that stimulate the protein–protein interactions.

It is now established from a variety of studies that proteolytic fermentation increases the water-holding capacity of protein by altering the protein structure and configuration to enhance the hydrophilicity of protein. Xing *et al.* (2020) revealed that 67% higher water-holding capacity in sourdough fermented with *Pediococcus pentosaceus* and *Pediococcus acidilactici* at 37 °C for 72 h as compared to non-fermented flour as a result of exposing the hydrophilic sites in protein. In Li *et al.* (2022) study, proso millet bran (5%) fermented with *Lactobacillus bulgaricus* (1.38×10^{10} cfu g^{-1}) and *Streptococcus thermophilus* (1.38×10^{10} cfu g^{-1}) at a ratio of 1:1 for 24 h at 37 °C showed higher water holding capacity and water swelling capacity due to the proteolysis of protein into small molecular substances increasing the surface area, thus generating more polar groups and forming more hydrogen bonds or dipole with water, increasing the water holding capacity and water swelling capacity. Çabuk *et al.* (2018) reported that the fermented pea-protein-enriched flour containing *L. plantarum* (7 log CFU g^{-1}) at 32 °C for 11 h could hold more oil due to the partially unravelled protein exposing the hydrophobic groups with oil-holding ability.

Emulsion stability is important to preserve the quality and shelf life of a product as unstable emulsions cause the floating of droplets to the surface, cohesion between droplets, and eventually creaming and separation. The hydrophobicity and structural flexibility affect the emulsifying properties of the protein. Tian *et al.* (2021) study revealed that the emulsifying activity of egg yolk protein fermented by *Streptococcus thermophiles* and *Lactobacillus bulgaricus* at 42 °C was effectively improved after 3 h of fermentation due to the enhancement of the surface electrostatic charge and solubility of the protein. In another study by Klupsaite *et al.* (2017) emulsifying properties of narrow-leaved lupine (*Lupinus angustifolius* L.) protein fermented with *Pediococcus pentosaceus* (9.2 log

CFU mL^{-1}) for 72 h at 35 °C was improved due to the increase in soluble protein concentration through proteolytic fermentation, where the soluble protein helps in better oil droplet entrapment, and thus, enhances its emulsion characteristic.

The foaming properties, such as foaming capacity and stability, are one of the key functional properties of proteins. The food industry has paid close attention to the foam's properties because of its distinctive mouthfeel and sensory characteristics. Several food products in daily life have been developed based on foam including beer, bread, cakes, and soufflés. The foaming capacity of proteins is influenced by a variety of physicochemical characteristics including surface tension and hydrophobicity, electrostatic repulsion, and molecular weight. Pauly *et al.* (2014) observed that since fermented dough has higher ionic strength and a lower pH, it produces more foam of higher stability than unfermented flour-water dough.

The incorporation of proteolytic LAB into the fermentation of milk reduces the pH to allow the coagulation of milk and improve the gelling behaviour, and thus, produce different fermented dairy products. The acid coagulation of milk protein is an irreversible and complicated process followed by demineralisation, reduction of electrostatic interactions between protein molecules, and aggregation of caseins *via* hydrophobic interaction and calcium bridging (Li & Zhao, 2019). In Rui *et al.* (2019) study, the soymilk yogurt fermented with *L. plantarum* B1-6 (3% v/v) at 37 °C had high hardness and gumminess values at low pH (5.1–5.4), indicating high gel strength and dense structure of the gel due to the hydrophobic interactions. The exopolysaccharides produced during fermentation play a significant role in the microstructure and elasticity of gels, and enhance the emulsifying and thickening characteristics of the products (Nikitina *et al.*, 2023). All in all, proteolytic fermentation breaks down the protein into smaller peptides, thus increasing its solubility. Depending on the peptides being released, it improves the water-holding capacity, oil-holding capacity, and foaming stability of the product. The souring of the product through proteolytic fermentation also causes coagulation and gel formation of proteins, producing diverse dairy-based products.

Effect on biological activities

Currently, the development of novel foods or nutraceuticals with health benefits is getting a lot of attention, which gives an alluring potential for the food and pharmaceutical industries. Foods that can provide health benefits beyond the provision of essential nutrients through fortification, enrichment, or enhancement, are known as functional foods. Fermented foods are increasingly recognised as functional foods due to their special functional properties providing some health benefits to consumers with the presence of functional microorganisms.

At this time, a special focus has been attributed to natural antioxidants, particularly those produced from natural sources such as protein hydrolysates, as a result of concern about the safety and side effects of synthetic antioxidants. Proteolytic fermentation could enhance the antioxidant capacity of fermented food due to the bioactive peptides and amino acids released from proteolysis showing antioxidant ability. Moreover, some of the antioxidant components were produced in the fermentation such as ascorbic acid, tocopherol, carotenoids, flavonoids, polyphenols, and glutathione (Wulandani *et al.*, 2020). During the last decades, researchers have confirmed the enhancement of antioxidative activity in food fermented with proteolytic LAB. Therefore, more recent attention has focused on the identification of *Lactobacillus* strains with excellent antioxidative activity, as well as the identification of antioxidative amino acids, peptide sequences, and molecular weight profile of these peptides. Sanjukta *et al.* (2021) in their study of antioxidant peptides of *kinema* (a fermented soybean food) fermented with proteolytic *Bacillus* spp. at 42 °C for 24 h, presented those peptides with antioxidative amino acids such as histidine, phenylalanine, methionine, tryptophan, and tyrosine improved the antioxidant activity. These studies observed that the peptide with SEDDVFVIPAAYPF sequence produced in *kinema* fermented using *Bacillus licheniformis* can be used as a functional food due to its enhanced antioxidant activities. Another study by Luan *et al.* (2021) reported that *L. plantarum* (10^7 CFU g^{-1}) enhanced the antioxidant activity in sausages fermented at 30 °C and 80% relative humidity for 48 h, where the peptide containing 5–27 amino acids with molecular weights below 3 kDa plays an important role in donating electrons for neutralising free radicals that contribute to the antioxidant capacity. Martí-Quijal *et al.* (2020) concluded that proteolytic fermentation of sea bass by-products by LAB isolated from sea bass viscera at 30 °C for 48 h synthesised phenolic acid with increased antioxidant capacity. All in all, the release of aromatic amino acids and the production of phenolic compounds through proteolytic fermentation enhances the antioxidant activities of the product.

Over the years, hypertension has become an increasing health concern worldwide since untreated hypertension increases the risk of heart failure, stroke, and other serious health problems. Synthetic antihypertensive drugs, including angiotensin-converting enzyme (ACE) inhibitors, angiotensin II receptor blockers, and calcium channel blockers effectively control hypertension but come with unpleasant side effects including dizziness, dysgeusia, headache, angioedema, and cough

(Mada *et al.*, 2020). Peptides derived from fermented food protein have the potential to become antihypertensive agents with negligible side effects. Begunova *et al.* (2021) study displayed that fermentation of 1% v/v *Lactobacillus helveticus* NK1, *Lacticaseibacillus rhamnosus* F and *Limosilactobacillus reuteri* LR1 at 37 °C for 72 h in milk promoted proteolytic hydrolysis and peptide formation with high ACE inhibitory, where the ACE-inhibitory peptides were found at the carboxyl-terminus of the αS2-casein. Huang *et al.* (2022) identified 11 novel peptides with high ACE inhibitory activity from sausage fermented with *L. plantarum* and *Staphylococcus simulans*, where VALSLSRP with X-Pro structure showed up to 75.36% ACE inhibition activity on 35 days on fermentation. Mazorra-Manzano *et al.* (2020) prepared a fermented cheese whey at 37 °C–42 °C and reported that microbiota in cheese whey can hydrolyse proteins and synthesised bioactive peptides through proteolytic fermentation that results in the increment of ACE-inhibitory activity by threefold after 120 h of fermentation. The proteolytic fermentation has the potential to release bioactive peptides that could interact with ACE and inhibit it, which in turn exhibits antihypertensive activities.

The prevalence of hyperglycaemia has dramatically increased during the past two decades and eventually become a major public health concern today. Although synthetic drugs such as metformin, acarbose, quercetin, and resveratrol inhibit α-amylase and control glucose levels, these synthetic inhibitors could cause undesirable side effects including diarrhoea, flatulence, pain, bloating, and loss of appetite (Khalid *et al.*, 2022). Many studies have reported the potential of proteolytic fermented food to work as an alternative therapy from a natural source for the management of hyperglycaemia. Ayyash *et al.* (2020) inspected the effect of camel sausage fermented with proteolytic *L. lactis* KX881782 (10^7–10^8 CFU kg^{-1}) for 48 h at 30 °C with relative humidity of 90% and found that the antihyperglycaemic activity of the camel sausage increased significantly up to 50% compared to camel sausage fermented with traditional commercial cultures of *Pediococcus pentosaceus* and *Staphylococcus carnosus*. In another study by Khakhariya *et al.* (2023), buffalo and camel milk fermented with *Lacticaseibacillus paracasei* (M11) in combination with yeast *Saccharomyce cerevisiae* (WBS2A) for 48 h at 37 °C synthesised antidiabetic peptides with DMPIQAFLLYQEPVLGPVR and FFIFTCLLAVVLAK sequences that showed antidiabetic activity.

Furthermore, Dharmisthaben *et al.* (2022) study found two novel peptides, which are LLNEK and IYTFPQPQSL, released from camel milk fermented with *Lacticaseibacillus casei* (NK9) (5×10^8 cfu mL^{-1}) at 37 °C for 24 h, showed remarkable anti-inflammatory activity. Ashokbhai *et al.* (2022) identified five novel antimicrobial peptides against *Enterococcus faecalis*, *Salmonella typhimurium*, *B. cereus*, and *E. coli* in sheep milk fermented with *L. fermentum* KGL at 48 h, including peptide FAWPQYLK. Elfahri *et al.* (2016) study found that skim milk (12%) fermented by proteolytic *Lactobacillus helveticus* strains (10^7 cells mL^{-1}) at 37 °C for 24 h showed anti-colon cancer activity by inhibiting up to 50.98% of colon cancer HT-29 cell line growth whereas the normal primary colon cells T4056 were unaffected. In consequence, proteolytic fermented food as a functional food displayed promising bioactivities such as antioxidative, antihypertensive, antihyperglycemic, anti-inflammatory, antimicrobial, and anticancer properties that potentially act as a natural alternative to synthetic chemicals or drugs.

Effect on sensory attributes

The proteolysis fermentation affects the sensory attribute by breaking down protein compounds into a variety of smaller molecules that can generate new flavour, texture, and colour in the food. The flavour compounds liberated by proteolysis fermentation are peptides, amino acids, keto acids, amine, and sulphur compounds (Emkani *et al.*, 2022). The existence of large hydrophobic peptides (Histidine, leucine, arginine, phenylalanine, isoleucine, lysine, and valine) are associated with the undesirable bitter taste of fermented food, and peptides and amino acids contribute to the fundamental taste of fermented foods, such as sweet (Alanine, glycine, threonine, serine, proline, and hydroxyproline), sour (Tyrosine, phenylalanine, and alanine), and salty or umami (Glutamic acid and aspartic acid) (Kayitesi *et al.*, 2023). Moreover, the branched-chain amino acids (Valine, leucine, and isoleucine) are converted into specific aldehydes that supply malty, fruity, alcoholic, and sweaty flavours; aromatic amino acids (Phenylalanine, tyrosine, and tryptophan) produce floral, chemical, and faecal flavours; aspartic acid is catabolised into buttery flavours and sulphur-containing amino acids (Methionine and cysteine) are transferred into compounds responsible for boiled cabbage, potato, meaty, egg, and garlic flavours (Chi *et al.*, 2021).

Numerous researches have shown that proteolytic fermentation enhances the sensory characteristics of food. Ben-harb *et al.* (2019) explained that the existence of roasting and grilling flavour in fermented pea protein comes from the pea vicilin being proteolysed LAB due to the peptides and amino acids liberated by the proteolytic activities. Papaioannou *et al.* (2021) reported that the volatiles including aldehydes, ketones, and carboxylic acids synthesised by the proteolysis of milk by *Lactobacillus acidophilus* and *Bifidobacterium* at 42 °C for 4–5 h affect the aroma and taste of the yogurt. Mamhoud *et al.* (2016) found that the bread produced by proteolytic fermented sourdough was saltier and less sweet compared to other bread, where the reduction in sweetness intensity is due to the conversion of sugar into lactic acid that contributes to sourness, whereas the saltiness could be associated with the proteolysis of the native wheat flour proteins that significantly increase the free amino acids, including aspartic acid and glutamic acid, that contribute to the flavour in the food matrix.

Besides imparting flavour to food, proteolytic fermentation can diminish the perception of the undesirable flavour or off-flavour by reducing the precursors of unpleasant volatile compounds or by forming a new compound that masks the unfavourable ones. This can be shown in Yin *et al*. (2019) study that reported the bitterness of soybean meal fermented with *Bacillus subtilis* (10% v/v) at 30 °C for 64 h reduced after the fermentation due to the reduction in hydrophobic peptide content, while the hydrophilic peptides are often associated with pleasant fermented soy flavour. In another research by Youssef *et al*. (2020), the proteolytic fermentation showed significant a reduction or masking effect of leguminous off-flavour attributes in pea proteins. Ma *et al*. (2021) reported moderate proteolysis can positively affect the tenderness and flavour of fermented meat, but excessive protein degradation leads to adverse effects on tenderness and overproduction of bitter amino acids and peptides like hypoxanthine. To sum up, proteolytic fermentation could be a powerful tool for the enhancement of sensory perception in the industry because this process can impart desirable flavour, texture, and colour or fix the sensory defects in food without using any artificial substances.

Applications of proteolytic fermentation in the food industry

The modern world intends to look for replacements or substitutions to raise the global standard of living. Today, proteolytic fermentation is an extremely important technology in various industries, such as the dairy, meat, bakery, and brewing industries, since microbial proteases are successfully accepted as a substitute for chemicals to produce safe, value-added, high-nutritional value, and eco-friendly food products. The usage of chemical or enzymatic proteases in industries throughout the world has grown significantly, but despite their effectiveness, it is notable that some of these substances have negative impacts on human health and the environment. Although enzymatic proteases are generally considered safe, some can cause side effects such as diarrhoea, nausea, rash, vomiting, stomach pain, fever, headache, liver disorders, diabetes acceleration, and abnormal cardiac function. However, due to the nature of enzymatic action which utilises a small amount of the enzyme in comparison to the substrate, the consumption of the protease enzyme, if at all present, would be a negligible amount, which renders its negative impacts muted.

Dairy industry

The proteolytic activity of LAB is commonly employed in dairy production to manufacture cheese, yogurt, kefir, and other fermented dairy products. The *Lactobacillus* spp. is extensively utilised as a starter culture due to the complex proteolysis system that allows them to breakdown casein into small peptides and free amino acids that contribute to the flavour development and texture improvement in various dairy products. In cheese production, some microbial proteases produced by LAB can replace chymosin, a protease with high specificity for casein, to coagulate milk proteins in the cheese-manufacturing process (Kieliszek *et al*., 2021). The proteolysis of milk protein enhances the digestibility of products, which is a desirable quality in the infant formula industry. Moreover, the proteolytic system of LAB can release immunomodulatory peptides that reduce allergic responses to dairy products (Zou *et al*., 2023). The LAB (*E. faecalis* VB43) isolated from Brazilian artisanal cheese has the potential to be used in the manufacture of hypoallergenic dairy products due to the ability to hydrolyse the allergenic proteins in milk (Biscola & Choiset, 2018). Many studies have indicated that proteolysis of milk by *Lactobacillus* spp. produce angiotensin-converting enzyme inhibitory peptides that can prevent cardiovascular disease related to hypertension (Şanlier *et al*., 2019). Nevertheless, the precise composition and molecular structure of fermented dairy products remain poorly understood as a result of the diversity of LAB strains and the complexity of the fermentation substrate. Hence, future studies should examine metabolomics to identify the detailed composition and molecular structure of fermented dairy products produced by different LAB strains to discover the biochemical changes due to bacterial activity during proteolytic fermentation.

Meat industry

Fermented meat products including salami, ham, and sausages, are often consumed in many regions worldwide. During the proteolytic fermentation, sarcoplasmic proteins in meat are hydrolysed to a significant extent, while the myofibrillar and connective tissue proteins are partially hydrolysed (Kieliszek *et al*., 2021). As a result, the meat turns juicy and tender with higher moisture content and thus improves the digestibility of protein. The breakdown of proteins in muscles into peptides and amino acids impart the characteristic flavour to meat, which improves the palatability of the meat. In recent years, there has been an increasing amount of literature on the positive impacts of proteolytic fermentation on meat texture, aroma, and colour. Xiao *et al.* (2020) inoculated *L. plantarum* and *Staphylococcus xylosus* into fermented sausages and found that proteolytic fermentation improved the flavour of fermented sausage by enhancing the microbiological quality and increasing the free amino acid content. Zhu *et al.* (2020) reported that *L. plantarum* could enhance the colour and gel characteristics of Chinese fermented sausage by stimulating protein unhelixation, hydrophobic interaction, β-folding, and hydrogen bonding forces between protein and water, and by producing nitroso that reacts with myoglobin in the meat, producing bright red nitrosomyoglobin. Apart from enhancing the quality of meat, proteolytic fermentation can increase the shelf life of meat by delaying lipid oxidation and microbial growth due to the lower pH and production of antimicrobial substances. Fermented meat is often associated with high sodium, and considering the growing demand for healthier food, it is relevant to reformulate fermented meat products for the further development of innovative and functional products.

Baking industry

In the baking industry, proteolytic fermentation is utilised for the production of bread, pastry, crackers, and waffles. Proteases from LAB can reduce the residual amount of reactive gluten during fermentation by degrading the gluten proteins into small peptides with lower immunological activity. This provides an alternative to produce gluten-free baked products that are suitable for gluten-intolerant patients. The degradation of gluten also increases the free amino acids that result in the improvement in product flavour, affecting the rheological quality of sour wheat dough and the texture of the product (Pei *et al.*, 2020). LAB and their proteolytic enzyme alter the gluten network structure, which enhances the yeast's dough-raising ability and results in the bread of higher loaf volume in a shorter time. *Fructilactobacillus sanfranciscensis* is a dominant LAB species in the baking industry due to the special characteristic of this strain, expressed in terms of excellent proteolytic ability, which results in higher loaf volume and softer loaves (Akamine *et al.*, 2023). Moreover, proteolytic fermentation enhances the nutritional value of whole-wheat baked goods by slowing down the starch digestibility for a low glycaemic response, increasing protein digestion to control the concentration and bioaccessibility of bioactive compounds, and enhancing the bioavailability of mineral substances (Ma *et al.*, 2021).To achieve these rheological and organoleptic properties, more investigation should be done on the sourdough ecosystem regarding the dynamic of the interaction among the LAB, such as the quorum sensing process and the metabolic regulation of sourdough.

Brewing industry

In the brewery sector, LAB are utilised to regulate microbial populations, acidify wort, and produce traditional sour beer, such as the Lambic, Gueuze, Berliner Weisse, Flemish red ale, Gose, and kettle-sour beers. The dominant genera of LAB used in the production of sour beers are *Lactobacillus* and *Pediococcus*, although *Lactococcus*, *Leuconostoc*, *Oenococcus*, and other LAB can be inoculated to produce sour beers (Bossaert *et al.*, 2019). LAB contributes to sour beers of better quality by improving the aroma, enhancing the colour, and stabilising the final products. The proteolytic activity of LAB can break down the proteins in beers, reducing haze formation. Haze formation can be a major quality issue that significantly reduces the shelf life and affect the flavour of the beer. The presence of LAB are favourable for the manufacture of sour beers, but it can deteriorate non-sour beer. Maintaining proper fermentation conditions is crucial for the reproduction of beers and for preventing contamination of beers since the main microbial components for the production of sour beers are generally considered spoilage organisms in non-sour beer styles. Therefore, advanced approaches to better monitor metabolic pathways during sour beer brewing and to provide information about the microbial composition are required to develop next-generation sour beers.

Conclusion

This review provides a comprehensive overview of the importance of proteolytic fermentation in the production of functional food. The role of LAB in utilising their complex proteolytic systems to hydrolyse proteins and generate metabolites that can improve several parameters, such as physicochemical and functional properties, bioactivities, and sensory attributes of food, that are linked to the overall quality of fermented foods was highlighted. With the current knowledge and technology, proteolytic fermentation has expanded the range of food products with widespread application in food industries. Although the corresponding research on proteolytic fermentation focused mainly on *Lactobacillus* spp. is relatively advanced, bear in mind that regardless of the up-to-date technological revolution in the fields of food science, there are still secrets in proteolytic fermentation that have yet to be explored and discovered, particularly those related to the regulation of proteolysis pathways and mechanism. Thus, the future will bring us a boom in omic technologies and novel product development that will help to reveal unravelled challenges in the area of proteolytically fermented foods.

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Author contributions

Zhi Yin Ter: Conceptualization; methodology; data curation; investigation; resources; writing – original draft. **Lee Sin Chang:** Conceptualization; data curation; visualization; validation; resources; writing – review and editing. **Abdul Salam Babji:** Conceptualization; supervision; writing – review and editing. **Nurul Aqilah Mohd Zaini:** Conceptualization; writing – review and editing; supervision. **Shazrul Fazry:** Writing – review and editing; conceptualization; supervision. **Shahrul Razid Sarbini:** Validation; writing – review and editing. **Clemens Karl Peterbauer:** Validation; writing – review and editing. **Seng Joe Lim:** Conceptualization; supervision; validation; funding acquisition; project administration; resources; writing – review and editing.

Ethical guidelines

Ethics approval was not required for this article.

Declarations of interest

None.

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Data availability

Data sharing is not applicable to this article as no new data were created or analysed in this study.

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