



Role of lactic acid bacteria in flavor development in traditional Chinese fermented foods: A review

Yingying Hu, Lang Zhang, Rongxin Wen, Qian Chen & Baohua Kong

To cite this article: Yingying Hu, Lang Zhang, Rongxin Wen, Qian Chen & Baohua Kong (2020): Role of lactic acid bacteria in flavor development in traditional Chinese fermented foods: A review, Critical Reviews in Food Science and Nutrition, DOI: [10.1080/10408398.2020.1858269](https://doi.org/10.1080/10408398.2020.1858269)

To link to this article: <https://doi.org/10.1080/10408398.2020.1858269>



Published online: 30 Dec 2020.



Submit your article to this journal [↗](#)



Article views: 387



View related articles [↗](#)



View Crossmark data [↗](#)



Citing articles: 2 View citing articles [↗](#)

REVIEW



Role of lactic acid bacteria in flavor development in traditional Chinese fermented foods: A review

Yingying Hu, Lang Zhang, Rongxin Wen, Qian Chen, and Baohua Kong

College of Food Science, Northeast Agricultural University, Harbin, Heilongjiang, China

ABSTRACT

Traditional Chinese fermented foods are favored by consumers due to their unique flavor, texture and nutritional values. A large number of microorganisms participate in the process of fermentation, especially lactic acid bacteria (LAB), which are present in almost all fermented foods and contribute to flavor development. The formation process of flavor is complex and involves the biochemical conversion of various food components. It is very important to fully understand the conversion process to direct the flavor formation in foods. A comprehensive link between the LAB community and the flavor formation in traditional Chinese fermented foods is reviewed. The main mechanisms involved in the flavor formation dominated by LAB are carbohydrate metabolism, proteolysis and amino acid catabolism, and lipolysis and fatty acid metabolism. This review highlights some useful novel approaches for flavor enhancement, including the application of functional starter cultures and metabolic engineering, which may provide significant advances toward improving the flavor of fermented foods for a promising market.

KEYWORDS

Traditional Chinese fermented foods; bacterial diversity; lactic acid bacteria; flavor development; metabolic pathway

Introduction

Traditional Chinese fermented foods are strongly linked to Chinese tradition and culture. Traditional recipes are handed over from one generation to another to form a unique and diverse Chinese food fermentation culture. Being an effective preservation method available in ancient times, food fermentation plays an important role in the improvement of the sensory properties, shelf-life and nutritional value, and in the reduction of toxic and anti-nutritional factors of foods (Liu, Han, and Zhou 2011; Blandino et al. 2003). A variety of microorganisms participate in the fermentation process, which originate from the raw material, starter cultures, equipment and processing environment during preparation and fermentation (Hu et al. 2020). The microorganisms in fermented foods can breakdown the biochemical constituents of raw materials (e.g., lipids, proteins and sugars) thereby improving the digestibility and flavor, while imparting pharmacological and nutritional values (Tamang et al. 2015). Lactic acid bacteria (LAB) are commonly recognized as the key strains of microbiota, which have potent effects on the properties of many fermented foods (Salim-ur-Rehman, Paterson, and Piggott 2006).

LAB comprise a large bacterial group consisting of approximately 380 species in 40 genera of 6 families that phylogenetically belong to the order *Lactobacillales* within the phylum *Firmicutes*. *Lactobacillus* (*Lb*), *Lactococcus* (*Lc*), *Leuconostoc* (*Leu*), *Pediococcus*, *Streptococcus* and *Weissella* are the main genera of LAB in fermented foods (Tamang,

Watanabe, and Holzapfel 2016). The main function of LAB in fermented foods is to ferment carbohydrates into lactic acid that can rapidly acidify the food matrix to improve the shelf-life and microbial safety of the products. Moreover, the majority of LAB has the ability to contribute to the flavor formation in fermented foods (De Vuyst and Neysens 2005; Thierry et al. 2015).

Flavor is regarded as one of the most important food characteristics for consumers (Kumar Verma and Prakash Srivastav 2020). The process of flavor formation is very complex in foods and it is necessary to fully understand it. This review will focus on the methods for LAB community and flavor analyses of fermented foods. The roles of the LAB community in the flavor formation and flavor-generating routes in fermented foods will be summarized. The methods for flavor enhancement in the production of fermented foods will also be presented.

Methods for the analyses of the lactic acid bacterial community and flavor

Methods for the lactic acid bacterial community analysis

Microorganisms involved in fermented foods have been isolated and identified by culture-dependent and culture-independent methods in certain studies (Franciosa et al. 2018). However, culture-dependent methods are often time-consuming, can be only used for culturable microorganisms, and provide insufficient information about the microbial

structure. In addition, the culture-independent methods provide a deeper insight into the composition and potential function of bacteria, substantially exceeding the information provided by the culture-dependent methods (Afshari et al. 2020). Denaturing gradient gel electrophoresis (DGGE) and temperature gradient gel electrophoresis (TGGE) combined with polymerase chain reaction (PCR) have been widely used to characterize the microbial diversity and succession in fermented foods (Chen, Chen, and Lei 2017). However, PCR-DGGE is not appropriate for the identification of all microbial species and can also cause an overestimation of microbial diversity because there may be several heterogeneous copies of the 16S rRNA gene in the bacterial genome of the same species (García, Rendueles, and Díaz 2019; Cocolin et al. 2013).

At present, studies have been routinely performed directly on the microbiota using PCR-amplified 16S rRNA gene sequencing and metagenomics (Wang, Zhou, et al. 2020). Due to the low cost and relatively higher throughput of the method, PCR-amplified 16S rRNA genes sequencing has been extensively used for large-scale studies to display the succession of microbial community over time. This method also has certain drawbacks, such as the PCR amplification bias and low resolution of taxonomy assignment at the species level (Franzosa et al. 2015). Metagenome sequencing or shotgun metagenome sequencing is a technique where an entire mixed microbial community DNA is fragmented, prepared into a sequencing library and sequenced. This technique has the advantage in determination of the taxonomic composition of the food ecosystem and measuring the activities and functions of microorganisms and their relationships (van Hijum, Vaughan, and Vogel 2013; Tarnecki et al. 2017).

DNA is a chemically stable molecule that can be detected for a long time after cell death. However, RNA is more sensitive to degradation, especially in the fermented food ecosystem where enzymes, such as hydrolase, exist. DNA can provide a good overview of the microorganisms that are or were present in a given ecosystem; however, DNA cannot provide any information on what microbes are doing with regard to the metabolic activities and expression of factors (Cocolin et al. 2013). Therefore, analysis of RNA (transcriptomics), proteins (proteomics) and metabolites (metabonomics) preferably in an integrated framework is essential for the comprehensive description of microbial communities to monitor the fermentation process, guide preparation, and explore flavor variation in fermented foods dominated by LAB (Sirén et al. 2019; Chen, Chen, and Lei 2017).

Methods for flavor analysis

Flavor is a key attribute that defines the quality and the degree of consumer acceptance of fermented foods, which consists of the perception in taste (sweet, sour, bitter, salty and umami) and aroma produced by several volatile compounds (El Hadi et al. 2013; Diez-Simon, Mumm, and Hall 2019). Currently, over 2000 volatile compounds have been detected in fermented foods, including aldehydes, esters,

heterocycles, alcohols, acids, terpenes, ketones, nitrogen and sulfur compounds (Vénica et al. 2016; Diez-Simon, Mumm, and Hall 2019). There are two important steps involved in flavor analysis in fermented foods, including the extraction and identification. The methods for extraction of the volatile compounds mainly include solvent-assisted flavor evaporation (SAFE), supercritical fluid extraction (SFE), simultaneous distillation extraction (SDE), solid-phase microextraction (SPME), stir bar sorptive extraction (SBSE) and dynamic headspace sampling (DHS) (Kumar Verma and Prakash Srivastav 2020; Chen, Kong, et al. 2015). The identification methods mainly include spectroscopy, gas chromatography-mass spectrometry (GC-MS), gas chromatography-ion mobility spectrometry (GC-IMS) and gas chromatography-olfactometry-mass spectrometry (GC-O-MS) (Cordoba et al. 2020; Liu and Sun 2018). Each extraction and identification method has advantages and drawbacks in the analysis of fermented food flavor (Table 1). Therefore, these methods should be carefully selected with full consideration of their limitations.

It is well known that not all volatile compounds contribute to the flavor of the product; however, the key volatile compounds have a substantial effect on the flavor characteristics (Wang, Huang, et al. 2019). Odor activity values (OAVs) and flavor dilution factors (FDs) are proposed to determine the effect of individual volatile compounds on the flavor of the final products (Sumby, Grbin, and Jiranek 2010). The OAVs are the ratios between the concentrations and odor thresholds of the volatile compounds. The compounds with the values of OAVs over 1 are considered the key volatile compounds contributing to the aroma characteristics (Al-Dalali et al. 2020). The compounds that are sensed with the highest FDs of the products by GC-O-MS analysis are regarded as the key volatile compounds (Smit, Smit, and Engels 2005). Furthermore, omission tests and aroma reconstitution are commonly used to systemically and thoroughly characterize the key volatile compounds (Dongmo et al. 2016; Chen et al. 2019).

Correlation between LAB and volatile compounds in fermented food

It is commonly believed that LAB has a pronounced effect on the flavor of many Chinese fermented foods. There are numerous reports that established the relationship between the diversity of the LAB community and specific volatile compounds in many Chinese fermented foods (Cheng 2010; Lv et al. 2019; Yang et al. 2016; Liang et al. 2020). According to the typical raw materials commonly used in the Chinese staple diets, five main types of LAB fermentation are discussed in this part (Figure 1), and the detailed information on these fermented foods is listed in Table 2.

Fermented meat products

Fermented meat products are an important branch of traditional meat products in China and are deeply loved by consumers because of its unique flavor and rich nutrition.

Table 1. Various techniques of flavor analysis in fermented foods.

Techniques	Advantages	Drawbacks	References
Isolation techniques			
Simultaneous distillation extraction (SDE)	This isolation method can recover volatiles from a matrix and is often the best way to obtain the highest recovery of a wide range of compounds. It is also a better method for the analysis of compounds with low volatility.	This isolation method promotes the formation of artifacts by oxidization and Maillard reaction due to relatively high temperature and loss of heat-sensitive volatiles. The operation requirements for this method are complex.	Engel, Bahr, and Schieberle (1999); Chaintreau (2001).
Solvent-assisted flavor evaporation (SAFE)	This method is effective for less volatile and polar compounds without artifacts caused by secondary reactions. The use of the equipment for this method can also save time and reduce costs due to the stability of the compact distillation unit.	The elevated temperature applied during distillation may lead to artifact formation. The equipment is fragile.	Li et al. (2011)
Supercritical fluid extraction (SFE)	This method facilitates the recovery of solvent and has high solubility, selectivity and rates of mass transfer. It can also achieve high extraction yields in a short time without production of toxic waste and is very safe for humans and environment because it mainly uses CO ₂ .	The major limitation of this method is represented by the chemical properties of CO ₂ under supercritical conditions, which is similar to that of lipophilic solvents.	Yousefi et al. (2019); Molino et al. (2020).
Solid-phase microextraction (SPME)	This method is a solvent-free extraction technique with an effective, low cost, low solvent consumption and easily automated assay for high sample throughput. It is also more efficient in extracting low molecular weight and high volatility compounds.	The sensitivity, selectivity and accuracy should be improved.	Kataoka, Lord, and Pawliszyn (2000)
Stir-bar sorptive extraction (SBSE)	The advantages of this method include simplification, miniaturization, use of little or no solvent, and minimization of sample volume.	Procedure requires a prior extraction for analysis of solid food samples and full automation.	Kawaguchi et al. (2013)
Dynamic headspace sampling (DHS)	This method is especially suitable for the determination of volatile compounds in a wide range of concentrations because of its flexibility (such as sampled volume, equilibrium temperature, sampling time and purge time).	Flexibility requires more complex instrumentation and sampling procedures and high standardization of several parameters to obtain good sampling reproducibility. Procedures required for quantitative analysis are complex.	Bicchi et al. (2008); Soria, García-Sarrió, and Sanz (2015)
Identification techniques			
Gas chromatography-mass spectrometry (GC-MS)	This method is effective for obtaining structural information on volatile compounds by comparison of the fragments of the target compounds with those of the standard references from the database available in the GC-MS system.	The method cannot determine the odor property of the compounds and its contribution to the sample and requires vacuum.	Song and Liu (2018)
Gas chromatography-olfactometry-mass spectrometry (GC-O-MS)	The method is particularly favorable and efficient for identification or picking-up of aroma-active compounds from numerous volatile constituents.	When this method is used in evaluation of the odor of the aroma-active compounds, the evaluation of the odor is often influenced by the eluents with very similar retention time.	d'Acampora Zellner et al. (2008); Song and Liu (2018)
Gas chromatography-ion mobility spectrometry (GC-IMS)	The advantages of this method include fast detection speed, high sensitivity, easy operation, low cost and portable equipment. It works at atmospheric pressure.	IMS response is non-linear, which means that assays of concentrations at the ppbv and pptv levels may be challenging. There is no complete database of GC-IMS.	Wang, Chen, and Sun (2020)

Chinese fermented meat products can be divided into two categories: one is made from whole pieces or slices of meat, such as sour meat, and the other is made from chopped or comminuted meat commonly known as sausage (Tamang, Watanabe, and Holzapfel 2016). The major genera of LAB related to the fermented meat products include *Lactobacillus*, *Leuconostoc*, *Weissella* and *Pediococcus*, which have an effect on the flavor formation because of their unique metabolic characteristics (Nguyen et al. 2013; Thierry et al. 2015). Lv et al. (2019) explored the effect of temperature on bacterial communities and metabolites and

their correlations in the process of sour meat fermentation. The results indicated that other genera were gradually replaced by *Lactobacillus* during fermentation. *Lactobacillus* contributed to the development of key volatile compounds, such as (E,E)-2,4-decadienal, nonanal, hexanal, octanal, 1-octen-3-ol and benzaldehyde. In traditional dry sausage, we explored the correlations between the bacterial communities and volatile compounds of dry sausages in various regions of Northeast China. *S. xylosus*, *Lb. sakei*, *W. hellenica*, *Leu. citreum*, *Lc. raffinolactis* and *Lb. plantarum* were found to be the predominant bacterial species. *Lc. lactis*, *W. hellenica*,

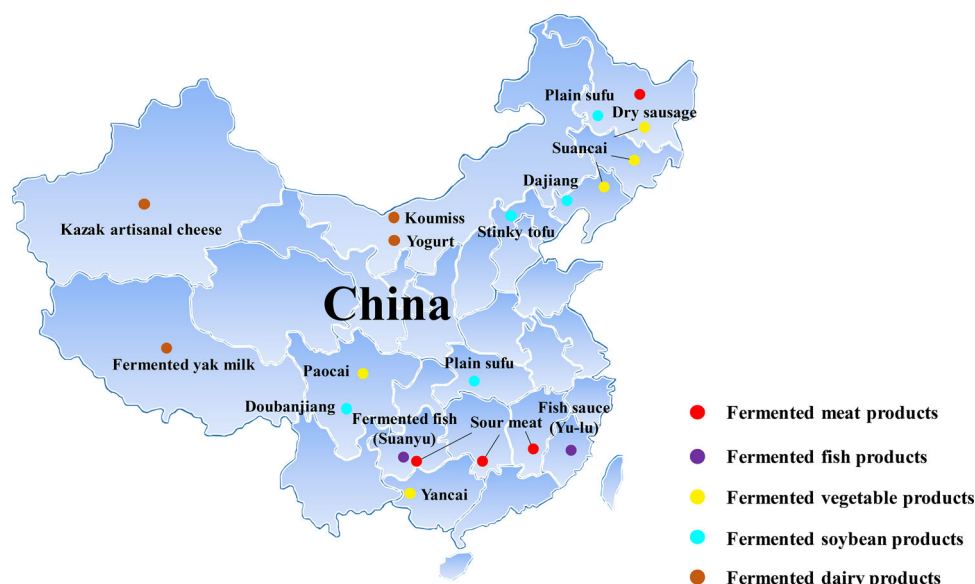


Figure 1. Distribution of traditional fermented foods in China. Source: Authors

Lb. plantarum, *Lb. sakei* and *Lb. alimentarius* were positively correlated with alcohols and carboxylic acids, and *Lb. alimentarius*, *Lb. plantarum* and *Lc. Lactis* were positively correlated with ketones, esters and aldehydes (Hu et al. 2020). We also explored the succession of the bacterial community in Harbin dry sausages (a type of naturally dry fermented sausage in Northeast China) during fermentation and its correlations with the sausage flavor. According to 16s rRNA gene analysis, *S. xylosus* and *Lb. sakei* were the predominant bacterial species during fermentation. The correlations between the core bacteria and the key volatile compounds showed that the core bacterial species (*Lb. sakei*, *S. xylosus* and *W. hellenica*) were significantly correlated with the major volatile compounds, such as 2,3-butanediol, ethanol, acetoin, ethyl hexanoate and ethyl lactate (Unpublished results).

Fermented fish products

Fermented fish products are becoming popular globally owing to their high nutritive value, bioavailability of minerals, easy digestibility and organoleptic characteristics (Das, Kumar, and Nayak 2020; Zang et al. 2018; Skåra et al. 2015). The dominant genera of LAB in the fermented fish products include *Lactobacillus*, *Lactococcus* and *Tetragenococcus* that are responsible for the flavor formation (Zang et al. 2018; Zang et al. 2020; Wang, Li, et al. 2020; Wang et al. 2018). Zang et al. (2018) explored the diversity and succession of microbial community of fermented fish (Suanyu). *Lactobacillus*, *Macrococcus* and *Staphylococcus* were found to be the predominant bacteria throughout the whole fermentation process. Zang et al. (2020) then evaluated the correlation between microbiota succession and flavor formation in Suanyu inoculated with mixed starter cultures (*S. xylosus* 135, *Lb. plantarum* 120 and *Saccharomyces cerevisiae* 31). The results showed that *Lactobacillus* contributed to the production of benzaldehyde, hexanoic and butanoic acids, ethyl octanoate, ethyl lactate,

and *Lactococcus* possibly contributed to the production of lactic, malic, acetic and tartaric acids during Suanyu fermentation. In addition, fish sauce (Yu-lu) is an appreciated, amber-colored, and very popular naturally fermented condiment. Wang, Li, et al. (2020) explored the dynamic changes in volatile flavor compounds and microbial communities and their correlations of Chinese fish sauce. They found that *Halanaerobium*, *Halomonas*, *Tetragenococcus*, *Halococcus*, and *Candidatus Frackibacter* were not only the primary influencers of fish sauce fermentation but also represented the core microbiota related to the formation of flavor compounds.

Fermented vegetable products

Fermented vegetable products are closely related to Chinese diet, which can be dated back to the third century B.C. (Caplice and Fitzgerald 1999). The harvested vegetables can be preserved for a long time, especially in winter, when vegetables are limited in some areas of China (Liu, Han, and Zhou 2011). The traditional storage method is to place vegetables into clean containers and add ingredients, such as salt, hot red peppers, garlic, ginger and Chinese prickly ash, for spontaneous fermentation. The most famous fermented vegetables in China are Dongbei suancai, Sichuan paocai and Jiangxi yancai (Yang et al. 2016; Guan et al. 2020; Xiao et al. 2018). The dominant genera of LAB in fermented vegetables include *Lactobacillus*, *Pediococcus*, *Leuconostoc*, *Weissella*, *Tetragenococcus* and *Lactococcus*, which are responsible for the flavor formation (Xiao et al. 2020; He et al. 2020). Xiao et al. (2018) investigated the microbial community succession and flavor compounds during Sichuan paocai fermentation. The results showed that the fermentation process was dominated by *Pediococcus*, *Streptococcus* and *Staphylococcus* followed by *Leuconostoc* and *Lactobacillus*. Correlation analysis indicated that the contribution of bacteria to flavor development was higher than the contribution of fungi. *Lactobacillus* was positively

Table 2. Lactic acid bacteria (LAB) and flavor compounds identified in different traditional Chinese fermented foods.

Fermented foods	Process of fermentation	Predominant LAB	Associated flavor compounds	References
Fermented meat products				
Fermented dry sausage	The fermented dry sausage is prepared from minced lean pork and pork back fat as materials that are mixed with the salts, sugars, nitrite, wine and spice, and stuffed into the natural pig intestine casings. Finally, the sausages are ripened at 15–37 °C and relative humidity of 65–85% for 10–20 d.	<i>Weissella hellenica</i> , <i>Lactobacillus sakei</i> , <i>Lactococcus lactis</i> , <i>Lactobacillus alimentarius</i> and <i>Lactobacillus plantarum</i>	3-Hydroxy-2-butanone, octanal, ethyl hexanoate and ethyl heptanoate.	Hu et al. (2019); Hu et al. (2020)
Sour meat	Sour meat is a traditional artisan fermented meat product popular in Dong, Miao and Tujia nationalities of China, which is made by mixing pork belly, salt, rice and other seasonings, and then naturally fermented in sealed jars at 10–25 °C and relative humidity of 50% for 15–30 d.	<i>Lactobacillus</i>	Hexanal, benzaldehyde, nonanal, (E,E)-2,4-decadienal, 1-octen-3-ol and octanal.	Lv et al. (2019)
Fermented fish products				
Fermented fish (Suanyu)	The fish is initially mixed with carbohydrates, salt, and spices and ripened at 10–30 °C for 40–60 d.	<i>Lactobacillus</i> and <i>Lactococcus</i>	Ethyl lactate, ethyl octanoate, benzaldehyde, hexanoic acid, butanoic acid, lactic acid and acetic acid.	Zang et al. (2018); Zang et al. (2020)
Fish sauce (Yu-lu)	Fish sauce is a clear brown liquid produced by spontaneous fermentation of diverse fish such as anchovies, sardines and menhaden, following the addition of salt (20–30% w/w).	<i>Tetragenococcus</i>	1-Octene-3-ol, 2-octenal, 3-methylbutanal, heptanal, 3-methylthiopropional, 2-butanone, 2-methylpropanal, 3,5-octadien-2-one and acetic acid.	Wang, Li, et al. (2020); Wang et al. (2018).
Fermented vegetable products				
Suancai	Dongbei suancai is usually fermented in winter in Northeast China. Cabbages are trimmed of outer leaves, washed, placed into a pot, seasoned with 2–3% salt for 8–15 h and spontaneously fermented in a jar at approximately 10 °C for approximately 20 d.	<i>Lactobacillus</i> , <i>Leuconostoc</i> , <i>Pediococcus</i> and <i>Weissella</i>	Esters, phenols, nitriles, sulfides, 1-hexanol, cis-hept-4-enol, 1-octanol, linalool, phenylethyl alcohol, 3-phenylpropanol and 2,5-dimethylbenzaldehyde.	Liang et al. (2020); Liu, Li, Wei, et al. (2019); He et al. (2020)
Paocai	Sichuan paocai is made from washed cabbage cut into small pieces and placed in a pickle jar with spices by spontaneous fermentation at an ambient temperature of approximately 23 °C for 4–7 d depending on the seasonal conditions.	<i>Lactococcus</i> , <i>Leuconostoc</i> , <i>Lactobacillus</i> , <i>Weissella</i> , <i>Fructobacillus</i> and <i>Pediococcus</i>	Lactic acid, formic acid, 3-mercaptohexyl butanoate, 1,2-propanediol diformate, 2-butenic acid, lavandulyl acetate, 3-(methylthio) propyl isothiocyanate and piperidine-2-thione.	Liu, She, et al. (2019); Xiao et al. (2018).
Yancai	Yancai is a traditional Chinese fermented vegetable. Jingxi yancai is made from various fresh vegetables that are washed and exposed to sunlight for 5–6 h to dehydrate. After seasoning with salt, semi-dried vegetables are placed into a jar with some water to allow spontaneous fermentation for 6–8 d.	<i>Lactobacillus</i> and <i>Pediococcus</i>	Isopentyl formate, sinapic acid, 2,4-ditert-butylbenzenethiol, sinapic acid, 2,4-ditert-butylbenzenethiol, 1,2,3,4-tetramethylbenzene, 3-methylhepta-1,6-dien-3-ol, and 5-amidino-2,5,8-trimethylnona-2,7-diene.	Xiao et al. (2020); Liu, Li, Huang, et al. (2019)
Fermented soybean products				
Doubanjiang	Generally, the production of Doubanjiang includes two stages. Initially, soybeans are softened under warm water and their 'shells' are removed. The cooled raw material is mixed with wheat flour, inoculated with <i>Aspergillus oryzae</i> , and then ferments for approximately two months.	<i>Tetragenococcus</i> , <i>Lactobacillus</i> and <i>Streptococcus</i>	Ethanol, isoamylol, furfuryl alcohol, ethyl hexanoate, ethyl phenylacetate and ethyl laurate.	Li et al. (2016); Li, Rui, et al. (2017); Zhang et al. (2020)
Stinky tofu	Soybeans are made into milk that then forms tofu during the first step. When the brine medium acquires a strong odor, an open fermentation is maintained for several days; then, tofu curds are immersed in a medium for a few hours to obtain the final product.	<i>Streptococcus lutetiensis</i> , <i>Lactococcus lactis</i>	–	Gu et al. (2018)
Plain sufu	The production of sufu involves preparation of tofu curds, inoculation of the tofu curds with microorganisms to form pehtzes, salting of pehtzes, and aging them in bottles with dressing mixture.	<i>Enterobacter</i> , <i>Tetragenococcus</i> , <i>Lactobacillus</i> , <i>Weissella</i>	Methional, ethyl (Z,Z)-9,12-octadecadienoate, phenol, hexanal, 2-pentylfuran and 1-hexanol.	He and Chung (2020)

(continued)

Table 2. Continued.

Fermented foods	Process of fermentation	Predominant LAB	Associated flavor compounds	References
Dajiang	The steps are as follows: (1) select high quality soybeans during the first or second month of the lunar year; (2) wash the soybeans and remove any impurities; (3) stew the beans in a pot under gentle heat until they can be easily mashed by hand-squeezing; (4) mash the boiled soybeans, mold into a bun-like, cylindrical or cuboid shape and wrap in paper; (5) place the wrapped mold on a cupboard or a top beam to allow free drop-in of microbes from the air. At this stage, the soybean paste is called bean sauce mash or paste brick; (6) four months later, rinse the mash and break into small gobbets; (7) put the gobbets into a jar together with water and salt, and (8) store the jar in an open place for natural fermentation during which a rake is used to remove the floating material. At this stage, soybean paste is called soy sauce mash. Soybean pastes become edible a month or more after this final step.	<i>Tetragenococcus</i> , <i>Weissella</i> , <i>Lactobacillus</i> and <i>Leuconostoc</i>	2-Methyl-1-propanol, 3-methyl-1-butanol, 2,5-dimethylpyrazine, 2,6-dimethylpyrazine, ethyl lactate, trimethylpyrazine, 3-methylthio-propionaldehyde, furfural, benzaldehyde, isovaleric acid, ethyl phenylacetate, 2-phenylethanol, 2-acetylpyrrole, 4-ethyl-2-methoxyphenol and 4-ethylphenol.	Sun et al. (2018); Yu and Bo (2020); Wu et al. (2018); Peng et al. (2014)
Fermented dairy products				
Koumiss	Koumiss is made from fresh mare milk using natural starters from the previous batch of koumiss and is fermented in wooden casks or porcelain urns. The raw milk is anaerobically fermented at ambient temperature for 1–3 d and stirred using a wooden stick.	<i>Lactobacillus helveticus</i> , <i>Streptococcus parauberis</i> and <i>Lactobacillus delbrueckii</i>	–	Mo et al. (2019)
Yogurt	Yogurt is produced with a starter culture added to skim milk, heating at 85 °C for 30 min and cooling to 42 °C. Fermentation proceeded at 42 °C in a water bath until the final pH 4.6 is reached. The yogurt bulk is cooled down to 10 °C before stirring. Then, the fermented matrix is stirred and finally stored at 4 °C in the dark for several days.	<i>Lactobacillus</i>	N-heptanol, 2-heptanone, 1-pentanol and hexanol.	Pan et al. (2014); Liu et al. (2016); Li, Song, et al. (2017)
Kazak artisanal Cheese	To produce Kazak artisanal cheese, milk is first pretreated by boiling for approximately 30–60 s, and old yogurt (a spontaneously fermented starter) is added to the milk at 28–30 °C. After 72 h of fermentation in goatskin bags, the fermented product is concentrated by boiling in a pan under constant stirring with a crabstick, and the whey is removed. The fermented thick yogurt is placed in a meshed canvas bag and suspended outdoors to remove the moisture. Subsequently, the fresh cheese is processed by shaping and placed on a bamboo board for 30–0 d of ripening at an average temperature from 5 °C to 10 °C and 85–90% humidity. Finally, the mature cheese is successfully obtained.	<i>Lactobacillus</i> and <i>Streptococcus</i>	2-Nonanone, acetoin, benzaldehyde, 1-hexanol, 2-heptanone, 2-nonanol, benzyl alcohol, ethyl hexanoate, ethyl nonanoate and ethyl octanoate.	Zheng, Liu, Shi, et al. (2018); Zheng, Liu, Li, et al. (2018); Wang, Wu, et al. (2019)
Fermented yak milk	Fermented yak milk is a traditional dairy product in North-western China generally prepared using qula (starter culture); the product is prepared by defatting, acidification, and air-drying yak milk with subsequent fermentation at 4–15 °C for 12–36 h.	<i>Lactobacillus</i> , <i>Streptococcus</i> , <i>Lactococcus</i> and <i>Leuconostoc</i>	Benzaldehyde, 2,3-pentanedione, ethanol and ethyl acetate.	Jiang et al. (2020)

correlated with lactic acid, formic acid, 3-mercaptopentyl butanoate, 1,2-propanediol diformate, 2-butenic acid, ethyl ester and 3-methoxy-thiophene, and *Leuconostoc* was positively associated with diamyl sulfite, dihexyl-3-methyl-ethylene oxide, 2,4-dimethylthiazole and lavandulyl acetate. The authors also evaluated the microbial communities of Dongbei suancai, Sichuan paocai and Jiangxi yancai and predicted the functional roles of the microbes and their associations with the flavor compounds (Xiao et al. 2020). The results indicated that *Lactobacillus* made up a large proportion of the species in all the three products analyzed and there were clear differences in the bacterial community structure between various fermented vegetables. *Lb. sakei*, *Lb. acetotolerans* and *P. pentosaceus* were found to be the markers of Dongbei suancai, Sichuan paocai, and Jiangxi yancai, respectively. Several *Lactobacillus* were closely associated with more than 20 flavor compounds. Among them, *Lb. sakei* was positively correlated with volatile compounds, such as ethyl esters, benzoic acid, lactic acid and (R)-3-hydroxybutyric acid. *Lb. acetotolerans* was correlated with volatile compounds, such as sinapic acid, linalool, terpinyl acetate, 3-methylhepta-1,6-dien-3-ol and lactic acid.

Dongbei suancai is a representative fermented vegetable product in the Northeast China that is usually fermented in winter at temperature approximately ranging from 10°C to 15°C for approximately 20 d. He et al. (2020) investigated the bacterial diversity and volatile compounds during suancai fermentation at various temperatures. *Leuconostoc* dominated the fermentation at 10°C and 15°C, while *Weissella* and *Lactococcus* were predominant at 20°C and 25°C. *Pseudoalteromonas*, *Lactobacillus*, *Pediococcus*, *Acinetobacter*, *Lactococcus*, *Brochothrix*, *Psychrobacter* and *Enterobacter* were the core bacteria correlated with volatile compounds formed during fermentation. The predominant genus *Lactobacillus* had significant positive correlation with 13 volatile compounds. *Leuconostoc* had significant positive correlation with 1-hexanol, linalool, phenylethyl alcohol, cis-hept-4-enol, 2,5-dimethylbenzaldehyde, 1-octanol, 3-phenylpropanol, etc. *Pediococcus* and *Lactococcus* were positively associated with 2,4-di-tert-butylphenol and 1-hexanol. *Pediococcus* was positively associated with (2-isothiocyanatoethyl)benzene and 1,3-bis(1,1-dimethylethyl)benzene.

Fermented soybean products

China has more than 2000 years of soybean production tradition, and fermented soybean products with high nutrition and high health value have attracted considerable attention. During fermentation, useful active substances are released through the metabolic process of microorganisms, providing additional health benefits. Doubanjiang and plain sufu are the representative fermented soybean products with characteristic flavors partially generated by LAB (Sun et al. 2018; Xie et al. 2019; Liu, Han, and Zhou 2011). The dominant genera of LAB in the fermented soybean products include *Streptococcus*, *Lactococcus*, *Tetragenococcus*, *Lactobacillus*, *Leuconostoc* and *Weissella* that are responsible for the flavor formation (Gu et al. 2018; Li, Rui, et al. 2017; Niu et al.

2020). Li et al. (2016) identified the core bacterial communities and volatile compounds and investigated their relationships in Doubanjiang. The core microbiota was identified by the 16S rRNA gene sequencing, which mainly included *Leuconostoc*, *Weissella*, *Lactobacillus*, *Staphylococcus*, *Leuconostocaceae*, *Lactobacillaceae* and *Bacillales*. Correlation analysis showed that 3-octanone was associated with *Leuconostoc*, *Weissella*, *Lactobacillus*, *Leuconostocaceae* and *Lactobacillaceae*. Li, Rui, et al. (2017) further investigated bacterial community succession and metabolite changes using the 16S rRNA gene sequencing and ¹H-NMR in Doubanjiang. The study of bacterial community showed that the genera *Staphylococcus*, *Tetragenococcus*, *Acinetobacter*, *Streptococcus*, *Lactobacillus* and *Pseudomonas* dominated the whole fermentation process. Correlation analysis revealed that *Tetragenococcus* had significant association with guanidoacetate and phenylalanine; *Streptococcus* had significant association with carbonic compounds (arabinose, ribose, glycerol, fructose, lactate and acetate) and nitrogen-containing compounds (aspartate, glutamate, alanine, glycine, threonine, guanidoacetate, valine and phenylalanine); *Lactobacillus* was associated only with lactate, and not associated with free sugars, acetate or mannitol.

Plain sufu is another famous traditional Chinese solid-state fermented soybean curd with highly flavor, white-yellow color and soft and creamy cheese-like texture (Chung, Fung, and Kim 2005). He and Chung (2020) investigated the core functional microbiota related to the flavor compounds involved in production of naturally fermented soybean curd (plain sufu). Nine bacterial (*Trabulsibacteria*, *Bacillus*, *Enterobacter*, *Tetragenococcus*, *Lactobacillus*, *Stenotrophomonas*, *Sphingobacterium*, *Weissella* and unclassified) and six fungal (*Alternaria*, *Actinomyces*, *Fusarium*, *Sterigmatomyces*, *Debaryomyces* and *Candida*) genera were identified as the core functional microbiota that had an effect on the production of the flavor compounds. The Pearson's correlation analysis indicated that *Tetragenococcus* and *Lactobacillus* were positively associated with 12 free amino acids, excluding arginine, histidine and cysteine. With regards to the formation of volatile compounds, these genera contributed to the formation of ethyl (Z,Z)-9,12-octadecadienoate; however, only *Tetragenococcus* contributed to the formation of methional. In addition, these genera contributed to the formation of two fatty acids, C22:0 and C15:1, and *Lactobacillus* contributed to the formation of C21:0. In contrast, *Weissella* and *Bacillus* had significantly negative correlation with all these flavor compounds, indicating that these genera inhibited the production of the flavor compounds.

Fermented dairy products

Fermented dairy products developed by nomadic people are fermented with raw materials, such as cow, sheep and yak milk. China is a multi-ethnic country with nomadic people living in Xinjiang, Inner Mongolia and other provinces and thus, abundant resources of fermented dairy products have been developed, such as koumiss, yoghurt, cheese and

fermented yak milk (Liu, Han, and Zhou 2011; Liu et al. 2016; Li, Song, et al. 2017). Typical LAB members in the fermented dairy products belong to the genera *Lactobacillus*, *Pediococcus*, *Leuconostoc* and *Lactococcus*, which are naturally present in containers, raw material and air and are responsible for the fermentation (Parente and Cogan 2004; Pan et al. 2014; Mo et al. 2019). Jiang et al. (2020) analyzed the microbial composition and flavor profile of traditional fermented yak milk. The results indicated that *Lactobacillus* was the most abundant genus in the majority of fermented yak milk samples, which displayed a significant correlation with volatile compounds, such as 2,3-pentanedione, ethanol, benzaldehyde and ethyl acetate. However, the samples with relatively high abundance of *Streptococcus* and *Lactococcus* had relatively low contents of volatile compounds. Zheng, Liu, Shi, et al. (2018) evaluated the microbiota community diversity and their relationships with fatty acids, volatile compounds and amino acids of cheese. The results indicated that *Torulaspora*, *Streptococcus*, *Kluyveromyces* and *Lactobacillus* predominated through the entire process of cheese ripening. Correlation analysis based on bidirectional orthogonal partial least squares showed that contributions of bacteria to flavor formation is higher than that of fungi. The abundance of *Staphylococcus*, *Bacillus*, *Lactococcus* and *Acetobacter* was positively correlated with 2-nonanone, acetoin and benzaldehyde. However, *Lactobacillus* was negatively correlated with volatile compounds, such as 1-hexanol, benzyl alcohol, 2-heptanone, ethyl hexanoate, 2-nonanol, ethyl nonanoate and ethyl octanoate. The authors also determined the microbial community composition and flavor profiles of 10 cheese samples from various regions of Xinjiang in China (Zheng, Liu, Li, et al. 2018). *Debaryomyces*, *Lactobacillus*, *Issatchenkia*, *Streptococcus* and *Kluyveromyces* were the core bacteria, and *Torulaspora* and *Pichia* were the key fungi in cheeses from various regions. The correlation analysis showed that *Lactobacillus* was positively associated with alanine, ethanol and two short chain fatty acids (acetic acid and butanoic acid); *Streptococcus* contributed to the production of acetoin, ethyl lactate and ethyl-2-methylbutanoate.

Analysis of the correlations between the LAB community and volatile compounds indicated that LAB was highly associated with the flavor formation in Chinese traditional fermented foods. Overall, *Lactobacillus*, *Lactococcus*, *Leuconostoc*, *Pediococcus*, *Weissella*, *Tetragenococcus*, *Streptococcus* and *Enterococcus* were the major genera in Chinese traditional fermented foods and they contributed to the formation of esters, aldehydes, acids, ketones and alcohols. However, the microbial community and the associated flavor has certain differences between various Chinese traditional fermented foods, which may be due to the activities of microorganisms interacting with each other and with the abiotic environment and to the differences in raw materials and processing conditions (Peláez and Requena 2005; Irlinger and Mounier 2009). A better understanding of how flavor is influenced by LAB and the metabolic pathways of LAB in fermented matrix is required.

Key metabolic pathways of LAB for flavor formation

LAB enzymes can hydrolyze numerous food components (including carbohydrates, proteins and lipids) into flavor precursors and convert them into the aroma compounds. Three key metabolic pathways of LAB are involved in the production of volatile compounds: (1) carbohydrate metabolism; (2) proteolysis and amino acid catabolism; and (3) lipolysis and fatty acid metabolism (Bintsis 2018). A general overview of the main metabolic pathways leading to the formation of volatile compounds in fermented foods is presented in Figure 2.

Carbohydrate metabolism

LAB metabolize carbohydrates by fermentation to produce ATP by substrate-level phosphorylation without the involvement of a membrane or electron transport system. There are two types of carbohydrate fermentation pathways in LAB that generate different metabolites; the pathways include homo-fermentation and hetero-fermentation depending on the substrate, LAB species and the environmental conditions (Sharma et al. 2020). Homo-fermentative LAB species include *Pediococcus*, *Lactococcus*, *Enterococcus*, *Streptococcus* and certain species of *Lactobacillus* (e.g., *Lb. casei*, *Lb. curvatus*, *Lb. acidophilus* and *Lb. helveticus*). Hetero-fermentative LAB include *Weissella*, *Leuconostoc*, *Oenococcus* and *Lactobacillus* species (e.g., *Lb. brevis*, *Lb. fermentum* and *Lb. reuteri*). For homo-fermentative LAB species, the sugars enter the pathways through the Embden-Meyerhof-Parnas (EMP) pathway to produce pyruvate, which is subsequently reduced to lactic acid as the sole product (Bintsis 2018). In hetero-fermentative LAB species, the sugars enter the pathways through the phosphoketolase pathway (PKP) to produce glucose-6-phosphate, an important intermediate for the formation of pyruvate, which can form metabolites in addition to lactic acid as the end product of fermentation, including acetic acid, ethanol and carbon dioxide (Wu and Li 2018). Acetic acid is the key flavor component in fermented dairy products and can be an off-flavor at higher concentrations (McAuliffe, Kilcawley, and Stefanovic 2019). Citrate is present in fermented vegetable and dairy products and is used as an additive for the production of fermented sausages; citrate can be co-metabolized with sugars by citrate-utilizing LAB (e.g., *Lc. lactis* and *Leu. mesenteroides*) (Hugenholtz 1993). Citrate can be converted into oxaloacetate and acetate by the enzyme citrate lyase. Oxaloacetate is subsequently converted by oxaloacetate decarboxylase to produce carbon dioxide and pyruvate. The subsequent dissipation of pyruvate may produce volatile compounds, such as 2,3-butanediol, diacetyl and acetoin, which may have a profound impact on the aroma of fermented food (Erkus et al. 2013; Collins 1972). Diacetyl with a buttery aroma has a positive effect on the flavor of a series of fermented dairy products, such as yogurt and cheese (Routray and Mishra 2011; Lo et al. 2018).

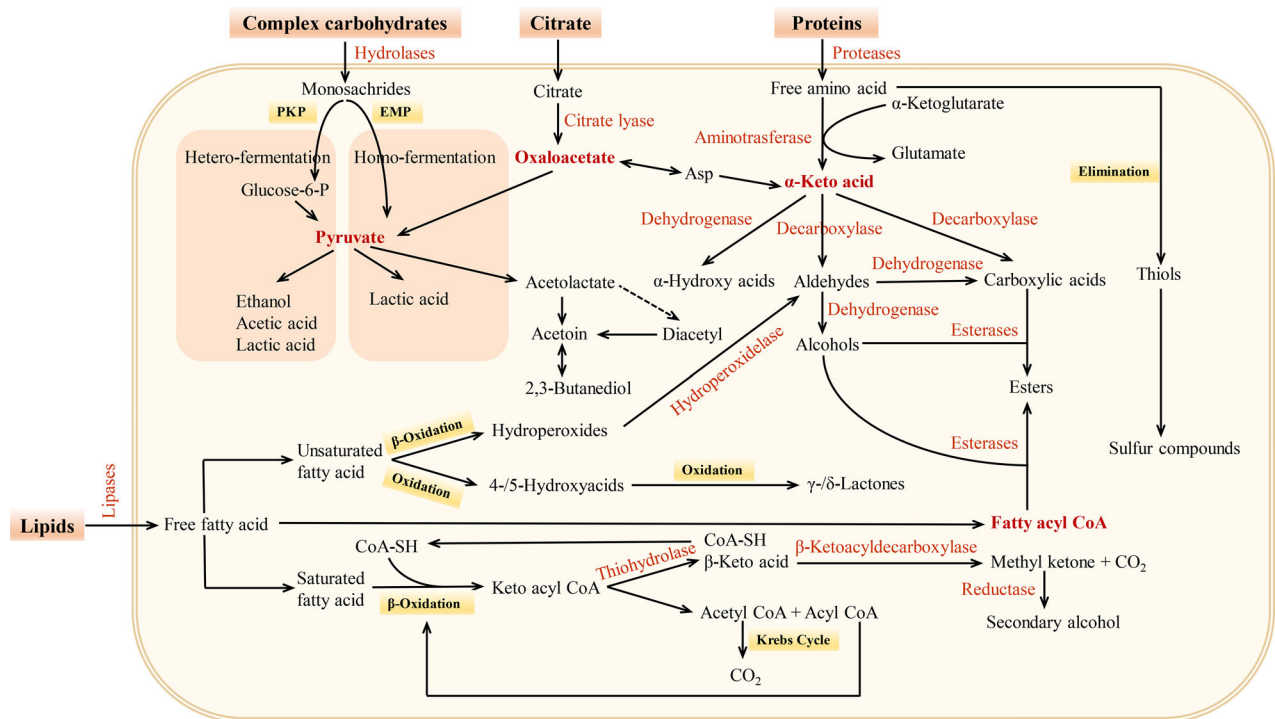


Figure 2. Overview of general conversion pathways relevant for flavor formation by lactic acid bacteria in fermented foods (based on Cheng 2010; De Vuyst, Van Kerrebroeck, and Leroy 2017; Paul and McSweeney-Maria 2000).

Proteolysis and amino acid catabolism

Proteolysis is one of the major biochemical events in flavor development that occurs during the fermentation and maturation of fermented foods (Viana de Souza and Dias 2017). LAB, such as *Lb. casei*, *Lb. plantarum*, *Lb. curvatus* and *Lb. sakei*, possess a proteolytic ability that enables them to hydrolyze proteins into peptides and amino acids (Bintsis 2018). Large hydrophobic peptides are associated with (undesirable) bitter taste and peptides and amino acids contribute to the basic taste of fermented foods, including sour (Tyr, Phe and Ala), bitter (His, Leu, Arg, Phe, Ile, Lys and Val), sweet (Ala, Gly, Thr, Ser, Pro and Hyp) and umami/salty (Glu and Asp) (Ramalingam, Zhen, and Hwang 2019; Bachmanov et al. 2016). Moreover, free amino acids can be used as substrates for subsequent flavor formation.

Two main pathways are involved in the conversion of free amino acids into volatile compounds: elimination reactions catalyzed by amino acid lyase and pathways initiated by amino acid aminotransferases. The elimination route has been described for methionine and threonine; the activity by carbon-sulfur lyases results in the release of thiols, which can be subsequently converted to the sulfur compounds (garlic, cabbage and boiled potato odours) (Liu et al. 2008; McAuliffe, Kilcawley, and Stefanovic 2019). The transamination route is initiated by aminotransferases that convert α -ketoglutarate into glutamate and simultaneously convert amino acids into the corresponding α -keto acid flavor precursors. α -Ketoglutarate is the preferred amino group acceptor (co-substrate) for transamination. Improving the availability of this co-substrate leads to increased conversion of amino acids. Yvon, Berthelot, and Gripon (1998) demonstrated that the addition of α -ketoglutarate significantly

increased amino acid conversion of *Lb. sakei*, *Lb. plantarum* and *Lc. Lactis* in cheese curd. Generated α -keto acids can undergo various enzymatic reactions including a reduction catalyzed by hydroxy acid dehydrogenase to generate α -hydroxy acids and decarboxylation to form aldehydes. The aldehydes can be further reduced to alcohols by alcohol dehydrogenase and oxidized to organic acid by aldehyde dehydrogenase or undergo oxidative decarboxylation to form acyl-CoA and carboxylic acids (Thierry et al. 2015; Viana de Souza and Dias 2017). The corresponding alcohols or organic acids can be used as the substrates to produce esters by esterases and acyltransferases.

Lipolysis and fatty acid metabolism

Lipolysis and oxidation of fatty acids in fermented foods are the major sources of flavor compounds. The hydrolysis of lipids (such as triglycerides, diglycerides and monoglycerides) releases free fatty acids that are important aroma compounds in the majority of fermented foods (Murtaza et al. 2014). These free fatty acids can be generated by lipases that are present in relatively high levels in the *Lactococcus* and *Lactobacillus* species (Kamaly and Marth 1989). Short and medium-chain free fatty acids (4-12 carbon atoms) give a characteristic flavor note due to their considerably lower perception thresholds. For example, butanoic acid has rancid and cheesy aroma; hexanoic acid has a pungent aroma; octanoic acid has a waxy, soapy, goaty, musty, rancid and fruity note. However, long-chain free fatty acids (>12 carbon atoms) with high perception thresholds have a minor effect on flavor (Molimard and Spinnler 1996).

Free fatty acids, including saturated fatty acids and unsaturated fatty acids, act as precursors of catabolic reactions

leading to the production of certain volatile compounds, such as alkanes, methyl ketones, esters, secondary alcohols and lactones, through lipid oxidation (Smit, Smit, and Engels 2005; Collins, McSweeney, and Wilkinson 2003). Saturated fatty acids produce the odd-carbon methyl ketones by decarboxylation of β -keto acids via β -oxidation (Cheng 2010). Methyl ketones can be reduced to the corresponding secondary alcohols by reductases (Molimard and Spinnler 1996). Two pathways are responsible for the oxidation of unsaturated fatty acids; one of the pathways involves oxidation of unsaturated fatty acids in the presence of free radicals to form hydroperoxides via β -oxidation. Another pathway of unsaturated fatty acid metabolism can lead to the formation of 4-/5-hydroxy acids, which are converted to γ -/ δ -lactones that provide strong fruity flavors (Wu et al. 2018). Furthermore, LAB have a number of esterases that can directly synthesize flavor esters from glycerides and alcohols via an alcoholysis reaction. For example, LAB can esterify ethanol with butyric and hexanoic acids to produce ethyl butanoate and ethyl hexanoate (Holland et al. 2005).

Enhancement of flavor formation

A number of factors, such as temperature, pH, water activity, oxygen, salt and substrate availability, influence the flavor formation of fermented foods by LAB (Ardö 2006). In response to environmental stresses that impact their metabolism and survival, LAB use various strategies to resist harsh conditions and sudden environmental changes to improve or maintain the quality and flavor of fermented foods (Wu, Huang, and Zhou 2017). However, these fermentation parameters generally cannot be changed and are hard to control, thus leading to inconsistency of the final product flavor quality. To address this problem in modern large-scale production and maintain the inherent characteristics of fermented foods, application of functional starter cultures and metabolic engineering have been used as the effective approaches to enhance flavor formation for fermented food production (Devanthi and Gkatzionis 2019).

Application of functional starter cultures

LAB are commonly used as functional starter cultures for flavor improvement in fermented foods (Dongmo et al. 2016). The products inoculated with starter cultures have the typical characteristics of fermented foods, better flavor and higher product quality compared with foods prepared by spontaneous fermentation. The single strain inoculation can accelerate the ripening time, inhibit pathogens and spoilage bacteria, and alleviate the changes in organoleptic quality and microbiological stability in indigenous fermented foods to improve the overall quality of the products (Han et al. 2014). Single strains of *Lactobacillus* and *Lactococcus* are commonly used as industrial cultures to produce unique flavor profiles (Ayad et al. 1999). Zheng et al. (2020) found that *Lb. harbinensis* M1 can produce high levels of the desirable flavor compounds, 2,3-butanedione and acetoin, in fermented soymilk. Luo et al. (2018) demonstrated that adding

Lc. lactis ssp. *lactis* F9 significantly increased 3-methylbutanal content and enhanced the nutty flavor of the cheese without impairing its textural properties. Additionally, we assessed the roles of single LAB strains of *P. pentosaceus*, *Lb. fermentum*, *Lb. curvatus* and *Lb. brevis* isolated from Harbin dry sausage in the protein hydrolysis and flavor development, and the results showed that *P. pentosaceus* and *Lb. curvatus* promoted the development of acids, alcohols and aldehydes (Chen, Liu, et al. 2015). However, the application of single LAB strains may be susceptible to several factors, such as substrate availability, salt stress, temperature and pH changes during fermentation (Gatti et al. 2014).

Mixed starter cultures may be more resilient and display a more robust performance, which is enhanced by the presence of a rich consortium of microbes (Erkus et al. 2013). Thus, the mixed starter cultures may be a good alternative for the enhancement of flavor. Rodríguez et al. (1996) found that mixed starter culture containing *Lb. plantarum*, *Lb. casei* subsp. *casei*, *Lc. lactis* subsp. *lactis*, *Leu. paramesenteroides* and *Leu. mesenteroides* subsp. *dextranicum* provided cheese with better aroma. Lee et al. (2020) investigated the effects of combining lactic acid bacteria (*Leu. mesenteroides* and *Lb. sakei*) as a starter culture on the flavor of kimchi, and found that the high-rate *Leu. mesenteroides* inoculation treatment that has hetero-fermentative characteristics, led to the formation of acetic acid, mannitol and lactic acid; however, high-rate *L. sakei* inoculation treatment that has homo-fermentative characteristics, led to the formation of less acetic acid and mannitol but more lactic acid. Hence, using mixed LAB starter strains is advantageous since it strengthens, and in some cases compensates, the weaknesses of the LAB strains. The availability and standardized manufacturing of kimchi have demonstrated the value of mixed LAB starters during production. In our previous study, the influences of single and mixed strains of *P. pentosaceus*, *Lb. curvatus*, *Lb. sakei* and *S. xylosus* on the flavor profile of Harbin dry sausages were investigated, and the results indicated that the starter culture mixture of *P. pentosaceus*, *Lb. curvatus* and *S. xylosus* can promote lipid and protein hydrolysis, inhibit lipid autooxidation and improve fermented flavor development (Chen et al. 2017; Chen et al. 2016; Hu et al. 2019). Therefore, application of beneficial strains used as starter cultures is one of the prerequisites for establishment of industrial production of fermented foods.

Metabolic engineering

Metabolic engineering is a powerful tool to improve flavor compounds associated with LAB (Chaves et al. 2002). Metabolic engineering of strains is a common strategy for the production of flavor compounds via the modification of one or multiple genes/enzymes (Li et al. 2020). Enhanced precision of the metabolic engineering modifications can be achieved by gene overexpression, gene knockouts, precursor optimization and transporter engineering (Sharma et al. 2020). Chaves et al. (2002) reported that overexpression of the *glyA* gene encoding serine hydroxymethyltransferase (SHMT), which has threonine aldolase activity and converts

threonine to glycine and acetaldehyde, resulted in overproduction of acetaldehyde by 80–90% in *Streptococcus thermophilus* compared with the values observed in the parental strains in yoghurt. Acetaldehyde is an industrially valuable metabolite widely used for imparting flavor in fermented dairy products. Kyla-Nikkila et al. (2000) constructed two *ldhD*-negative *Lb. helveticus* CNRZ32 strains using gene replacement to develop a host for the production of pure L-(1)-isomer of lactic acid. One of the strains was constructed by deleting the promoter region of the *ldhD* gene and another strain was constructed by replacing the structural gene of *ldhD* with an additional copy of the structural gene (*ldhL*) of L-LDH of the same species. Two D-LDH-negative strains produced only L-(1)-lactic acid in an amount equal to the total lactate produced by the wild type. The maximum L-LDH activity was found to be 53 and 93% higher in GRL86 and GRL89, respectively, than that in the wild-type strain. Vaidyanathan et al. (2011) metabolically engineered *Lb. reuteri* by the expression of *Escherichia coli* alcohol dehydrogenase that is known to efficiently convert the precursor 3-hydroxypropionaldehyde to 1,3-propanediol. The results showed that specific productivity of 1,3-propanediol was increased 34% and molar yield was enhanced by 13% relative to the native strain. Guo et al. (2012) reported a novel strategy to precisely control the pyruvate distribution for fine tuning of lactate and diacetyl production in *L. lactis* through promoter engineering. Using selected promoters for the constitutive expression of the NADH oxidase gene, NADH oxidase activity increased to 58.17-fold of the wild-type strain under aerobic conditions. Via an altered NADH/NAD⁺ ratio, the reduced pyruvate to lactate flux was rerouted to diacetyl and production increased from 1.07 ± 0.03 mM to 4.16 ± 0.06 mM. Wang et al. (2016) compared the metabolic capacity of an engineered isolate of *L. plantarum* with its parent isolate, and found that the engineered isolate had a greater capacity to manipulate aspartate metabolism by enriching higher amounts of the intracellular aspartate.

Metabolic engineering has made significant progress in microbial strain improvement; however, its impact on commercial application has not been reported. Future studies, need to consider the effect of gene modification on the whole metabolic pathway responsible for cell function and overall fermentation performance and on food safety.

Conclusions and future prospects

Traditional Chinese fermented foods are an abundant LAB resource and have a long history in China with unique and appealing characteristics. Koumiss, Suancai, plain sufu and Chinese fermented sausage are representative fermented foods consumed in China. This review presented the emerging technologies for identification of the flavor compounds, bacterial community, and correlations between flavor compounds and LAB in the fermentation process. Key metabolic pathways of LAB for flavor formation and the methods for enhancement of flavor development in traditional Chinese fermented foods were also reviewed.

Studies of flavor improvement in the immediate future may help to elucidate metabolic contributions, promote the manufacturing process, and enhance flavor of fermented foods and can be directed toward: 1) identification of the key aroma compounds in the final products and determination of the main LAB involved in their formation; 2) investigation of the fermentation process parameters as tool for generation and modulation of targeted aroma compounds, such as pH, salt, water activity, temperature, oxygen and substrate availability; 3) study of interactions within the microbial community in the fermentation progress; and 4) study of the functionality and metabolic mechanism of LAB by metagenomics, metatranscriptomics and metaproteomics.

Disclosure statement

No potential conflict of interest was reported by the authors.

Author contributions

Yingying Hu identified and interpreted the literature sources and drafted the manuscript. Lang Zhang and Rongxin Wen collected relevant research and review papers, and designed the figure and prepared the content of tables. Qian Chen and Baohua Kong completed proof-reading and final editing of the manuscript.

Funding

This study was funded by the National Natural Science Foundation of China (31972139 and 31771990) and the National Key Research and Development Program during the 13th Five-year Plan in China (2016YFD0401504-03).

References

- Afshari, R., C. J. Pillidge, D. A. Dias, A. M. Osborn, and H. Gill. 2020. Cheesomics: The future pathway to understanding cheese flavour and quality. *Critical Reviews in Food Science and Nutrition* 60 (1): 33–47. doi: [10.1080/10408398.2018.1512471](https://doi.org/10.1080/10408398.2018.1512471).
- Al-Dalali, S., F. P. Zheng, B. G. Sun, and F. Chen. 2020. Characterization and comparison of aroma profiles and aroma-active compounds between traditional and modern Sichuan vinegars by molecular sensory science. *Journal of Agricultural and Food Chemistry* 68 (18):5154–67. doi: [10.1021/acs.jafc.0c00470](https://doi.org/10.1021/acs.jafc.0c00470).
- Ardö, Y. 2006. Flavour formation by amino acid catabolism. *Biotechnology Advances* 24 (2):238–42. doi: [10.1016/j.biotechadv.2005.11.005](https://doi.org/10.1016/j.biotechadv.2005.11.005).
- Ayad, E. H., A. Verheul, C. de Jong, J. T. Wouters, and G. Smit. 1999. Flavour forming abilities and amino acid requirements of *Lactococcus lactis* strains isolated from artisanal and non-dairy origin. *International Dairy Journal* 9 (10):725–35. doi: [10.1016/S0958-6946\(99\)00140-5](https://doi.org/10.1016/S0958-6946(99)00140-5).
- Bachmanov, A. A., N. P. Bosak, J. I. Glendinning, M. Inoue, X. Li, S. Manita, S. A. McCaughey, Y. Murata, D. R. Reed, M. G. Tordoff, et al. 2016. Genetics of amino acid taste and appetite. *Advances in Nutrition (Bethesda, MD)* 7 (4):806S–22S. doi: [10.3945/an.115.011270](https://doi.org/10.3945/an.115.011270).
- Bicchi, C., C. Cordero, E. Liberto, B. Sgorbini, and P. Rubiolo. 2008. Headspace sampling of the volatile fraction of vegetable matrices. *Journal of Chromatography A* 1184 (1–2):220–33. doi: [10.1016/j.chroma.2007.06.019](https://doi.org/10.1016/j.chroma.2007.06.019).

- Bintsis, T. 2018. Lactic acid bacteria as starter cultures: An update in their metabolism and genetics. *AIMS Microbiology* 4 (4):665–84. doi: [10.3934/microbiol.2018.4.665](https://doi.org/10.3934/microbiol.2018.4.665).
- Blandino, A., M. E. Al-Aseeri, S. S. Pandiella, D. Cantero, and C. Webb. 2003. Cereal-based fermented foods and beverages. *Food Research International* 36 (6):527–43. doi: [10.1016/S0963-9969\(03\)00009-7](https://doi.org/10.1016/S0963-9969(03)00009-7).
- Caplice, E., and G. F. Fitzgerald. 1999. Food fermentations: Role of microorganisms in food production and preservation. *International Journal of Food Microbiology* 50 (1–2):131–49. doi: [10.1016/S0168-1605\(99\)00082-3](https://doi.org/10.1016/S0168-1605(99)00082-3).
- Chaintreau, A. 2001. Simultaneous distillation-extraction: From birth to maturity-review. *Flavour and Fragrance Journal* 16 (2):136–48. doi: [10.1002/ffj.967](https://doi.org/10.1002/ffj.967).
- Chaves, A. C. S. D., M. Fernandez, A. L. S. Lerayer, I. Mierau, M. Kleerebezem, and J. Hugenholtz. 2002. Metabolic engineering of acetaldehyde production by *Streptococcus thermophilus*. *Applied and Environmental Microbiology* 68 (11):5656–62. doi: [10.1128/aem.68.11.5656-5662.2002](https://doi.org/10.1128/aem.68.11.5656-5662.2002).
- Chen, G., C. C. Chen, and Z. H. Lei. 2017. Meta-omics insights in the microbial community profiling and functional characterization of fermented foods. *Trends in Food Science & Technology* 65:23–31. doi: [10.1016/j.tifs.2017.05.002](https://doi.org/10.1016/j.tifs.2017.05.002).
- Chen, Q., B. H. Kong, Q. Han, Q. Liu, and L. Xu. 2016. The role of bacterial fermentation in the hydrolysis and oxidation of sarcoplasmic and myofibrillar proteins in Harbin dry sausages. *Meat Science* 121:196–206. doi: [10.1016/j.meatsci.2016.06.012](https://doi.org/10.1016/j.meatsci.2016.06.012).
- Chen, Q., B. H. Kong, Q. Han, X. F. Xia, and L. Xu. 2017. The role of bacterial fermentation in lipolysis and lipid oxidation in Harbin dry sausages and its flavour development. *LWT* 77:389–96. doi: [10.1016/j.lwt.2016.11.075](https://doi.org/10.1016/j.lwt.2016.11.075).
- Chen, Q., B. H. Kong, Q. X. Sun, F. J. Dong, and Q. Liu. 2015. Antioxidant potential of a unique LAB culture isolated from Harbin dry sausage: In vitro and in a sausage model. *Meat Science* 110:180–8. doi: [10.1016/j.meatsci.2015.07.021](https://doi.org/10.1016/j.meatsci.2015.07.021).
- Chen, Q., Q. Liu, Q. X. Sun, B. H. Kong, and Y. L. Xiong. 2015. Flavour formation from hydrolysis of pork sarcoplasmic protein extract by a unique LAB culture isolated from Harbin dry sausage. *Meat Science* 100:110–7. doi: [10.1016/j.meatsci.2014.10.001](https://doi.org/10.1016/j.meatsci.2014.10.001).
- Chen, S., C. Wang, M. Qian, Z. Li, and Y. Xu. 2019. Characterization of the key aroma compounds in aged Chinese rice wine by comparative aroma extract dilution analysis, quantitative measurements, aroma recombination, and omission studies. *Journal of Agricultural and Food Chemistry* 67 (17):4876–84. doi: [10.1021/acs.jafc.9b01420](https://doi.org/10.1021/acs.jafc.9b01420).
- Cheng, H. 2010. Volatile flavor compounds in yogurt: A review. *Critical Reviews in Food Science and Nutrition* 50 (10):938–50. doi: [10.1080/10408390903044081](https://doi.org/10.1080/10408390903044081).
- Chung, H. Y., P. K. Fung, and J. S. Kim. 2005. Aroma impact components in commercial Plain Sufu. *Journal of Agricultural and Food Chemistry* 53 (5):1684–91. doi: [10.1021/jf048617d](https://doi.org/10.1021/jf048617d).
- Cocolin, L., V. Alessandria, P. Dolci, R. Gorra, and K. Rantsiou. 2013. Culture independent methods to assess the diversity and dynamics of microbiota during food fermentation. *International Journal of Food Microbiology* 167 (1):29–43. doi: [10.1016/j.ijfoodmicro.2013.05.008](https://doi.org/10.1016/j.ijfoodmicro.2013.05.008).
- Collins, E. B. 1972. Biosynthesis of flavor compounds by microorganisms. *Journal of Dairy Science* 55 (7):1022–8. doi: [10.3168/jds.S0022-0302\(72\)85615-7](https://doi.org/10.3168/jds.S0022-0302(72)85615-7).
- Collins, Y. F., P. L. H. McSweeney, and M. G. Wilkinson. 2003. Lipolysis and free fatty acid catabolism in cheese: A review of current knowledge. *International Dairy Journal* 13 (11):841–66. doi: [10.1016/S0958-6946\(03\)00109-2](https://doi.org/10.1016/S0958-6946(03)00109-2).
- Cordoba, N., M. Fernandez-Alduenda, F. L. Moreno, and Y. Ruiz. 2020. Coffee extraction: A review of parameters and their influence on the physicochemical characteristics and flavour of coffee brews. *Trends in Food Science & Technology* 96:45–60. doi: [10.1016/j.tifs.2019.12.004](https://doi.org/10.1016/j.tifs.2019.12.004).
- d'Acamora Zellner, B., P. Dugo, G. Dugo, and L. Mondello. 2008. Gas chromatography-olfactometry in food flavour analysis. *Journal of Chromatography A* 1186 (1–2):123–43. doi: [10.1016/j.chroma.2007.09.006](https://doi.org/10.1016/j.chroma.2007.09.006).
- Das, O., S. H. Kumar, and B. B. Nayak. 2020. Relative abundance of halophilic archaea and bacteria in diverse salt-fermented fish products. *LWT* 117:108688. doi: [10.1016/j.lwt.2019.108688](https://doi.org/10.1016/j.lwt.2019.108688).
- De Vuyst, L., and P. Neysens. 2005. The sourdough microflora: Biodiversity and metabolic interactions. *Trends in Food Science & Technology* 16 (1–3):43–56. doi: [10.1016/j.tifs.2004.02.012](https://doi.org/10.1016/j.tifs.2004.02.012).
- De Vuyst, L., S. Van Kerrebroeck, and F. Leroy. 2017. Microbial ecology and process technology of sourdough fermentation. *Advances in Applied Microbiology* 100:49–160. doi: [10.1016/bs.aambs.2017.02.00](https://doi.org/10.1016/bs.aambs.2017.02.00).
- Devanthi, P. V. P., and K. Gkatzionis. 2019. Soy sauce fermentation: Microorganisms, aroma formation, and process modification. *Food Research International (Ottawa, Ont.)* 120:364–74. doi: [10.1016/j.foodres.2019.03.010](https://doi.org/10.1016/j.foodres.2019.03.010).
- Diez-Simon, C., R. Mumm, and R. D. Hall. 2019. Mass spectrometry-based metabolomics of volatiles as a new tool for understanding aroma and flavour chemistry in processed food products. *Metabolomics* 15 (3):14. doi: [10.1007/s11306-019-1493-6](https://doi.org/10.1007/s11306-019-1493-6).
- Dongmo, S. N., S. Procopio, B. Sacher, and T. Becker. 2016. Flavor of lactic acid fermented malt based beverages: Current status and perspectives. *Trends in Food Science & Technology* 54:37–51. doi: [10.1016/j.tifs.2016.05.017](https://doi.org/10.1016/j.tifs.2016.05.017).
- El Hadi, M., F. J. Zhang, F. F. Wu, C. H. Zhou, and J. Tao. 2013. Advances in fruit aroma volatile research. *Molecules (Basel, Switzerland)* 18 (7):8200–29. doi: [10.3390/molecules18078200](https://doi.org/10.3390/molecules18078200).
- Engel, W., W. Bahr, and P. Schieberle. 1999. Solvent assisted flavour evaporation - A new and versatile technique for the careful and direct isolation of aroma compounds from complex food matrices. *European Food Research and Technology* 209 (3–4):237–41. doi: [10.1007/s002170050486](https://doi.org/10.1007/s002170050486).
- Erkus, O., V. C. de Jager, M. Spus, I. J. van Alen-Boerrigter, I. M. van Rijswijk, L. Hazelwood, P. W. M. Janssen, S. A. T. van Hijum, M. Kleerebezem, and E. J. Smid. 2013. Multifactorial diversity sustains microbial community stability. *The ISME Journal* 7 (11):2126–36. doi: [10.1038/ismej.2013.108](https://doi.org/10.1038/ismej.2013.108).
- Franciosa, I., V. Alessandria, P. Dolci, K. Rantsiou, and L. Cocolin. 2018. Sausage fermentation and starter cultures in the era of molecular biology methods. *International Journal of Food Microbiology* 279:26–32. doi: [10.1016/j.ijfoodmicro.2018.04.038](https://doi.org/10.1016/j.ijfoodmicro.2018.04.038).
- Franzosa, E. A., T. Hsu, A. Sirota-Madi, A. Shafquat, G. Abu-Ali, X. C. Morgan, and C. Huttenhower. 2015. Sequencing and beyond: Integrating molecular “omics” for microbial community profiling. *Nature Reviews. Microbiology* 13 (6):360–72. doi: [10.1038/nrmicro3451](https://doi.org/10.1038/nrmicro3451).
- García, C., M. Rendueles, and M. Díaz. 2019. Liquid-phase food fermentations with microbial consortia involving lactic acid bacteria: A review. *Food Research International (Ottawa, Ont.)* 119:207–20. doi: [10.1016/j.foodres.2019.01.043](https://doi.org/10.1016/j.foodres.2019.01.043).
- Gatti, M., B. Bottari, C. Lazzi, E. Neviani, and G. Mucchetti. 2014. Invited review: Microbial evolution in raw-milk, long-ripened cheeses produced using undefined natural whey starters. *Journal of Dairy Science* 97 (2):573–91. doi: [10.3168/jds.2013-7187](https://doi.org/10.3168/jds.2013-7187).
- Gu, J. S., T. J. Liu, F. A. Sadiq, H. Y. Yang, L. Yuan, G. H. Zhang, and G. Q. He. 2018. Biogenic amines content and assessment of bacterial and fungal diversity in stinky tofu - A traditional fermented soy curd. *LWT* 88:26–34. doi: [10.1016/j.lwt.2017.08.085](https://doi.org/10.1016/j.lwt.2017.08.085).
- Guan, Q. Q., W. D. Zheng, T. Huang, Y. S. Xiao, Z. G. Liu, Z. Peng, D. M. Gong, M. Y. Xie, and T. Xiong. 2020. Comparison of microbial communities and physicochemical characteristics of two traditionally fermented vegetables. *Food Research International (Ottawa, Ont.)* 128:108755. doi: [10.1016/j.foodres.2019.108755](https://doi.org/10.1016/j.foodres.2019.108755).
- Guo, T. T., J. Kong, L. Zhang, C. C. Zhang, and S. M. Hu. 2012. Fine tuning of the lactate and diacetyl production through promoter engineering in *Lactococcus lactis*. *PLoS One* 7 (4):e36296. doi: [10.1371/journal.pone.0036296](https://doi.org/10.1371/journal.pone.0036296).
- Han, X., H. X. Yi, L. W. Zhang, W. W. Huang, Y. C. Zhang, L. L. Zhang, and M. Du. 2014. Improvement of fermented Chinese cabbage characteristics by selected starter cultures. *Journal of Food Science* 79 (7):M1387–92. doi: [10.1111/1750-3841.12495](https://doi.org/10.1111/1750-3841.12495).

- He, W. M., and H. Y. Chung. 2020. Exploring core functional microbiota related with flavor compounds involved in the fermentation of a natural fermented plain sufu (Chinese fermented soybean curd). *Food Microbiology* 90:103408. doi: [10.1016/j.fm.2019.103408](https://doi.org/10.1016/j.fm.2019.103408).
- He, Z., H. Y. Chen, X. Y. Wang, X. P. Lin, C. F. Ji, S. J. Li, and H. P. Liang. 2020. Effects of different temperatures on bacterial diversity and volatile flavor compounds during the fermentation of suancai, a traditional fermented vegetable food from northeastern China. *LWT* 118:108773. doi: [10.1016/j.lwt.2019.108773](https://doi.org/10.1016/j.lwt.2019.108773).
- Holland, R., S. Q. Liu, V. L. Crow, M. L. Delabre, M. Lubbers, M. Bennett, and G. Norris. 2005. Esterases of lactic acid bacteria and cheese flavour: Milk fat hydrolysis, alcoholysis and esterification. *International Dairy Journal* 15 (6–9):711–8. doi: [10.1016/j.idairyj.2004.09.012](https://doi.org/10.1016/j.idairyj.2004.09.012).
- Hu, Y. Y., L. Zhang, Q. Liu, Y. Wang, Q. Chen, and B. H. Kong. 2020. The potential correlation between bacterial diversity and the characteristic volatile flavour of traditional dry sausages from Northeast China. *Food Microbiology* 91:103505. doi: [10.1016/j.fm.2020.103505](https://doi.org/10.1016/j.fm.2020.103505).
- Hu, Y. Y., Q. Chen, R. X. Wen, Y. Wang, L. G. Qin, and B. H. Kong. 2019. Quality characteristics and flavor profile of Harbin dry sausages inoculated with lactic acid bacteria and *Staphylococcus xylosum*. *LWT* 114:108392. doi: [10.1016/j.lwt.2019.108392](https://doi.org/10.1016/j.lwt.2019.108392).
- Hugenholtz, J. 1993. Citrate metabolism in lactic acid bacteria. *FEMS Microbiology Reviews* 12 (1–3):165–78. doi: [10.1111/j.1574-6976.1993.tb00017.x](https://doi.org/10.1111/j.1574-6976.1993.tb00017.x).
- Irlinger, F., and J. Mounier. 2009. Microbial interactions in cheese: Implications for cheese quality and safety. *Current Opinion in Biotechnology* 20 (2):142–8. doi: [10.1016/j.copbio.2009.02.016](https://doi.org/10.1016/j.copbio.2009.02.016).
- Jiang, Y., N. Li, Q. Wang, Z. M. Liu, Y. K. Lee, X. M. Liu, J. X. Zhao, H. Zhang, and W. Chen. 2020. Microbial diversity and volatile profile of traditional fermented yak milk. *Journal of Dairy Science* 103 (1):87–97. doi: [10.3168/jds.2019-16753](https://doi.org/10.3168/jds.2019-16753).
- Kamaly, K. M., and E. H. Marth. 1989. Enzyme activities of lactic Streptococci and their role in maturation of cheese: A review. *Journal of Dairy Science* 72 (8):1945–66. doi: [10.3168/jds.S0022-0302\(89\)79318-8](https://doi.org/10.3168/jds.S0022-0302(89)79318-8).
- Kataoka, H., H. L. Lord, and J. Pawliszyn. 2000. Applications of solid-phase microextraction in food analysis. *Journal of Chromatography A* 880 (1–2):35–62. doi: [10.1016/S0021-9673\(00\)00309-5](https://doi.org/10.1016/S0021-9673(00)00309-5).
- Kawaguchi, M., A. Takatsu, R. Ito, and H. Nakazawa. 2013. Applications of stir-bar sorptive extraction to food analysis. *TrAC Trends in Analytical Chemistry* 45:280–93. doi: [10.1016/j.trac.2013.01.007](https://doi.org/10.1016/j.trac.2013.01.007).
- Kumar Verma, D., and P. Prakash Srivastav. 2020. A paradigm of volatile aroma compounds in rice and their product with extraction and identification methods: A comprehensive review. *Food Research International (Ottawa, Ont.)* 130:108924. doi: [10.1016/j.foodres.2019.108924](https://doi.org/10.1016/j.foodres.2019.108924).
- Kyla-Nikkila, K., M. Hujanen, M. Leisola, and A. Palva. 2000. Metabolic engineering of *Lactobacillus helveticus* CNRZ32 for production of pure L-(+)-lactic acid. *Applied Environmental Microbiology* 66 (9):3835–41. doi: [10.1128/aem.66.9.3835-3841.2000](https://doi.org/10.1128/aem.66.9.3835-3841.2000).
- Lee, J. J., Y. J. Choi, M. J. Lee, S. J. Park, S. J. Oh, Y. R. Yun, S. G. Min, H. Y. Seo, S. H. Park, and M. A. Lee. 2020. Effects of combining two lactic acid bacteria as a starter culture on model kimchi fermentation. *Food Research International (Ottawa, Ont.)* 136:109591. doi: [10.1016/j.foodres.2020.109591](https://doi.org/10.1016/j.foodres.2020.109591).
- Li, C. K., J. H. Song, L. Y. Kwok, J. C. Wang, Y. Dong, H. J. Yu, Q. C. Hou, H. P. Zhang, and Y. F. Chen. 2017. Influence of *Lactobacillus plantarum* on yogurt fermentation properties and subsequent changes during postfermentation storage. *Journal of Dairy Science* 100 (4):2512–25. doi: [10.3168/jds.2016-11864](https://doi.org/10.3168/jds.2016-11864).
- Li, M. J., C. Q. Liu, J. M. Yang, R. Nian, M. Xian, F. L. Li, and H. B. Zhang. 2020. Common problems associated with the microbial productions of aromatic compounds and corresponding metabolic engineering strategies. *Biotechnology Advances* 41:107548. doi: [10.1016/j.biotechadv.2020.107548](https://doi.org/10.1016/j.biotechadv.2020.107548).
- Li, N., F. P. Zheng, H. T. Chen, S. Y. Liu, C. Gu, Z. Y. Song, and B. G. Sun. 2011. Identification of volatile components in Chinese Sinkiang fermented camel milk using SAFE, SDE, and HS-SPME-GC/MS. *Food Chemistry* 129 (3):1242–52. doi: [10.1016/j.foodchem.2011.03.115](https://doi.org/10.1016/j.foodchem.2011.03.115).
- Li, Z., L. Dong, Q. Huang, and X. Wang. 2016. Bacterial communities and volatile compounds in Doubanjiang, a Chinese traditional red pepper paste. *Journal of Applied Microbiology* 120 (6):1585–94. doi: [10.1111/jam.13130](https://doi.org/10.1111/jam.13130).
- Li, Z., J. Rui, X. Li, J. Li, L. Dong, Q. Huang, C. Huang, Z. Wang, L. Li, P. Xuan, et al. 2017. Bacterial community succession and metabolite changes during doubanjiang-meju fermentation, a Chinese traditional fermented broad bean (*Vicia faba* L.) paste. *Food Chemistry* 218:534–42. doi: [10.1016/j.foodchem.2016.09.104](https://doi.org/10.1016/j.foodchem.2016.09.104).
- Liang, H. P., Z. He, X. Y. Wang, G. Song, H. Y. Chen, X. P. Lin, C. F. Ji, and S. J. Li. 2020. Effects of salt concentration on microbial diversity and volatile compounds during suancai fermentation. *Food Microbiology* 91:103537. doi: [10.1016/j.fm.2020.103537](https://doi.org/10.1016/j.fm.2020.103537).
- Liu, H. L., and B. G. Sun. 2018. Effect of fermentation processing on the flavor of Baijiu. *Journal of Agricultural and Food Chemistry* 66 (22):5425–32. doi: [10.1021/acs.jafc.8b00692](https://doi.org/10.1021/acs.jafc.8b00692).
- Liu, L., X. She, Y. Qian, Y. L. Li, Y. F. Tao, Z. M. Che, G. R. Liu, and Y. Rao. 2019. Effect of different fermenting containers on the deterioration of Sichuan pickle. *LWT* 111:829–36. doi: [10.1016/j.lwt.2019.05.024](https://doi.org/10.1016/j.lwt.2019.05.024).
- Liu, M. J., A. Nauta, C. Francke, and R. J. Siezen. 2008. Comparative genomics of enzymes in flavor-forming pathways from amino acids in lactic acid bacteria. *Applied and Environmental Microbiology* 74 (15):4590–600. doi: [10.1128/aem.00150-08](https://doi.org/10.1128/aem.00150-08).
- Liu, S. N., Y. Han, and Z. J. Zhou. 2011. Lactic acid bacteria in traditional fermented Chinese foods. *Food Research International* 44 (3): 643–51. doi: [10.1016/j.foodres.2010.12.034](https://doi.org/10.1016/j.foodres.2010.12.034).
- Liu, W. J., J. Yu, Z. H. Sun, Y. Q. Song, X. N. Wang, H. M. Wang, T. Y. Wuren, M. S. Zha, B. L. G. Menghe, and H. P. Zhang. 2016. Relationships between functional genes in *Lactobacillus delbrueckii* ssp. *bulgaricus* isolates and phenotypic characteristics associated with fermentation time and flavor production in yogurt elucidated using multilocus sequence typing. *Journal of Dairy Science* 99 (1): 89–103. doi: [10.3168/jds.2015-10209](https://doi.org/10.3168/jds.2015-10209).
- Liu, Z. G., J. Y. Li, B. L. Wei, T. Huang, Y. S. Xiao, Z. Peng, M. Y. Xie, and T. Xiong. 2019. Bacterial community and composition in Jiangshui and Suan-cai revealed by high-throughput sequencing of 16S rRNA. *International Journal of Food Microbiology* 306:108271. doi: [10.1016/j.ijfoodmicro.2019.108271](https://doi.org/10.1016/j.ijfoodmicro.2019.108271).
- Liu, Z. G., J. Y. Li, T. Huang, Y. S. Xiao, Z. Peng, M. Y. Xie, and T. Xiong. 2019. Comparison of the bacterial communities in home-made Nanfeng yancai with and without salt. *Food Research International* 125:108509. doi: [10.1016/j.foodres.2019.108509](https://doi.org/10.1016/j.foodres.2019.108509).
- Lo, R., V. T. T. Ho, N. Bansal, and M. S. Turner. 2018. The genetic basis underlying variation in production of the flavour compound diacetyl by *Lactobacillus rhamnosus* strains in milk. *International Journal of Food Microbiology* 265:30–9. doi: [10.1016/j.ijfoodmicro.2017.10.029](https://doi.org/10.1016/j.ijfoodmicro.2017.10.029).
- Luo, J., C. B. Jiang, L. Zhao, M. Zhang, F. Wang, E. N. Sun, and F. Z. Ren. 2018. Keto acid decarboxylase and keto acid dehydrogenase activity detected during the biosynthesis of flavor compound 3-methylbutanal by the nondairy adjunct culture *Lactococcus lactis* ssp. *lactis* F9. *Journal of Dairy Science* 101 (11):9725–35. doi: [10.3168/jds.2018-14760](https://doi.org/10.3168/jds.2018-14760).
- Lv, J., Z. X. Yang, W. H. Xu, S. J. Li, H. P. Liang, C. F. Ji, C. X. Yu, B. W. Zhu, and X. P. Lin. 2019. Relationships between bacterial community and metabolites of sour meat at different temperature during the fermentation. *International Journal of Food Microbiology* 307:108286. doi: [10.1016/j.ijfoodmicro.2019.108286](https://doi.org/10.1016/j.ijfoodmicro.2019.108286).
- McAuliffe, O., K. Kilcawley, and E. Stefanovic. 2019. Symposium review: Genomic investigations of flavor formation by dairy microbiota. *Journal of Dairy Science* 102 (1):909–22. doi: [10.3168/jds.2018-15385](https://doi.org/10.3168/jds.2018-15385).
- Mo, L. X., J. Yu, H. Jin, Q. C. Hou, C. Q. Yao, D. Y. Ren, X. N. An, T. Tsogtgerel, and H. P. Zhang. 2019. Investigating the bacterial microbiota of traditional fermented dairy products using propidium monoazide with single-molecule real-time sequencing. *Journal of Dairy Science* 102 (5):3912–23. doi: [10.3168/jds.2018-15756](https://doi.org/10.3168/jds.2018-15756).

- Molimard, P., and H. E. Spinnler. 1996. Review: Compounds involved in the flavour of surface mould-ripened cheeses: Origins and properties. *Journal of Dairy Science* 79 (2):169–84. doi: [10.3168/jds.S0022-0302\(96\)76348-8](https://doi.org/10.3168/jds.S0022-0302(96)76348-8).
- Molino, A., S. Mehariya, G. D. Sanzo, V. Larocca, M. Martino, G. P. Leone, T. Marino, S. Chianese, R. Balducci, and D. Musmarra. 2020. Recent developments in supercritical fluid extraction of bioactive compounds from microalgae: Role of key parameters, technological achievements and challenges. *Journal of CO2 Utilization* 36: 196–209. doi: [10.1016/j.jcou.2019.11.014](https://doi.org/10.1016/j.jcou.2019.11.014).
- Murtaza, M. A., S. Ur-Rehman, F. M. Anjum, N. Huma, and I. Hafiz. 2014. Cheddar cheese ripening and flavor characterization: A review. *Critical Reviews in Food Science and Nutrition* 54 (10):1309–21. doi: [10.1080/10408398.2011.634531](https://doi.org/10.1080/10408398.2011.634531).
- Nguyen, D. T. L., K. Van Hoorde, M. Cnockaert, E. de Brandt, K. de Bruyne, B. T. Le, and P. Vandamme. 2013. A culture-dependent and -independent approach for the identification of lactic acid bacteria associated with the production of nem chua, a Vietnamese fermented meat product. *Food Research International* 50 (1):232–40. doi: [10.1016/j.foodres.2012.09.029](https://doi.org/10.1016/j.foodres.2012.09.029).
- Niu, C. T., Y. Xue, Y. Jia, T. B. Xu, C. F. Liu, F. Y. Zheng, J. J. Wang, and Q. Li. 2020. Analysis of bacterial community dynamics in the manufacture process of lajiaojiang (red chili paste). *LWT* 122: 108976. doi: [10.1016/j.lwt.2019.108976](https://doi.org/10.1016/j.lwt.2019.108976).
- Pan, D. D., Z. Wu, T. Peng, X. Q. Zeng, and H. Li. 2014. Volatile organic compounds profile during milk fermentation by *Lactobacillus pentosus* and correlations between volatiles flavor and carbohydrate metabolism. *Journal of Dairy Science* 97 (2):624–31. doi: [10.3168/jds.2013-7131](https://doi.org/10.3168/jds.2013-7131).
- Parente, E., and T. M. Cogan. 2004. Starter cultures: General aspects. *Cheese: Chemistry, Physics and Microbiology* 1:123–47. doi: [10.1016/S1874-558X\(04\)80065-4](https://doi.org/10.1016/S1874-558X(04)80065-4).
- Paul, L. H., and J. S. McSweeney-Maria. 2000. Biochemical pathways for the production of flavour compounds in cheeses during ripening: A review. *Le Lait* 80 (3):293–324. doi: [10.1051/lait:2000127](https://doi.org/10.1051/lait:2000127).
- Peláez, C., and T. Requena. 2005. Exploiting the potential of bacteria in the cheese ecosystem. *International Dairy Journal* 15 (6–9):831–44. doi: [10.1016/j.idairyj.2004.12.001](https://doi.org/10.1016/j.idairyj.2004.12.001).
- Peng, X. Y., X. Li, X. D. Shi, and S. T. Guo. 2014. Evaluation of the aroma quality of Chinese traditional soy paste during storage based on principal component analysis. *Food Chemistry* 151:532–8. doi: [10.1016/j.foodchem.2013.11.095](https://doi.org/10.1016/j.foodchem.2013.11.095).
- Ramalingam, V., S. Zhen, and I. Hwang. 2019. The potential role of secondary metabolites in modulating the flavor and taste of the meat. *Food Research International (Ottawa, Ont.)* 122:174–82. doi: [10.1016/j.foodres.2019.04.007](https://doi.org/10.1016/j.foodres.2019.04.007).
- Rodríguez, J., T. Requena, H. Goudédranche, J. L. Maubois, and M. Juárez. 1996. Accelerated ripening of reduced fat semi-hard cheese from a mixture of cow's, goat's and ewe's ultrafiltrated milk by using a Lac-Prt-strain of lactococci. *Le Lait* 76 (6):513–22. doi: [10.1051/lait:1996640](https://doi.org/10.1051/lait:1996640).
- Routray, W., and H. N. Mishra. 2011. Scientific and technical aspects of yogurt aroma and taste: A review. *Comprehensive Reviews in Food Science and Food Safety* 10 (4):208–20. doi: [10.1111/j.1541-4337.2011.00151.x](https://doi.org/10.1111/j.1541-4337.2011.00151.x).
- Salim-Ur-Rehman, A., Paterson, and J. R. Piggott. 2006. Flavour in sourdough breads: A review. *Trends in Food Science & Technology* 17 (10):557–66. doi: [10.1016/j.tifs.2006.03.006](https://doi.org/10.1016/j.tifs.2006.03.006).
- Sharma, A., G. Gupta, T. Ahmad, B. Kaur, and K. R. Hakeem. 2020. Tailoring cellular metabolism in lactic acid bacteria through metabolic engineering. *Journal of Microbiological Methods* 170:105862. doi: [10.1016/j.mimet.2020.105862](https://doi.org/10.1016/j.mimet.2020.105862).
- Sirén, K., S. S. T. Mak, U. Fischer, L. H. Hansen, and M. T. P. Gilbert. 2019. Multi-omics and potential applications in wine production. *Current Opinion in Biotechnology* 56:172–8. doi: [10.1016/j.copbio.2018.11.014](https://doi.org/10.1016/j.copbio.2018.11.014).
- Skåra, T., L. Axelsson, G. Stefánsson, B. Ekstrand, and H. Hagen. 2015. Fermented and ripened fish products in the northern European countries. *Journal of Ethnic Foods* 2 (1):18–24. doi: [10.1016/j.jef.2015.02.004](https://doi.org/10.1016/j.jef.2015.02.004).
- Smit, G., B. A. Smit, and W. J. M. Engels. 2005. Flavour formation by lactic acid bacteria and biochemical flavour profiling of cheese products. *FEMS Microbiology Reviews* 29 (3):591–610. doi: [10.1016/j.femsre.2005.04.002](https://doi.org/10.1016/j.femsre.2005.04.002).
- Song, H. L., and J. B. Liu. 2018. GC-O-MS technique and its applications in food flavor analysis. *Food Research International (Ottawa, Ont.)* 114:187–98. doi: [10.1016/j.foodres.2018.07.037](https://doi.org/10.1016/j.foodres.2018.07.037).
- Soria, A. C., M. J. García-Sarrió, and M. L. Sanz. 2015. Volatile sampling by headspace techniques. *Trac Trends in Analytical Chemistry* 71:85–99. doi: [10.1016/j.trac.2015.04.015](https://doi.org/10.1016/j.trac.2015.04.015).
- Sumby, K. M., P. R. Grbin, and V. Jiranek. 2010. Microbial modulation of aromatic esters in wine: Current knowledge and future prospects. *Food Chemistry* 121 (1):1–16. doi: [10.1016/j.foodchem.2009.12.004](https://doi.org/10.1016/j.foodchem.2009.12.004).
- Sun, X. D., G. Z. Lu, Y. S. Luan, Z. H. Zhao, H. Yang, and D. Su. 2018. Analyses of microbial community of naturally homemade soybean pastes in Liaoning Province of China by Illumina Miseq Sequencing. *Food Research International (Ottawa, Ont.)* 111:50–7. doi: [10.1016/j.foodres.2018.05.006](https://doi.org/10.1016/j.foodres.2018.05.006).
- Tamang, J., N. Thapa, B. Tamang, A. Rai, and R. Chettri. 2015. Microorganisms in fermented foods and beverages. In *Health Benefits of Fermented Foods and Beverages*, ed. J. P. Tamang, 1–110. 1st ed. Florida: CRC Press. doi: [10.1201/b18279-2](https://doi.org/10.1201/b18279-2).
- Tamang, J. P., K. Watanabe, and W. H. Holzapfel. 2016. Review: Diversity of microorganisms in global fermented foods and beverages. *Frontiers in Microbiology* 7:377. doi: [10.3389/fmicb.2016.00377](https://doi.org/10.3389/fmicb.2016.00377).
- Tarnecki, A. M., F. A. Burgos, C. L. Ray, and C. R. Arias. 2017. Fish intestinal microbiome: Diversity and symbiosis unravelled by metagenomics. *Journal of Applied Microbiology* 123 (1):2–17. doi: [10.1111/jam.13415](https://doi.org/10.1111/jam.13415).
- Thierry, A., T. Pogačić, M. Weber, and S. Lortal. 2015. Production of flavor compounds by lactic acid bacteria in fermented foods. In *Biotechnology of Lactic Acid Bacteria: Novel Applications*, ed. F. Mozzi, R. R. Raya, and G. M. Vignolo, 314–40. 2nd ed. New Jersey: John Wiley & Sons. doi: [10.1002/9781118868386.ch19](https://doi.org/10.1002/9781118868386.ch19).
- Vaidyanathan, H., V. Kandasamy, G. Gopal Ramakrishnan, K. Ramachandran, G. Jayaraman, and S. Ramalingam. 2011. Glycerol conversion to 1, 3-propanediol is enhanced by the expression of a heterologous alcohol dehydrogenase gene in *Lactobacillus reuteri*. *AMB Express* 1 (1):37–45. doi: [10.1186/2191-0855-1-37](https://doi.org/10.1186/2191-0855-1-37).
- Van Hijum, S. A. F. T., E. E. Vaughan, and R. F. Vogel. 2013. Application of state-of-art sequencing technologies to indigenous food fermentations. *Current Opinion in Biotechnology* 24 (2):178–86. doi: [10.1016/j.copbio.2012.08.004](https://doi.org/10.1016/j.copbio.2012.08.004).
- Vénica, C. I., I. V. Wolf, C. V. Bergamini, and M. C. Perotti. 2016. Influence of lactose hydrolysis on galacto-oligosaccharides, lactose, volatile profile and physicochemical parameters of different yogurt varieties. *Journal of the Science of Food and Agriculture* 96 (15): 4929–39. doi: [10.1002/jsfa.7870](https://doi.org/10.1002/jsfa.7870).
- Viana de Souza, J., and F. S. Dias. 2017. Protective, technological, and functional properties of select autochthonous lactic acid bacteria from goat dairy products. *Current Opinion in Food Science* 13:1–9. doi: [10.1016/j.cofs.2017.01.003](https://doi.org/10.1016/j.cofs.2017.01.003).
- Wang, J., M. Q. Huang, J. J. Zhang, and J. H. Wu. 2019. Flavor chemistry in Baijiu with sesame flavor: A review. In *Sex, Smoke, and Spirits: The Role of Chemistry*, ed. B. Guthrie, J. D. Beauchamp, A. Buettner, S. Toth, and M. C. Qian, 177–224. ACS Publications. doi: [10.1021/bk-2019-1321.ch013](https://doi.org/10.1021/bk-2019-1321.ch013).
- Wang, J., T. Wu, X. B. Fang, and Z. N. Yang. 2019. Manufacture of low-fat Cheddar cheese by exopolysaccharide-producing *Lactobacillus plantarum* JLK0142 and its functional properties. *Journal of Dairy Science* 102 (5):3825–14. doi: [10.3168/jds.2018-15154](https://doi.org/10.3168/jds.2018-15154).
- Wang, J. C., W. Y. Hui, C. X. Cao, R. L. Jin, C. X. Ren, H. P. Zhang, and W. Y. Zhang. 2016. Proteomic analysis of an engineered isolate of *Lactobacillus plantarum* with enhanced raffinose metabolic capacity. *Scientific Reports* 6 (1):31403. doi: [10.1038/srep31403](https://doi.org/10.1038/srep31403).
- Wang, S. Q., H. T. Chen, and B. G. Sun. 2020. Recent progress in food flavor analysis using gas chromatography-ion mobility spectrometry (GC-IMS). *Food Chemistry* 315:126158. doi: [10.1016/j.foodchem.2019.126158](https://doi.org/10.1016/j.foodchem.2019.126158).

- Wang, Y. Q., C. S. Li, L. H. Li, X. Q. Yang, Y. Y. Wu, Y. Q. Zhao, and Y. Wei. 2018. Effect of bacterial community and free amino acids on the content of biogenic amines during fermentation of Yu-lu, a Chinese fermented fish sauce. *Journal of Aquatic Food Product Technology* 27 (4):496–507. doi: [10.1080/10498850.2018.1450573](https://doi.org/10.1080/10498850.2018.1450573).
- Wang, Y. Q., C. S. Li, Y. Q. Zhao, L. H. Li, X. Q. Yang, Y. Y. Wu, S. J. Chen, J. W. Cen, S. L. Yang, and D. Q. Yang. 2020. Novel insight into the formation mechanism of volatile flavor in Chinese fish sauce (Yu-lu) based on molecular sensory and metagenomics analyses. *Food Chemistry* 323:126839. doi: [10.1016/j.foodchem.2020.126839](https://doi.org/10.1016/j.foodchem.2020.126839).
- Wang, Y. Q., Y. T. Zhou, X. Xiao, J. Zheng, and H. Zhou. 2020. Metaproteomics: A strategy to study the taxonomy and functionality of the gut microbiota. *Journal of Proteomics* 219:103737. doi: [10.1016/j.jprot.2020.103737](https://doi.org/10.1016/j.jprot.2020.103737).
- Wu, C. D., J. Huang, and R. Q. Zhou. 2017. Genomics of lactic acid bacteria: Current status and potential applications. *Critical Reviews in Microbiology* 43 (4):393–404. doi: [10.1080/1040841X.2016.1179623](https://doi.org/10.1080/1040841X.2016.1179623).
- Wu, J. R., T. Tian, Y. M. Liu, Y. X. Shi, D. B. Tao, X. Q. Yue, and R. N. Wu. 2018. The dynamic changes of chemical components and microbiota during the natural fermentation process in Da-Jiang, a Chinese popular traditional fermented condiment. *Food Research International (Ottawa, Ont.)* 112:457–67. doi: [10.1016/j.foodres.2018.06.021](https://doi.org/10.1016/j.foodres.2018.06.021).
- Wu, W. Q., and H. T. Li. 2018. Metabolites of lactic acid bacteria. In *Lactic Acid Bacteria in Foodborne Hazards Reduction*, ed. W. Chen and A. Narbad, 87–113. Berlin: Springer. doi: [10.1007/978-981-13-1559-6_4](https://doi.org/10.1007/978-981-13-1559-6_4).
- Xiao, Y. S., T. Huang, C. L. Huang, J. Hardie, Z. Peng, M. Y. Xie, and T. Xiong. 2020. The microbial communities and flavour compounds of Jiangxi yancai, Sichuan paocai and Dongbei suancai: Three major types of traditional Chinese fermented vegetables. *LWT* 121:108865. doi: [10.1016/j.lwt.2019.108865](https://doi.org/10.1016/j.lwt.2019.108865).
- Xiao, Y. S., T. Xiong, Z. Peng, C. G. Liu, T. Huang, H. Yu, and M. Y. Xie. 2018. Correlation between microbiota and flavours in fermentation of Chinese Sichuan Paocai. *Food Research International (Ottawa, Ont.)* 114:123–32. doi: [10.1016/j.foodres.2018.06.051](https://doi.org/10.1016/j.foodres.2018.06.051).
- Xie, M. J., F. Y. An, X. Q. Yue, Y. M. Liu, H. S. Shi, M. Yang, X. Y. Cao, J. R. Wu, and R. N. Wu. 2019. Characterization and comparison of metaproteomes in traditional and commercial dajiang, a fermented soybean paste in northeast China. *Food Chemistry* 301:125270. doi: [10.1016/j.foodchem.2019.125270](https://doi.org/10.1016/j.foodchem.2019.125270).
- Yang, H. Y., H. Wu, L. J. Gao, H. B. Jia, Y. Zhang, Z. J. Cui, and Y. H. Li. 2016. Effects of *Lactobacillus curvatus* and *Leuconostoc mesenteroides* on suan cai fermentation in Northeast China. *Journal of Microbiology and Biotechnology* 26 (12):2148–58. doi: [10.4014/jmb.1607.07010](https://doi.org/10.4014/jmb.1607.07010).
- Yousefi, M., M. Rahimi-Nasrabadi, S. M. Pourmortazavi, M. Wysokowski, T. Jesionowski, H. Ehrlich, and S. Mirsadeghi. 2019. Supercritical fluid extraction of essential oils. *Trac Trends in Analytical Chemistry* 118:182–93. doi: [10.1016/j.trac.2019.05.038](https://doi.org/10.1016/j.trac.2019.05.038).
- Yu, H., and S. Bo. 2020. Analysis of bacterial diversity and biogenic amines content during fermentation of farmhouse sauce from Northeast China. *Food Control* 108 (106861). doi: [10.1016/j.foodcont.2019.106861](https://doi.org/10.1016/j.foodcont.2019.106861).
- Yvon, M., S. Berthelot, and J. C. Gripon. 1998. Adding α -ketoglutarate to semi-hard cheese curd highly enhances the conversion of amino acids to aroma compounds. *International Dairy Journal* 8 (10–11): 889–98. doi: [10.1016/S0958-6946\(99\)00011-4](https://doi.org/10.1016/S0958-6946(99)00011-4).
- Zang, J. H., Y. S. Xu, W. S. Xia, J. M. Regenstein, D. W. Yu, F. Yang, and Q. X. Jiang. 2020. Correlations between microbiota succession and flavor formation during fermentation of Chinese low-salt fermented common carp (*Cyprinus carpio* L.) inoculated with mixed starter cultures. *Food Microbiology* 90:103487. doi: [10.1016/j.fm.2020.103487](https://doi.org/10.1016/j.fm.2020.103487).
- Zang, J. H., Y. S. Xu, W. S. Xia, D. W. Yu, P. Gao, Q. X. Jiang, and F. Yang. 2018. Dynamics and diversity of microbial community succession during fermentation of Suan yu, a Chinese traditional fermented fish, determined by high throughput sequencing. *Food Research International* 111:565–73. doi: [10.1016/j.foodres.2018.05.076](https://doi.org/10.1016/j.foodres.2018.05.076).
- Zhang, L., Z. M. Che, W. Z. Xu, P. Yue, R. Li, Y. F. Li, X. F. Pei, and P. B. Zeng. 2020. Dynamics of physicochemical factors and microbial communities during ripening fermentation of Pixian Doubanjiang, a typical condiment in Chinese cuisine. *Food Microbiology* 86:103342. doi: [10.1016/j.fm.2019.103342](https://doi.org/10.1016/j.fm.2019.103342).
- Zheng, X. J., F. Liu, K. X. Li, X. W. Shi, Y. Q. Ni, B. K. Li, and B. Zhuge. 2018. Evaluating the microbial ecology and metabolite profile in Kazak artisanal cheeses from Xinjiang, China. *Food Research International* 111:130–6. doi: [10.1016/j.foodres.2018.05.019](https://doi.org/10.1016/j.foodres.2018.05.019).
- Zheng, X. J., F. Liu, X. W. Shi, B. Wang, K. X. Li, B. K. Li, and B. Zhuge. 2018. Dynamic correlations between microbiota succession and flavor development involved in the ripening of Kazak artisanal cheese. *Food Research International (Ottawa, Ont.)* 105:733–42. doi: [10.1016/j.foodres.2017.12.007](https://doi.org/10.1016/j.foodres.2017.12.007).
- Zheng, Y., Y. Fei, Y. Yang, Z. Jin, B. Yu, and L. Li. 2020. A potential flavor culture: *Lactobacillus harbinensis* M1 improves the organoleptic quality of fermented soymilk by high production of 2,3-butanediol and acetoin. *Food Microbiology* 91:103540. doi: [10.1016/j.fm.2020.103540](https://doi.org/10.1016/j.fm.2020.103540).