MINI-REVIEW

Kimchi microflora: history, current status, and perspectives for industrial kimchi production

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Abstract Kimchi, a traditional Korean food made by the fermentation of vegetables, has become popular globally because of its organoleptic, beneficial, and nutritional properties. Spontaneous kimchi fermentation in unsterilized raw materials leads to the growth of various lactic acid bacteria (LAB), which results in variations in the taste and sensory qualities of kimchi products and difficulties in the standardized industrial production of kimchi. Raw materials, kimchi varieties, ingredients, and fermentation conditions have significant effects on the microbial communities and fermentative characteristics of kimchi during fermentation. Heterofermentative LAB belonging to the genera Leuconostoc, Lactobacillus, and Weissella are likely to be key players in kimchi fermentation and have been subjected to genomic and functional studies to gain a better understanding of the fermentation process and beneficial effects of kimchi. The use of starter cultures has been considered for the industrial production of high quality, standardized kimchi. Here, we review the composition and biochemistry of kimchi microflora communities, functional and genomic studies of kimchi LAB, and perspectives for industrial kimchi production.

Keywords Kimchi · Fermentation · Microflora · Heterofermentative lactic acid bacteria · Genomics · Industrial kimchi production · Starter culture

Introduction

Kimchi is a traditional Korean food, which is made by the fermentation of vegetables such as cabbage, radish, and

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Department of Life Science, Chung-Ang University, 84, HeukSeok-RoDongjak-Gu Seoul 156-756, Republic of Korea e-mail: cojeon@cau.ac.kr cucumber with various seasonings including salts, red pepper powder, garlic, leek, and ginger. Based on the major raw materials and preparation methods, kimchi is classified into hundreds of varieties, which have their own unique features in biochemical, nutritional, and organoleptic properties (Cheigh et al. 1994). Kimchi production is processed through fermentation of salted vegetables by lactic acid bacteria (LAB), which produce various compounds including organic acids (lactic and acetic acids), carbon dioxide, ethanol, vitamins, bacteriocins, prebiotic factors, and other flavoring compounds (mannitol and amino acids) contributing to kimchi's health-promoting and sensory properties during fermentation (Cheigh et al. 1994; Lee et al. 1999b; Yun et al. 1996).

Because kimchi fermentation without specific inoculants or starters leads to the growth of various LAB species or strains, originated from raw materials, that have been widely considered to have potential health benefits or probiotic effects (Chang et al. 2010; Ji et al. 2013; Lee et al. 2011a), kimchi may be a good source of potentially probiotic LAB. However, spontaneous kimchi fermentation also results in variations in the taste and sensory qualities of kimchi products, which makes it difficult to control the fermentation processes for the industrial production of kimchi. The use of starter cultures has been considered as an alternative for the industrial production of high quality, standardized kimchi. Here, we will review the history and current knowledge of kimchi microflora and LAB and suggest perspectives for the industrial production of kimchi.

Kimchi microbial community structure

LAB are naturally present at very low numbers in raw materials (vegetables and seasonings); however, they rapidly dominate the kimchi fermentation owing to conditions that favor their growth, such as anaerobic and low temperature conditions and the presence of NaCl (1.5-4.0%). In the early studies on kimchi LAB communities, traditional methods based on the morphological and phenotypic identification of bacterial species grown on culture agar media were used, although they were often unsuccessful (Lee et al. 1992; Mheen and Kwon 1984; Shin et al. 1996). Enterococcus, Pediococcus (P.), and Streptococcus species that were often observed as the dominant genera in the kimchi LAB community based on the traditional methods have been rarely detected in recent studies (Cho et al. 2006; Jeong et al. 2013a, b, c; Jung et al. 2012c; Kim and Chun 2005; Park et al. 2010, 2012a). This is probably because of the inaccurate identification by the morphological and phenotypic approaches. Therefore, as alternatives to the traditional methods, molecular methods using the sequences of 16S ribosomal RNA (rRNA) genes for the identification of isolated strains have attracted the attention of many researchers. Diverse LAB including Leuconostoc (Leu.) mesenteroides, Leu. citreum, Leu. carnosum, Leu. gasicomitatum, Leu. inhae, Leu. gelidum, Leu. kimchii, Leu. miyukkimchii, Lactobacillus (Lb.) sakei, Lb. plantarum, Lb. brevis, Lb. curvatus, Weissella (W.) koreensis, W. cibaria, W. kimchii, W. soli, and W. confusa have been isolated from various kimchi varieties and characterized taxonomically (Cho et al. 2006; Choi et al. 2002; Kim et al. 2000, 2003; Lee et al. 2002, 2012). However, culture-dependent approaches are not suitable to monitor community dynamics (successions) of kimchi LAB overtime during fermentation

Fig. 1 Heatmaps showing snapshots of LAB communities in cabbage kimchi products. Kimchi samples *A*, *B*, and *C* were analyzed using PCR/clone library (Kim and Chun 2005), isolation/ PCR (Cho et al. 2006), and PCR/ clone library (Park et al. 2010) approaches based on 16S rRNA gene sequences, respectively. The heatmaps were generated using "gplots" package of R program (http://cran.r-project.org/web/ packages/gplots/index.html) because they are labor-intensive and time-consuming. Recently, culture-independent methods based on the direct analysis of 16S rRNA genes without any culturing step have been widely used for studying the kimchi LAB dynamics during fermentation. Especially, polymerase chain reaction (PCR)-denaturing gradient gel electrophoresis (DGGE) and PCR-pyrosequencing approaches have been popularly applied (Jeong et al. 2013a, b, c; Jung et al. 2012c, 2013; Lee et al. 2005b; Park et al. 2012a).

Until now, analyses of the kimchi LAB communities have shown that LAB belonging to the genera Leuconostoc, Lactobacillus, and Weissella are likely to be mainly responsible for kimchi fermentation, while members of the genera Lactococcus (Lc.) and Pediococcus were detected as minor populations (Fig. 1 and Table 1), which are basically similar to LAB communities of other fermented vegetables such as sauerkraut and pickles (Breidt et al. 2013). The kimchi LAB reduce the pH of the kimchi supernatant by producing organic acids from carbohydrates during fermentation, which causes striking changes of LAB communities depending on the kimchi fermentation stage (Table 1). Generally, members of Leuconostoc such as Leu. mesenteroides and Leu. citreum, which possess less acid tolerance and microaerophilic properties compared with other kimchi LAB, dominate the kimchi microflora during the early fermentation period, whereas members of Lactobacillus and Weissella such as Lb. sakei,



Table 1 Changes of kimchi lactic acid bacteria (LAB) communities depending on the fermentation stage

Kimchi varieties	Analysis ^a	Fermentation stage ^b	Lactic acid bacteria ^c	Reference
Cabbage kimchi	PCR/DGGE	Early Middle	Leu. citreum, W. confusa Leu. citreum, W. confusa, Lb. curvatus, Lb. sakei	Lee et al. (2005b)
		Late	Leu. citreum, W. confusa, Lb. sakei, Lb. curvatus	
Cabbage kimchi	Isolation/PCR	Early Middle	Leu. citreum, Leu. lactis, W. cibaria, Leu. mesenteroides, Leu. kimchii W. koreensis, Leu. gelidum, Leu. lactis, Lb. pentosus	Cho et al. (2006)
		Late	W. koreensis, Leu. gasicomitatum	
Watery kimchi	PCR/clone library	Early Middle	W. cibaria, W. confusa W. cibaria, W. confusa, Lb. brevis, Lb. alimentarius	Kim et al. (2012)
		Late	Lb. plantarum, W. cibaria, Lb. brevis, Leu. pseudomesenteroides	
Cabbage kimchi	PCR/pyrosequencing	Early Middle	Leu. mesenteroides, W. cibaria, Leu. citreum, Leu. lactis, Lb. sakei Lb. sakei, W. koreensis, Leu. mesenteroides, Leu. gelidum, Leu. carnosum	Jung et al. (2013b)
		Late	Lb. sakei, W. koreensis, Leu. gelidum, Leu. mesenteroides, Leu. carnosum	
Cabbage kimchi	PCR/pyrosequencing	Early Middle	Leu. citreum, Leu. hozapfelii, Leu. gasicomitatum, W. soli, Lc. lactis Lb. sakei, Leu. gasicomitatum, W. koreensis, Leu. gelidum	Jeong et al. (2013c)
		Late	Lb. sakei, Leu. gasicomitatum, W. koreensis, Leu. gelidum	
Watery kimchi	PCR/pyrosequencing	Early	Leu. citreum, Leu. gasicomitatum, W. cibaria, Leu. holzapfelii, Leu. lactis	Jeong et al. (2013a)
		Middle	Leu. gasicomitatum, Leu. gelidum, Lb. sakei	
		Late	Leu. gasicomitatum, Leu. gelidum, Lb. sakei	

^a All LAB communities were analyzed on the basis of 16S rRNA genes

^b Kimchi fermentation was arbitrarily divided into three stages in this review on the basis of pH; early, pH >5.2; middle, pH 4.5–5.2; late, pH <4.5

^c One representative community among LAB communities corresponding to each fermentation stage was selected, and the LAB community was described in order of population abundances in each sample

Lb. plantarum, and W. koreensis, which have more acid tolerance, become more dominant as the kimchi fermentation environment changes to more anaerobic and acidic conditions (Chang and Chang 2010). However, the absence of specific kimchi LAB in raw materials or different kimchi varieties, raw materials, ingredients, and fermentation conditions significantly affects the kimchi LAB successions, and there are many exceptions that do not follow the general LAB successions during fermentation. As shown in Table 1, members of Weissella such as W. cibaria and W. confusa are sometimes dominant even during the early fermentation stage, and members of Leuconostoc such as Leu. gelidum and Leu. gasicomitatum are dominant during the late fermentation stage; Leu. gasicomitatum and Leu. gelidum have more acid tolerance compared with Leu. mesenteroides and Leu. citreum (Jeong et al. 2013a).

It has been reported that LAB as well as yeasts play significant roles in kimchi fermentation and some yeasts might be the cause of off-flavor or food spoilage during kimchi fermentation (Chang et al. 2008). Diverse yeasts including *Saccharomyces, Candida, Pichia,* and *Kluyveromyces* have been isolated from kimchi, especially during the late fermentation stages, because they grow well at low pH (Chang et al. 2008; Jeong et al. 2013a, c). *Saccharomyces* species, in particular, consume free sugars and produce

ethanol as a major product and glycerol as a by-product after approximately 30 days of kimchi fermentation (Jeong et al. 2013a, c). Along with the decrease of kimchi LAB and *Saccharomyces*, the growth of *Candida*, which is suspected to cause spoilage during kimchi fermentation, is often observed during the late fermentation period (Chang et al. 2008; Jeong et al. 2013a, c).

Bacteriophage infection has been a well-recognized problem in industrial food fermentation, and a wide range of countermeasures have been employed for its controls (Kleppen et al. 2012; Moineau and Lévesque 2005). It has been reported that bacteriophages affect the bacterial community succession in food fermentation and are apparently responsible for the variability frequently observed in such vegetable fermentations (Kleppen et al. 2011; Lu et al. 2012). In a recent study, a high amount of bacteriophage DNA was found in kimchi, indicating that bacteriophages most probably also affect kimchi LAB succession (Jung et al. 2011; Park et al. 2011a). However, little is known about bacteriophages and the potential countermeasures against them in kimchi fermentation. Because previous studies suggest that kimchi LAB as well as yeasts and bacteriophages are important groups affecting the taste and quality of kimchi, more studies on yeasts and bacteriophages are a prerequisite for the industrial production of high-quality kimchi.

Factors affecting kimchi microflora

Many intrinsic, extrinsic, and processing-related factors affect kimchi microflora during fermentation, which eventually results in changes in the metabolites, taste, and nutritional and organoleptic properties of kimchi products. More specifically, fermentation temperature, raw materials (vegetable type, harvesting area and season, and cultivar), kimchi varieties, salt concentration, ingredients (seasonings), and starter cultures are important factors that affect the kimchi microflora.

The fermentation temperature is one of the most important factors influencing kimchi fermentation (Cho et al. 2006; Choi et al. 1998; Kim and Chang 2000; Mheen and Kwon 1984; Shin et al. 1996). Kimchi is generally fermented at low temperatures (2-6 °C) to ensure proper ripening and preservation, but sometimes, it is fermented at higher temperatures to accelerate the process. The growth of kimchi LAB occurs more rapidly at higher temperatures, which results in a quicker decrease of the pH during fermentation (Choi et al. 1998; Kim and Chang 2000; Mheen and Kwon 1984). The fermentation temperature also affects kimchi LAB communities because LAB present in raw materials have different growth properties depending on the temperature (Cho et al. 2006; Lee et al. 2005b; Shin et al. 1996), meaning that kimchi LAB successions can be different depending on the fermentation temperature despite the use of the same raw materials and preparation method. For example, Cho et al. (2006) reported that W. koreensis showing a relatively good psychrophilic growth predominated at -1 °C, while a short incubation at 15 °C enhanced the growth of the less psychrophilic Leuconostoc species, including Leu. citreum, thus delaying the growth of W. koreensis.

Salt concentration is another important factor affecting kimchi microflora. Kimchi is generally fermented at salt concentrations of approximately 2-3 %, which is favorable for the growth of LAB. It was reported that the acidification of kimchi occurred rapidly with the quick growth of kimchi LAB at low salt concentration (<2 %), whereas kimchi fermentation and ripening were delayed at high salt concentration (>3 %) (Mheen and Kwon 1984). So et al. (1996) showed, from the comparison of the lag phase time and doubling time of isolated kimchi LAB, that members of Leuconostoc grew well at low salt concentrations, while members of Lactobacillus grew well at high salt concentrations. Kimchi ingredients (seasonings) also affect the kimchi LAB communities because they are potential sources of LAB and differentially influence the growth of LAB during fermentation (Lee et al. 2008; No et al. 1995; Yi et al. 1998). When kimchi contained more garlic, the population of kimchi LAB significantly increased, while that of other aerobic bacteria decreased (Cho et al. 1988; Lee et al. 2008), indicating that garlic might be an important source of kimchi LAB or contain carbohydrates and nutrients that promote the growth of kimchi LAB. Red pepper powder delayed the kimchi fermentation progress, including the growth of LAB and metabolite production, especially during the early fermentation period (Jeong et al. 2013b). Red pepper powder also influenced the kimchi LAB communities during fermentation (Jeong et al. 2013b); the proportion of *Weissella* was higher in kimchi with red pepper powder than in kimchi without red pepper powder, while the proportions of *Leuconostoc* and *Lactobacillus* were lower in kimchi with red pepper powder.

Until now, studies on kimchi have been mainly focused on the effects of the fermentation conditions and kimchi ingredients on the microbial community, although the LAB populations present in raw materials are also important in determining the kimchi LAB successions, because kimchi is generally processed by spontaneous fermentation. Studies on the microflora present in raw materials have rarely been explored, but further investigations on this topic will contribute to a better understanding of the kimchi microflora and the estimation of kimchi LAB successions during fermentation. Currently, some LAB species belonging to Leuconostoc and Lactobacillus are being used as starter cultures for industrial kimchi production in some Korean kimchi companies. The use of Leuconostoc and Lactobacillus species as starter cultures inhibited the growth of E. coli and Gram-negative bacteria during kimchi fermentation, and Leuconostoc species produced less acidic kimchi than Lactobacillus species (Chang and Chang 2010, 2011; Choi et al. 2003). The use of Leu. mesenteroides as a kimchi starter accelerated the fermentation process, including metabolite production and affected kimchi LAB communities (Jung et al. 2012c). Compared with nonstarter kimchi, in starter kimchi inoculated with Leu. mesenteroides, the relative abundances of Leuconostoc as well as Weissella increased, while that of Lactobacillus decreased, suggesting that kimchi quality and microflora can be controlled by using starter cultures.

Metabolism of kimchi lactic acid bacteria

The list of the dominant kimchi LAB shown in Fig. 1 and Table 1 suggests that kimchi fermentation is generally processed by obligately (*Leuconostoc* and *Weissella* species and *Lb*. *brevis*) or facultatively (*Lb. sakei, Lb. plantarum*, and *Lb. curvatus*) heterofermentative LAB. Heterofermentative LAB produce lactic acid, ethanol, and carbon dioxide from glucose through the 6-phosphogluconate/phosphoketolase pathway under anaerobic conditions; net 1 mol of ATP per mole of glucose is produced (Fig. 2). Glucose and fructose are detected in kimchi as major free sugars (Jeong et al. 2013a, b, c; Jung et al. 2011, 2012c); fructose can be metabolized via its conversion from fructose-6-P to glucose-6-P by heterofermentative LAB. The production of mannitol, a naturally occurring sixcarbon polyol that imparts a refreshing taste to kimchi fermentation

Fig. 2 A proposed pathway for glucose and fructose metabolism of heterofermentative lactic acid bacteria (Leuconostoc species) during kimchi fermentation [modified from Wisselink et al. (2002)]. All genes coding transporters and metabolic enzymes in the pathway were found in the genomes of Leuconostoc species (Jung et al. 2012a, b, d; Lee et al. 2011b; Oh et al. 2010). (1) phosphoketolase (2) glucose phosphate isomerase (3) mannitol dehydrogenase. PTS phosphotransferase transport system





(Jeong et al. 2013a, b, c; Jung et al. 2011, 2012c; Yun et al. 1996). Mannitol is synthesized through fructose reduction with the consumption of NADH by mannitol dehydrogenase (Wisselink et al. 2002), resulting in the production of acetate instead of ethanol; 1 mol of ATP per 2 mol of mannitol is additionally produced (Fig. 2), meaning that mannitol-producing LAB can be more competitive in the presence of fructose. This may explain that *Leuconostoc* species, known as the major mannitol-producing LAB, are dominant in many kimchi microflora, even though they are less acid tolerant.

Besides lactate and acetate as the major organic acids, other diverse organic acids such as propionic acid, butanoic acid, 2methylpropionic acid, fumaric acid, succinic acid, and tartaric acid are produced as minor components during kimchi fermentation (Shim et al. 2012); these might be produced by kimchi LAB or other kimchi microflora under anaerobic conditions. Moreover, amino acids that play an essential role as important taste compounds in kimchi products accumulate during fermentation (Jeong et al. 2013a, c). Proteases derived from raw materials and spontaneous kimchi microflora, especially various kimchi LAB, may be responsible for the amino acid accumulation. It has been reported that kimchi LAB, like other LAB, are able to produce γ -aminobutyric acid (GABA), vitamins, and volatile flavoring compounds contributing to the organoleptic, health, and nutritional properties of kimchi products. GABA, a four-carbon nonprotein amino acid that functions as a major inhibitory neurotransmitter in the central nervous system, is primarily produced from glutamate by glutamate decarboxylase during kimchi fermentation. It has been reported that Lactobacillus species are major GABA producers during kimchi fermentation (Cho et al. 2007, 2011; Jeong et al. 2013c; Kook et al. 2010; Seok et al. 2008). Therefore, Lactobacillus species including Lb. sakei and Lb. buchneri have been considered as kimchi starters for the production of GABA-enriched kimchi (Cho et al. 2007, 2011; Seok et al. 2008). Although it is known that kimchi has

high vitamin content, there is no report about the vitamin production by kimchi LAB. However, genes involved in the synthesis of vitamin B group (e.g., riboflavin and folate) were found in the genomes of Leu. mesenteroides and Lb. sakei (Jung et al. 2012d, 2013), meaning that kimchi LAB may produce vitamins during kimchi fermentation. Flavoring compounds are also important to determine the tastes of kimchi products even though their content is very low in kimchi. The main metabolic activity in kimchi fermentation is the formation of lactate, acetate, carbon dioxide, and mannitol; however, other minor organic compounds such as diacetyl, acetoin, acetaldehyde, secondary alcohols, esters, and lactones are also produced from carbohydrates or fatty acids by kimchi microflora (Cha et al. 1998; Kang et al. 2003). The main metabolites as well as various flavoring compounds contribute to the typical organoleptic properties of kimchi. The production of bacteriocins, low-molecular-mass peptides or proteins, has been identified in kimchi LAB including Leu. mesenteroides (Yang et al. 2002), Leu. citreum (Chang and Chang 2010, 2011), Lb. plantarum (Chung et al. 2010), Lb. sakei (Kim et al. 2004), Lc. lactis (Jeong et al. 2011; Kim et al. 2006; Lee et al. 1999a), and P. acidilactici (Shin et al. 2008). The production of bacteriocins in kimchi could be important because they can prevent spoilage and overripening of kimchi products and inhibit the growth of foodborne pathogens (Chang and Chang 2010, 2011). Nisin, a representative bacteriocin produced by kimchi LAB (Lc. lactis subsp. lactis), inhibits the growth of Clostridium perfringens, Listeria monocytogenes, vancomycin-resistant Enterococcus, and methicillin-resistant Staphylococcus aureus, as well as some closely related LAB (Park et al. 2003).

Functional properties of kimchi

Kimchi products that are mainly made by heterofermentative LAB from mixtures of vegetables and seasonings have been regarded as functional foods with high concentrations of probiotic LAB and beneficial substances (e.g., antioxidants, vitamins, dietary fibers, and minerals) (Park and Rhee 2005). A large number of health benefit or function associated with kimchi LAB (e.g., Lb. acidophilus, Lb. plantarum, Lb. brevis, Lb. sakei) or kimchi products, e.g., antimutagenic activity against diverse mutagens (Rhee and Park 2001), antioxidant activities (Lee et al. 2005a; Park et al. 2011b), amelioration of cyclophosphamide-induced immunosuppression effects (Jang et al 2013), prevention or alleviation of allergies (Han et al. 2012; Kim et al. 2013), growth inhibition of Helicobacter pylori (Ki et al. 2010), antidiabetic effect (Islam and Choi 2009), and antiobesity effect (Ji et al. 2012; Park et al. 2012b), have been reported. Although many scientific evidence supporting potential probiotic effects and health benefits of kimchi LAB and products have been accumulated, their clear evidence in humans are still lacking because they have been mostly tested in vitro or in mouse experiments. Therefore, further studies on probiotic effects and health benefits of kimchi LAB and products in humans are necessary, which will enhance kimchi's status as a healthful food.

Genomic studies on kimchi LAB

Because LAB are industrially important bacterial group that has been used for a variety of applications, including fermentation of dairy food and production of macromolecules, enzymes, and metabolites, and as probiotics, and the genome sequencing has provided insights into the genetic and metabolic capacities of LAB, genome sequencing of many LAB has been performed (de Vos 2011; Makarova et al. 2006; Pfeiler and Klaenhammer 2007). The first complete genome sequencing of kimchi LAB was only performed on Leu. citreum KM20 in 2008 (Kim et al. 2008), and recently, extensive genome sequencing of many kimchi LAB also has been performed due to the development of new sequencing technologies (Jung et al. 2012a, b, d; Lee et al. 2011b, c; Oh et al. 2010). However, the functional and comparative studies on the sequenced kimchi LAB genomes to uncover genetic and metabolic capacities are rarely performed. Because genome sequences alone are insufficient to understand kimchi microflora, genomic and functional studies of kimchi LAB coupled with new analyses such as metabolomics, metagenomics, and metatranscriptomics have to be performed to achieve a better understanding of complex kimchi microflora. Recently, the microbial successions as well as overall genetic and metabolic features of complex kimchi microflora during kimchi fermentation were investigated using metagenomic and metatranscriptomic analyses (Jung et al. 2011, 2013). These analyses revealed that kimchi LAB had high metabolic potential with respect to heterotrophic lactic acid fermentations and that bacteriophage infection influenced kimchi fermentation.

Perspectives for industrial kimchi productions

As kimchi has become a globally popular food because of its taste and health-promoting properties and its commercial market size has gradually increased [Korean kimchi market size in 2012 was approximately 2,300 million USD; Nonghyup economic research institute (http://www.nheri.re.kr/)], Korean kimchi companies began to recognize the necessity of industrial production of uniform quality kimchi. However, because kimchi is generally fermented by various naturally occurring LAB derived from raw materials, the quality of the kimchi products varies depending on the raw materials even though it is processed under controlled conditions. The use of starter cultures has been suggested as an alternative for quality development and uniform kimchi production; therefore,

currently, kimchi LAB including Leu. mesenteroides, Leu. citreum, and Lb. plantarum featured properties such as mannitol production, antimicrobial activity, and acid and bile tolerances are being used as kimchi fermentation starters (Kim et al. 2011; Ryu et al. 2011, 2012). However, kimchi fermentation using starter cultures is not always successful because the starters used sometimes fail to outcompete naturally occurring LAB under the kimchi fermentation conditions. Therefore, the adaptability to kimchi fermentation conditions (low temperature, salts, and low pH) to confer advantageous competitive growth against LAB present in raw materials is an important consideration for the successful development of kimchi starters. Besides the adaptability of kimchi starters to kimchi fermentation conditions, the production of major organic acids (lactate and acetate) and mannitol as well as other components such as minor organic acids, amino acids, flavoring compounds, vitamins, biogenic amines, and bacteriocins should be carefully considered for the development of kimchi starters because these substances significantly affect the taste, organoleptic, and health-promoting and nutritional properties of kimchi products.

Genetic manipulations or mutagenic treatments providing kimchi starters with new physiological properties or functions have been used to improve the adaptability and functionalities of kimchi starters. For example, Lb. plantarum ldhL gene encoding L-(+)-lactate dehydrogenase was cloned into the Dlactate producer Leu. citreum to increase the ratio of L-(+)lactate (Jin et al. 2009), and nitrosoguanidine was treated to kimchi starters to improve their acid tolerance (Kim et al. 2005). However, genetic manipulations and mutagen treatments for the development of kimchi starters in food industry have some limitations including regulatory issues or antipathy of the consumers to the use of genetically modified organisms (GMO) and mutagen treatments. Presently, most of the LAB starters that have been widely utilized for the industrial fermentation of a broad range of food products, ranging from vegetable fermentation to cheese production, have been developed by domestication over a long period. Due to their short generation times, microorganisms are well suited for the investigation of evolutionary strategies in a laboratory setting for the development of starter cultures (Dragosits and Mattanovich 2013). For instance, domesticated Lc. lactis strains with significant increase in the acidification rates and biomass yields in milk were obtained by the propagation in milk for only 1,000 generations of a Lc. lactis strain isolated from a plant (Bachmann et al. 2012), showing that adaptive laboratory evolution can be a good approach to develop kimchi starters from natural LAB. Bacteriophages are frequently observed during kimchi fermentation (Jung et al. 2011; Kleppen et al. 2012; Park et al. 2011a), and their infection probably influences kimchi LAB succession and quality. The acquired knowledge on kimchi bacteriophages and the genome sequencing of kimchi LAB will provide insights into the molecular processes involved in phage-host interactions and ultimately lead to the development of phageresistant kimchi starters. Our understanding of the kimchi microflora has increased exponentially by the applications of "omics" technologies, which will open up new horizons in the industrial production of kimchi with good taste and high quality.

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References

- Bachmann H, Starrenburg MJ, Molenaar D, Kleerebezem M, van Hylckama Vlieg JE (2012) Microbial domestication signatures of *Lactococcus lactis* can be reproduced by experimental evolution. Genome Res 22:115–124
- Breidt F, McFeeters RF, Perez-Diaz I, Lee CH (2013) Fermented vegetables. In: Doyle MP, Beuchat LR (eds) Food microbiology: fundamentals and frontiers, 4th edn. ASM Press, Washington DC, pp 783–793
- Cha YJ, Kim H, Cadwallader KR (1998) Aroma-active compounds in kimchi during fermentation. J Agric Food Chem 46:1944–1953
- Chang JY, Chang HC (2010) Improvements in the quality and shelf life of kimchi by fermentation with the induced bacteriocin-producing strain, *Leuconostoc citreum* GJ7 as a starter. J Food Sci 75:M103– M110
- Chang JY, Chang HC (2011) Growth inhibition of foodborne pathogens by kimchi prepared with bacteriocin-producing starter culture. J Food Sci 76:M72–M78
- Chang HW, Kim KH, Nam YD, Roh SW, Kim MS, Jeon CO, Oh HM, Bae JW (2008) Analysis of yeast and archaeal population dynamics in kimchi using denaturing gradient gel electrophoresis. Int J Food Microbiol 126:159–166
- Chang JH, Shim YY, Cha SK, Chee KM (2010) Probiotic characteristics of lactic acid bacteria isolated from kimchi. J Appl Microbiol 109: 220–230
- Cheigh HS, Park KY, Lee CY (1994) Biochemical, microbiological, and nutritional aspects of kimchi (Korean fermented vegetable products). Crit Rev Food Sci Nutr 34:175–203
- Cho NC, Jhon DY, Shin MS, Hong YH, Lim HS (1988) Effect of garlic concentrations on growth of microorganisms during kimchi fermentation. Kor J Food Sci Technol 20:231–235
- Cho J, Lee D, Yang C, Jeon J, Kim J, Han H (2006) Microbial population dynamics of kimchi, a fermented cabbage product. FEMS Microbiol Lett 257:262–267
- Cho YR, Chang JY, Chang HC (2007) Production of γ-aminobutyric acid (GABA) by *Lactobacillus buchneri* isolated from kimchi and its neuroprotective effect on neuronal cells. J Microbiol Biotechnol 17: 104–109
- Cho SY, Park MJ, Kim KM, Ryu JH, Park HJ (2011) Production of high γ-aminobutyric acid (GABA) sour kimchi using lactic acid bacteria isolated from *mukeunjee* kimchi. Food Sci Biotechnol 20:403–408
- Choi SY, Lee MK, Choi KS, Koo YJ, Park WS (1998) Changes of fermentation characteristics and sensory evaluation of kimchi on different storage temperature. Kor J Food Sci Technol 30:644–649
- Choi HJ, Cheigh CI, Kim SB, Lee JC, Lee DW, Choi SW, Park JM, Pyun YR (2002) Weissella kimchii sp. nov., a novel lactic acid bacterium from kimchi. Int J Syst Evol Microbiol 52:507–511

- Choi IK, Jung SH, Kim BJ, Park SY, Kim J, Han HU (2003) Novel Leuconostoc citreum starter culture system for the fermentation of kimchi, a fermented cabbage product. Antonie Van Leeuwenhoek 84:247–253
- Chung JH, Bae Y, Kim Y, Lee JH (2010) Characteristics of bacteriocin produced by a *Lactobacillus plantarum* strain isolated from kimchi. Kor J Microbiol Biotechnol 38:481–485
- de Vos WM (2011) System solutions by lactic acid bacteria: from paradigms to practice. Microb Cell Fact 10:S2
- Dragosits M, Mattanovich D (2013) Adaptive laboratory evolution principles and applications for biotechnology. Microb Cell Fact 12:17
- Han Y, Kim B, Ban J, Lee J, Kim BJ, Choi BS, Hwang S, Ahn K, Kim J (2012) A randomized trial of *Lactobacillus plantarum* CJLP133 for the treatment of atopic dermatitis. Pediatr Allergy Immunol 23:667– 673
- Islam MS, Choi H (2009) Antidiabetic effect of Korean traditional Baechu (Chinese cabbage) kimchi in a type 2 diabetes model of rats. J Med Food 12:292–297
- Jang SE, Joh EH, Lee HY, Ahn YT, Lee JH, Huh CS, Han MJ, Kim DH (2013) Lactobacillus plantarum HY7712 ameliorates cyclophosphamide-induced immunosuppression in mice. J Microbiol Biotechnol 23:414–421
- Jeong SY, Park CS, Choi NS, Yang HJ, Kim CY, Yoon BD, Kang DO, Ryu YW, Kim MS (2011) Characteristics of bacteriocin produced by *Lactococcus lactis* ET45 isolated from kimchi. Kor J Microbiol 47: 74–80
- Jeong SH, Jung JY, Lee SH, Jin HM, Jeon CO (2013a) Microbial succession and metabolite changes during fermentation of dongchimi, traditional Korean watery kimchi. Int J Food Microbiol 164:46–53
- Jeong SH, Lee HJ, Jung JY, Lee SH, Seo HY, Park WS, Jeon CO (2013b) Effects of red pepper powder on microbial communities and metabolites during kimchi fermentation. Int J Food Microbiol 160:252– 259
- Jeong SH, Lee SH, Jung JY, Choi EJ, Jeon CO (2013c) Microbial succession and metabolite changes during long-term storage of kimchi. J Food Sci 78:M763–M769
- Ji YS, Kim HN, Park HJ, Lee JE, Yeo SY, Yang JS, Park SY, Yoon HS, Cho GS, Franz CM, Bomba A, Shin HK, Holzapfel WH (2012) Modulation of the murine microbiome with a concomitant antiobesity effect by *Lactobacillus rhamnosus* GG and *Lactobacillus sakei* NR28. Benef Microbes 1:13–22
- Ji Y, Kim H, Park H, Lee J, Lee H, Shin H, Kim B, Franz CMAP, Holzapfel WH (2013) Functionality and safety of lactic bacterial strains from Korean kimchi. Food control 31:467–473
- Jin Q, Jung JY, Kim YJ, Eom HJ, Kim SY, Kim TJ, Han NS (2009) Production of L-lactate in *Leuconostoc citreum* via heterologous expression of L-lactate dehydrogenase gene. J Biotechnol 144: 160–164
- Jung JY, Lee SH, Kim JM, Park MS, Bae J, Hahn Y, Madsen EL, Jeon CO (2011) Metagenomic analysis of kimchi, a traditional Korean fermented food. Appl Environ Microbiol 77:2264–2274
- Jung JY, Lee SH, Jeon CO (2012a) Complete genome sequence of *Leuconostoc carnosum* strain JB16, isolated from kimchi. J Bacteriol 194:6672
- Jung JY, Lee SH, Jeon CO (2012b) Complete genome sequence of Leuconostoc gelidum strain JB7, isolated from kimchi. J Bacteriol 194:6665
- Jung JY, Lee SH, Lee HJ, Seo HY, Park WS, Jeon CO (2012c) Effects of Leuconostoc mesenteroides starter cultures on microbial communities and metabolites during kimchi fermentation. Int J Food Microbiol 153:378–387
- Jung JY, Lee SH, Lee SH, Jeon CO (2012d) Complete genome sequence of *Leuconostoc mesenteroides* subsp. *mesenteroides* strain J18, isolated from kimchi. J Bacteriol 194:730

- Jung JY, Lee SH, Jin HM, Hahn Y, Madsen EL, Jeon CO (2013) Metatranscriptomic analysis of lactic acid bacterial gene expression during kimchi fermentation. Int J Food Microbiol 163:171–179
- Kang JH, Lee JH, Min S, Min DB (2003) Changes of volatile compounds, lactic acid bacteria, pH, and headspace gases in kimchi, a traditional Korean fermented vegetable product. J Food Sci 68:849–854
- Ki MR, Ghim SY, Hong IH, Park JK, Hong KS, Ji AR, Jeong KS (2010) In vitro inhibition of *Helicobacter pylori* growth and of adherence of cagA-positive strains to gastric epithelial cells by *Lactobacillus paraplantarum* KNUC25 isolated from kimchi. J Med Food 13: 629–634
- Kim MH, Chang MJ (2000) Fermentation property of Chinese cabbage kimchi by fermentation temperature and salt concentration. J Kor Soc Agric Chem Biotechnol 43:7–11
- Kim M, Chun J (2005) Bacterial community structure in kimchi, a Korean fermented vegetable food, as revealed by 16S rRNA gene analysis. Int J Food Microbiol 103:91–96
- Kim J, Chun J, Han HU (2000) Leuconostoc kimchii sp. nov., a new species from kimchi. Int J Syst Evol Microbiol 50:1915–1919
- Kim B, Lee J, Jang J, Kim J, Han H (2003) Leuconostoc inhae sp. nov., a lactic acid bacterium isolated from kimchi. Int J Syst Evol Microbiol 53:1123–1126
- Kim HT, Park JY, Lee GG, Kim JH (2004) Isolation of a bacteriocinproducing *Lactobacillus sakei* strain from kimchi. J Kor Soc Food Sci Nutr 33:560–565
- Kim YH, Kim HZ, Kim JY, Choi TB, Kang SM (2005) Strain improvement of *Leuconostoc mesenteroides* as a acid-resistant mutant and effect on kimchi fermentation as a starter. Kor J Microbiol Biotechnol 33:41–50
- Kim YS, Kim MJ, Kim P, Kim JH (2006) Cloning and production of a novel bacteriocin, lactococcin K, from *Lactococcus lactis* subsp. *lactis* MY23. Biotechnol Lett 28:357–362
- Kim JF, Jeong H, Lee JS, Choi SH, Ha M, Hur CG, Kim JS, Lee S, Park HS, Park YH, Oh TK (2008) Complete genome sequence of *Leuconostoc citreum* KM20. J Bacteriol 190:3093–3094
- Kim BJ, Oh JY, Kwon MS, Jung HW, Lee KP (2011) Novel Leuconostoc citreum, fermentation foods and compositions comprising the same. Korean patent. 10-1099924
- Kim B, Seo WT, Kim MG, Yun HD, Cho KM (2012) Metagenomic lactic acid bacterial diversity during *mulkimchi* fermentation based on 16S rRNA sequence. J Kor Soc Appl Biol Chem 55:787–792
- Kim JY, Park BK, Park HJ, Park YH, Kim BO, Pyo S (2013) Atopic dermatitis-mitigating effects of new *Lactobacillus* strain, *Lactobacillus sakei* probio 65 isolated from kimchi. J Appl Microbiol 115:517–526
- Kleppen HP, Bang T, Nes IF, Holo H (2011) Bacteriophages in milk fermentations: Diversity fluctuations of normal and failed fermentations. Int Dairy J 21:592–600
- Kleppen HP, Holo H, Jeon SR, Nes IF, Yoon SS (2012) Novel Podoviridae family bacteriophage infecting Weissella cibaria isolated from kimchi. Appl Environ Microbiol 78:7299–7308
- Kook MC, Seo MJ, Cheigh CI, Lee SJ, Pyun YR, Park H (2010) Enhancement of γ-aminobutyric acid production by *Lactobacillus* sakei B2-16 expressing glutamate decarboxylase from *Lactobacillus* plantarum ATCC 14917. J Kor Soc Appl Biol Chem 53:816–820
- Lee CW, Ko CY, Ha DM (1992) Microfloral changes of the lactic acid bacteria during kimchi fermentation and identification of the isolates. Kor J Appl Microbiol Biotechnol 20:102–109
- Lee HJ, Joo YJ, Park CS, Kim SH, Hwang IK, Ahn JS, Mheen TI (1999a) Purification and characterization of a bacteriocin produced by *Lactococcus lactis* subsp. *lactis* H-559 isolated from kimchi. J Biosci Bioeng 88:153–159
- Lee HJ, Park CS, Joo YJ, Kim SH, Yoon JH, Park YH, Hwang IK, Ahn JS, Mheen TI (1999b) Identification and characterization of bacteriocin-producing lactic acid bacteria isolated from kimchi. J Microbiol Biotechnol 9:282–291

- Lee JS, Lee KC, Ahn JS, Mheen TI, Pyun YR, Park YH (2002) Weissella koreensis sp. nov., isolated from kimchi. Int J Syst Evol Microbiol 52:1257–1261
- Lee J, Hwang KT, Heo MS, Lee JH, Park KY (2005a) Resistance of *Lactobacillus plantarum* KCTC 3099 from kimchi to oxidative stress. J Med Food 8:299–304
- Lee JS, Heo GY, Lee JW, Oh YJ, Park JA, Park YH, Pyun YR, Ahn JS (2005b) Analysis of kimchi microflora using denaturing gradient gel electrophoresis. Int J Food Microbiol 102:143–150
- Lee JY, Choi MK, Kyung KH (2008) Reappraisal of stimulatory effect of garlic on kimchi fermentation. Kor J Food Sci Technol 40:479–484
- Lee H, Yoon H, Ji Y, Kim H, Park H, Lee J, Shin H, Holzapfel WH (2011a) Functional properties of *Lactobacillus* strains isolated from kimchi. Int J Food Microbiol 145:155–161
- Lee SH, Jung JY, Lee SH, Jeon CO (2011b) Complete genome sequence of *Leuconostoc kimchii* strain C2, isolated from kimchi. J Bacteriol 193:5548
- Lee SH, Jung JY, Lee SH, Jeon CO (2011c) Complete genome sequence of *Weissella koreensis* KACC 15510, isolated from kimchi. J Bacteriol 193:5534
- Lee SH, Park MS, Jung JY, Jeon CO (2012) *Leuconostoc miyukkimchii* sp. nov., isolated from brown algae (*Undaria pinnatifida*) kimchi. Int J Syst Evol Microbiol 62:1098–1103
- Lu Z, Pérez-Diaz IM, Hayes JS, Breidt F (2012) Bacteriophage ecology in a commercial cucumber fermentation. Appl Environ Microbiol 78:8571–8578
- Makarova K, Slesarev A, Wolf Y, Sorokin A, Mirkin B, Koonin E, Pavlov A, Pavlova N, Karamychev V, Polouchine N, Shakhova V, Grigoriev I, Lou Y, Rohksar D, Lucas S, Huang K, Goodstein DM, Hawkins T, Plengvidhya V, Welker D, Hughes J, Goh Y, Benson A, Baldwin K, Lee JH, Díaz-Muñiz I, Dosti B, Smeianov V, Wechter W, Barabote R, Lorca G, Altermann E, Barrangou R, Ganesan B, Xie Y, Rawsthorne H, Tamir D, Parker C, Breidt F, Broadbent J, Hutkins R, O'Sullivan D, Steele J, Unlu G, Saier M, Klaenhammer T, Richardson P, Kozyavkin S, Weimer B, Mills D (2006) Comparative genomics of the lactic acid bacteria. Proc Natl Acad Sci U S A 103:15611–15616
- Mheen TI, Kwon TW (1984) Effect of temperature and salt concentration on kimchi fermentation. Kor J Food Sci Technol 16:443–450
- Moineau S, Lévesque C (2005) Control of bacteriophages in industrial fermentations. In: Kutter E, Sulakvelidze A (eds) Bacteriophages: biology and applications. CRC Press, Boca Raton, pp 286–296
- No HK, Lee SH, Kim SD (1995) Effects of ingredients on fermentation of Chinese cabbage kimchi. J Kor Soc Food Nutr 24:642–650
- Oh HM, Cho YJ, Kim BK, Roe JH, Kang SO, Nahm BH, Jeong G, Han HU, Chun J (2010) Complete genome sequence analysis of *Leuconostoc kimchii* IMSNU 11154. J Bacteriol 192:3844–3845
- Park KY, Rhee SH (2005) Functional foods from fermented vegetable products; Kimchi (Korean fermented vegetables) and functionality. In: Shi J, Ho CT, Shahidi F (eds) Asian Functional Foods. CRC Press, Boca Raton, pp 341–380
- Park SH, Itoh K, Kikuchi E, Niwa H, Fujisawa T (2003) Identification and characteristics of nisin Z-producing *Lactococcus lactis* subsp. *lactis* isolated from kimchi. Curr Microbiol 46:385–588
- Park JM, Shin JH, Lee DW, Song JC, Suh HJ, Chang UJ, Kim JM (2010) Identification of the lactic acid bacteria on kimchi according to initial

and over-ripened fermentation using PCR and 16S rRNA gene sequence analysis. Food Sci Biotechnol 19:541–546

- Park EJ, Kim KH, Abell GCJ, Kim MS, Roh SW, Bae JW (2011a) Metagenomic analysis of the viral communities in fermented foods. Appl Environ Microbiol 77:1284–1291
- Park JM, Shin JH, Gu JG, Yoon SJ, Song JC, Jeon WM, Suh HJ, Chang UJ, Yang CY, Kim JM (2011b) Effect of antioxidant activity in kimchi during a short-term and over-ripening fermentation period. J Biosci Bioeng 112:356–359
- Park EJ, Chun J, Cha CJ, Park WS, Jeon CO, Bae JW (2012a) Bacterial community analysis during fermentation of ten representative kinds of kimchi with barcoded pyrosequencing. Food Microbiol 30:197– 204
- Park JA, Tirupathi Pichiah PB, Yu JJ, Oh SH, Daily JW 3rd, Cha YS (2012b) Anti-obesity effect of kimchi fermented with *Weissella koreensis* OK1-6 as starter in high-fat diet-induced obese C57BL/ 6J mice. J Appl Microbiol 113:1507–1516
- Pfeiler EA, Klaenhammer TR (2007) The genomics of lactic acid bacteria. Trends Microbiol 15:546–553
- Rhee CH, Park HD (2001) Three glycoproteins with antimutagenic activity identified in *Lactobacillus plantarum* KLAB21. Appl Environ Microbiol 67:3445–3449
- Ryu BH, Sim GS, Lee JH, Ha WK (2011) Novel Leuconostoc mesenteroides DSR 218 and use thereof. Korean patent. 10-1055949
- Ryu BH, Sim GS, Lee JH, Ha WK (2012) Plant originated *Lactobacillus* plantarum DSR CK10, DSR M2 to keep freshness and use thereof. Korean patent. 10-1124056
- Seok JH, Park KB, Kim YH, Bae MO, Lee MK, Oh SH (2008) Production and characterization of kimchi with enhanced levels of γ-aminobutyric acid. Food Sci Biotechnol 17:940–946
- Shim SM, Kim JY, Lee SM, Park JB, Oh SK, Kim YS (2012) Profiling of fermentative metabolites in kimchi: volatile and non-volatile organic acids. J Kor Soc Appl Biol Chem 55:463–469
- Shin DH, Kim MS, Han JS, Lim DK, Bak WS (1996) Changes of chemical composition and microflora in commercial kimchi. Kor J Food Sci Technol 28:137–145
- Shin MS, Han SK, Ryu JS, Kim KS, Lee WK (2008) Isolation and partial characterization of a bacteriocin produced by Pediococcus pentosaceus K23-2 isolated from kimchi. J Appl Microbiol 105: 331–339
- So MH, Lee YS, Kim HS, Cho EJ, Yea MJ (1996) An influence of salt concentrations on growth rates of lactic acid bacteria isolated from kimchi. Kor J Food Nutr 9:341–347
- Wisselink HW, Weusthuis RA, Eggink G, Hugenholtz J, Grobben GJ (2002) Mannitol production by lactic acid bacteria: a review. Int Dairy J 12:151–161
- Yang EJ, Chang JY, Lee HJ, Kim JH, Chung DK, Lee JH, Chang HC (2002) Characterization of the antagonistic activity against *Lactobacillus plantarum* and induction of bacteriocin production. Kor J Food Sci Technol 34:311–318
- Yi JH, Cho Y, Hwang IK (1998) Fermentative characteristics of kimchi prepared by addition of different kinds of minor ingredients. Kor J Soc Food Sci 14:1–8
- Yun JW, Kang SC, Song SK (1996) Mannitol accumulation during fermentation of kimchi. J ferment Bioeng 81:279–280