Arginine metabolism and the role of arginine deiminase-producing microorganisms in kimchi fermentation

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HIGHLIGHTS

- The abundance of Weissella members increased the arginine deiminase (ADI) metabolite levels.
- ADI activity affects the nitrogen cycle during kimchi fermentation.
- Nitrate content reduced dramatically in kimchi containing Leuconostoc mesenteroides.
- Bacteria with low ADI metabolite activity may reduce nitrite production in fermentation.

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ABSTRACT

In this study, we evaluated the correlation between the arginine deiminase (ADI) pathway and nitrogen cycle during cabbage kimchi fermentation. Nitrite used as a food additive can be converted to carcinogenic N-nitroso compounds via reactions with secondary amines under specific conditions; thus, high nitrate- and nitrite-containing foods present a potential risk to human health. We monitored the bacterial community, levels of ADI metabolites, and nitrogen compounds present in kimchi that contained bacteria that showed low ADI activity during fermentation. The dominant growth of microorganisms with weak ADI activity reduced arginine degradation and ornithine production. Furthermore, nitrite production in kimchi samples was affected by ADI activity. The ornithine and nitrite contents in the control kimchi were 1.7- and 2.6-fold higher at week 2 than at week 1. These results suggest that ADI-associated metabolism is correlated with the nitrogen cycle in kimchi and that the addition of bacteria with weak ADI activity may reduce nitrite production in kimchi.

1. Introduction

Kimchi is a representative Korean fermented food comprising salted cabbage, radish, ginger, garlic, and red pepper powder. Kimchi and other fermented foods have been reported to have beneficial effects on health, and this is believed to be associated with probiotic lactic acid bacteria (LAB) and postbiotic fermented metabolites (Hwang and Lee, 2019; Park and Bae, 2016; Patra et al., 2016; Sharon et al., 2014).

Kimchi is a non-sterilized fermented food, and its bacterial composition may be influenced by diverse raw ingredients. Many studies have shown that LAB in kimchi mainly originates from garlic, ginger, red pepper, and cabbage (S. Lee et al., 2015). Garlic, in particular, is an important source of LAB in kimchi (Cho et al., 2006; Hwang et al., 2019; Lee et al., 2017; S. Lee et al., 2015), while red pepper has been reported as a source of Weissella cibaria and Weissella koreensis (Jung et al., 2021; Kang et al., 2016). Despite the differences in the main ingredients, Lactobacillus, Leuconostoc, and
Weissella spp. are the dominant LAB groups in various types of kimchi (Jung et al., 2021; Kim et al., 2012; S. Lee et al., 2015). Nitrate and nitrite are abundant in green leafy vegetables and are generally regarded as safe for consumption and have beneficial effects on human health (Papadia et al., 2018; Salehzadeh et al., 2020). Nitrate is also found in the other fermented food such as Japanese sake (Japanese wine), and cheese (Kyrakiakis et al., 1997; Sasaki et al., 2020). However, nitrate can react with amines under certain conditions and can be converted to carcinogenic N-nitrosamine compounds (Liu et al., 2014). Therefore, high nitrate- and nitrite-containing foods may pose potential risks to human health (Gangolli et al., 1994), and it is important to evaluate the mechanism of nitrate and nitrite production in food products.

Nitriﬁcation involves the oxidation of ammonia to nitrite (NO2
- ) which is further oxidized to nitrate (NO3
- ) (Barth et al., 2020; Tiso and Schechter, 2015). The catalytic reduction of ammonia to produce nitrate has been detected in diverse bacteria, including LAB (Tiso and Schechter, 2015). Therefore, it is of great interest to investigate the relationship between arginine deiminase (ADI) pathway metabolites and nitrate/nitrite during kimchi fermentation. The ADI pathway is an energy pathway used by bacteria in low-oxygen conditions and comprises ADI, ornithine transcarbamylase (OTC), and carbamate kinase (CK) (Hwang and Lee, 2018; Novak et al., 2016). The ADI pathway catalyzes the conversion of arginine to ornithine, citrulline, ammonia, and carbon dioxide, while generating adenosine triphosphate (ATP) from adenosine diphosphate and phosphate (Jung et al., 2021). The distribution of genes associated with the ADI pathway varies among bacteria. Members of the Weissella genus exhibit high arginine catabolic activity among the kimchi-derived LAB, with Weissella growth inducing arginine degradation to ornithine and ammonia during kimchi fermentation (Jung et al., 2021).

In this study, we investigated the correlation between ADI metabolites and nitrate/nitrite production by comparing nitrate/nitrite compounds between control kimchi and kimchi supplemented with LAB showing low ADI activity.

2. Materials and methods

2.1. Sample preparation and analysis of the physicochemical properties of kimchi

Kimchi was prepared using the following raw materials obtained from a local market (w/w): salted cabbage (75%), red pepper (3.8%), radish (1.8%), onions (1.2%), small green onions (1.2%), fish sauce (5.3%), glutinous rice (0.6%), and water (11.1%). The ingredients were mixed prior to fermentation.

Kimchi samples A (control, without bacteria) and B (with bacteria) were prepared and stored at 4 °C for 4 weeks. Leuconostoc mesenteroides WiKim32, which was previously isolated from kimchi (Lee et al., 2020), was cultivated in de Man, Rogosa, and Sharpe (MRS) medium (Difco Laboratories, Detroit, MI, USA) for 24 h at 30 °C and added to kimchi B at a final concentration of 6 log colony forming units (CFU)/g. The bacterial cells were serially diluted in sterilized sodium chloride solution (0.85%). The cells were spread on MRS agar or Petrifilm AC plates (3M, St Paul, MN, USA) and incubated at 30 °C for 12 h. The number of bacteria in kimchi was counted as CFU/mL.

To analyze the physicochemical properties and metabolites of kimchi, the samples were homogenized using a hand blender (Philips, Eindhoven, Netherlands) and filtered using sterilized gauze. The pH value was determined using a pH meter (Mettler Toledo, Columbus, OH, USA), and total acidity was calculated as lactic acid (%) via titration with 0.1 N sodium hydroxide up to an endpoint of pH 8.3. All experiments were performed once a week during the four-week fermentation period.

2.2. Bacterial community analysis

Genomic DNA was extracted from the kimchi samples using a genomic DNA extraction kit (Qiagen, Hilden, Germany). The bacterial communities were analyzed via pyrosequencing of the 16S rDNA. The samples were analyzed by TheraGen (Suwon, Korea) using an Illumina MiSeq sequencing system (Illumina, San Diego, CA, USA). A 16S rDNA-sequencing library was constructed using the 16S metagenomic sequencing library preparation protocol (Illumina). The V3 and V4 hypervariable regions of the 16S rDNA gene were amplified using the KAPA HiFi HotStart ReadyMix kit (KAPA Biosystems, Wilmington, MA, USA) and purified using the Agencourt AMPure XP system (Beckman Coulter, Brea, CA, USA). The prepared library sequences were run on the MiSeq system (Illumina) with 2 x 300 bp paired-end reads. The reads were sorted using unique barcodes for PCR products, after which the barcode, linker, and primer sequences were removed from the original sequencing reads. Potential chimeric sequences were detected using the Bellerophon method. The number of operational taxonomic units (OTUs) were calculated from the pre-processed reads and determined by clustering the sequences using the QIIME software (v.1.8.0). Taxonomic abundance was counted with an RDP Classifier v1.1 which was also used for normalization of microbial composition.

2.3. Metabolite analysis

Metabolites were extracted from 50 g of each kimchi sample, which was homogenized using a hand blender. After centrifugation at 5,000 × g for 20 min, salicin (0.5 mM) was added to clear supernatants as an internal standard, and the solution was extracted using 50% acetonitrile. The kimchi extracts (10 μL) were analyzed using ultra-high-performance liquid chromatography-tandem mass spectrometry. The metabolites were evaluated using an Acquity UPLC system (Waters, Milford, MA, USA) coupled with a Triple TOF 5600 Plus MS instrument (AB SCIEX, Redwood City, CA, USA), and separated on an ACQUITY BEH C18 column (2.1 × 100 mm, 1.7 μm particles; Waters). The analytical conditions were as follows: solvent A, distilled water containing 0.01 M ammonium acetate; solvent B, acetonitrile containing 0.01 M ammonium acetate; injection volume, 10 μL; flow rate, 0.4 mL/min; spray voltage, -4.5 kV; scan rate, 10 spectra/sec; collision energy, -30 eV; source temperature, 300 °C; mass range, m/z 50–1,000. Multiple reaction monitoring mass spectra generated the following transitions: arginine, m/z 173 → 123; ornithine, m/z 131 → 131; citrulline, m/z 174 → 131; salicin (internal standard), m/z 285 → 123. The metabolite peak areas obtained were normalized to those of the internal standard using the SCIEX OS software (Sciei, Framingham, MA, USA).

2.4. Measurement of nitrogen compound contents

The supernatants extracted from the kimchi samples were filtered using disposable syringes containing 0.2 μm pore size filters (Millipore, Bedford, MA, USA). The contents of each component were measured in 100 μL of supernatant. The absorbance of nitrate and nitrite at 540 nm was measured using a colorimetric nitrite/nitrate assay (Sigma-Aldrich, St. Louis, MO, USA). The standard for the colorimetric detection of nitrite/nitrate was serially diluted to concentrations of 0 (blank), 2, 4, 8, and 10 nmol/well. The concentration of ammonia was determined by measuring absorbance at 340 nm using a colorimetric ammonia assay kit (Sigma-Aldrich).

2.5. Statistical analysis

All experiments were performed in triplicate and data are presented as the mean ± standard deviation. Two-way analysis of variance was performed using GraphPad Prism v7 (GraphPad Software, San Diego, CA, USA) with Tukey’s multiple comparison test. Values of p < 0.05 were considered significant.

3. Results

3.1. Changes in the bacterial community during kimchi fermentation

Kimchi samples were collected weekly, and their physicochemical properties and fermented compounds were evaluated. The addition of
L. mesenteroides increased the total bacterial count and acidity of kimchi B (Figure 1). The LAB content increased from 5.4 to 7.9 log CFU/mL in kimchi A and from 8.3 to 9.0 log CFU/mL in kimchi B (Figure 1a). The acidity and lactic acid content of kimchi B were also higher than kimchi A during fermentation (Figure 1b and c).

To identify the dominant bacterial group present during the fermentation process, the bacterial community in kimchi A and B was analyzed via pyrosequencing analysis (Figure 2). Both kimchi samples showed an increase in LAB abundance during fermentation. The LAB content was approximately 17.2% in kimchi A at the initial time point and comprised Lactobacillus, Lactococcus, Leuconostoc, and Weissella genera. The abundance of Weissella increased from the initial 3.9%-57.2% and 53.7% at weeks 1 and 2, respectively. The abundance of L. mesenteroides in kimchi B was 39.0% at the initial time point and increased to 72.0% and 76.6% at weeks 1 and 2, respectively (Figure 2a and b). The total bacterial loads in kimchi A and B were 6.3–6.8 and 8.3–8.9 log CFU/mL during fermentation, respectively. The ADI pathway genes were investigated and are listed in Figure 2c.

3.2. ADI metabolites in kimchi

ADI metabolites changes were analyzed during fermentation. The ADI metabolites differed in concentration between kimchi A and B (Figure 3a and b). There was a significant difference in arginine utilization ($p < 0.05$) between both kimchi samples. The arginine content was approximately 41.2 ± 0.6 and 41.9 ± 1.0 μg/mL in kimchi A and kimchi B at the initial time point, respectively. The arginine content in kimchi A reduced to 24.3 ± 1.6 and 2.5 ± 1.7 μg/mL at week 1 and week 2, respectively. In contrast, kimchi B contained 32.8 ± 3.0 μg/mL of arginine at week 2 (Figure 3a). An increase in ornithine content was observed, comparable to that of arginine reduction in both kimchi samples. Kimchi A and B contained 5.7 ± 0.1 and 6.2 ± 0.1 μg/mL ornithine at the initial time point, respectively. Ornithine content increased to 10.8 ± 0.5 μg/mL in kimchi A and 6.5 ± 1.3 μg/mL in kimchi B at week 2 (Figure 3b). The ammonia content increased slightly in both kimchi samples and ranged from 6.5–9.0 μg/mL during fermentation. However, the ammonia content did not differ between kimchi A and B (Figure 3c) ($p < 0.05$).

3.3. ADI activity of W. koreensis and L. mesenteroides

L. mesenteroides has been reported to exhibit weak ADI activity (Hwang and Lee, 2018). Therefore, we evaluated the ADI activity of L. mesenteroides and W. koreensis. The bacteria were cultivated in MRS media and ADI metabolite contents, including arginine, citrulline, and ornithine, were analyzed and compared (Figure 4). ADI activity was detected in W. koreensis alone. The arginine content in L. mesenteroides and W. koreensis cultures was 245.6 ± 13.3 and 224.1 ± 10.0 μg/mL at the initial time point, respectively; arginine content reduced to 73.1 ± 3.4 μg/mL in W. koreensis cultures and remained unchanged (219.6 ± 12.4 μg/mL) in L. mesenteroides cultures after 3 h of cultivation at 30 °C (Figure 4a). The citrulline and ornithine contents in the W. koreensis culture increased by approximately 3.5- and 4.5-fold, respectively, and remained unchanged in the L. mesenteroides cultures (Figure 4b and c).

3.4. Nitrate production

The nitrate and nitrite contents in kimchi A and B were analyzed (Figure 5). The nitrate content (33.5 μg/mL) was higher at the initial time point than at later time points. The nitrate content in kimchi A and B reduced to 0.8 ± 0.1 and 0.1 ± 0.0 μg/mL, respectively, at week 1 (Figure 5a). The nitrite content in both kimchi samples was 0.4 ± 0.1 μg/mL at the initial time point. At week 1, the nitrite content increased to 1.0 ± 0.1 μg/mL in kimchi A, whereas it was approximately 0.3 ± 0.1 μg/mL in kimchi B (Figure 5b).

4. Discussion

The bacterial ADI pathway is an energy generation pathway that produces ornithine, ATP, CO$_2$, and ammonia. Ammonia is further oxidized to nitrite or reduced to nitrate (Tiso and Schechter, 2015). Nitrate and nitrite inhibit microbial growth and are therefore used as food additives. These compounds also promote nitric oxide production, which improves cardiovascular health in humans. However, nitrite is converted to carcinogenic N-nitroso compounds via reactions with secondary amines in an acidic environment. Therefore, high nitrate- and nitrite-containing foods present a potential risk to human health (Ma et al., 2018).

Amino acid content in kimchi originates from diverse raw ingredients and serves as cell structural components and an energy source for bacteria (Lam et al., 2009; Mutaguchi et al., 2018). Notably, arginine is the only amino acid whose content decreased during the fermentation process; many LAB use arginine and citrulline as sources of energy (Choi et al., 2018). Fermentative environments are anaerobic conditions in which LAB can utilize arginine to generate energy, with ADI pathways being a major energy supply route for LAB (Pessione et al., 2010). Analysis of the ADI system of LAB showed that adi genes are abundant among Weissella spp. commonly identified in kimchi and that L. mesenteroides have weak ADI activity, implying that L. mesenteroides does not utilize arginine as a nutrient source (Jung et al., 2021; Yeong et al., 2020). In this study, we confirmed that kimchi enriched with Weissella contained a high ornithine content and that W. koreensis showed strong ADI activity (Figures 3 and 4).

Our analyses revealed that nitrite content increased only in kimchi A at the time where ADI metabolite production was at its maximum (Figure 5). These results suggest that ADI metabolites represent important elements in the nitrification process during kimchi fermentation. Both kimchi samples had a high nitrate content at the initial time point, possibly because cabbage and radish serve as sources of nitrate in kimchi (Jo et al., 2010). We observed a decrease in the nitrate content of both kimchi samples after 1 week of fermentation, and this was associated
with the maximum increase of LAB (Figure 5a). Several studies have shown that LAB reduce nitrate and nitrite content (Kim et al., 2017; Tiso and Schechter, 2015; Wang and Shao, 2018). Lactobacillus isolated from kimchi exhibit nitrate- and nitrite-depletion activity (Paik and Lee, 2014), which suggests that LAB contains a nitrite reductase enzyme system that may contribute to the conversion of nitrite to nitrogen dioxide (NO2), nitrous oxide, and N2 under anaerobic conditions (Baskaran et al., 2020; Gou et al., 2019; Oh et al., 2004; Tiso and Schechter, 2015).

In this study, we demonstrated that L. mesenteroides did not possess ADI activity and that kimchi with L. mesenteroides had a low nitrate content. L. mesenteroides have been widely used as kimchi starters in the kimchi industry (M. Lee et al., 2015); adding bacteria with weak ADI activity may prevent arginine catabolic activity and reduce the risk of further nitrate production. Therefore, LAB showing low ADI activity may be used as a kimchi starter to reduce nitrite production by bacteria. Overall, this study highlights an advantageous feature of kimchi starters in the kimchi industry.

Figure 2. Analysis of the bacterial community of kimchi. The bacterial communities in the kimchi samples were analyzed using pyrosequencing technology. Kimchi samples were stored at 4°C and collected once a week. The bacterial community was analyzed at the species level (a and b) and abundance of ADI pathway genes (c) in kimchi A and kimchi B. The orange bar in panel c indicates the abundance of species (%) with maximum cutoff of 5% and the grey box indicates the presence of genes.
Figure 2. (continued).

| Bacterial strain | Time (W) | Genes |
|------------------|----------|-------|
| Lactobacillus agilis | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Lactobacillus algidus | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Lactobacillus bronnieae | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Lactobacillus brevis | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Lactobacillus casei | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Lactobacillus casei K81 | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Lactobacillus fermentum | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Lactobacillus fischingeri | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Lactobacillus gasseri | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Lactobacillus hilgar | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Lactobacillus homorogus | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Lactobacillus hoshi | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Lactobacillus komagatae | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Lactobacillus leichmanii | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Lactobacillus reuteri | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Lactobacillus rhamnosus | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Lactobacillus sakei | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Lactobacillus salivarius | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Lactobacillus senega | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Lactobacillus microaerophilus | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Lactobacillus paracasei | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Lactobacillus periconiae | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Lactobacillus plantarum | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Lactobacillus plantarum | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Leuconostoc gelidum | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Leuconostoc cremoris | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Leuconostoc diacetylactis | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Leuconostoc in situ | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Leuconostoc mesenteroides | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Leuconostoc meyeri-Kimchi | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Leuconostoc pullis | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Leuconostoc pseudomesenteroides | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Leuconostoc rapi | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Weissella benjaminii | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Weissella diehlii | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Weissella fabarca | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Weissella haloplora | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Weissella kandleri | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Weissella koreensis | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Weissella minor | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Weissella oryzae | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Weissella paraplagiostercoides | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Weissella radii | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Weissella soli | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |
| Weissella viscosa | 0 1 2 3 4 | ✓ ✓ ✓ ✓ |

Figure 3. Analysis of ADI metabolites in the kimchi. The levels of ADI metabolites present in the kimchi samples were measured using LC-MS/MS and ammonia assay kit. (a) Arginine, (b) ornithine, and (c) ammonia. Significance was calculated by comparing kimchi B with the control kimchi A at the same fermentation time; statistical significance is represented as * (p < 0.05).
5. Conclusions

Nitrate and nitrite serve as valuable food additives in the production of diverse foods. However, these compounds may increase the risk of cancer development via the formation of nitrosamines. Nitrate and nitrite are abundant in green leafy vegetables and are produced via bacterial processes. In this study, we investigated the levels of ADI metabolites and nitrogen compounds in kimchi. The ADI pathway produces ammonia during kimchi fermentation and is involved in nitration and increases the nitrite content in kimchi. L. mesenteroides did not have ADI activity, and kimchi with the addition of L. mesenteroides showed low nitrate content. LAB showing low ADI activity may be used as a kimchi starter to reduce nitrite production.

Declarations

Author contribution statement

Sera Jung: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Ji Yoon Chang: Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data.

Jong-Hee Lee: Conceived and designed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

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Data availability statement

Data included in article/supp. material/referenced in article.

Declaration of interests statement

The authors declare no conflict of interest.

Additional information

No additional information is available for this paper.

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