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Tetragenococcus halophilus MJ4 as a starter culture for repressing biogenic amine (cadaverine) formation during saeu-jeot (salted shrimp) fermentation

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ABSTRACT

Biogenic amines (BAs) are frequently present in traditionally fermented salted foods. In this study, a *Tetragenococcus halophilus* strain (MJ4) with no BA-producing ability was isolated from a fish (anchovy) sauce. Strain MJ4 did not produce BAs from supplied precursors and no BA-producing genes were identified in its genome. Bacterial community analysis showed that in non-inoculated saeu-jeot (shrimp sauce) fermentation, *Tetragenococcus* predominated after 82 days, while in strain MJ4-inoculated saeu-jeot, *Tetragenococcus* predominated during the entire fermentation. Strain MJ4 repressed the growth of *T. muriaticus*, a known BA producer, during fermentation, but metabolite analysis demonstrated that metabolite profiles, including amino acids, were similar regardless of MJ4 inoculation. The metabolite analysis also showed that strain MJ4 clearly repressed the formation of cadaverine during fermentation. This study suggests that the use of strain MJ4 as a starter culture in salted fish fermentation may be a good strategy for the reduction of BA formation.

1. Introduction

Traditional fermented foods are generally produced through spontaneous fermentation of various raw ingredients, such as vegetables, fish, and meat, without sterilization (Patra et al., 2016). Therefore, microorganisms primarily derived from raw ingredients or surrounding environment proliferate during food fermentation (Guan et al., 2011; Jung et al., 2013, 2014; Lee et al., 2015) and produce various metabolites such as amino acids, organic acids, and active metabolites imparting nutritional values, health-benefits, and tastes to the consumers (Koo et al., 2016; Jung et al., 2016a; Tamang et al., 2016). However, the growth of these microorganisms occasionally generates undesirable and unexpected metabolites, such as biogenic amines (BAs) or toxins, during fermentation. In particular, BAs are frequently found in Korean traditional fermented foods such as fermented soybean paste (doenjang) and sauce (ganjang) and fermented salted fish (jeot) (Lee et al., 2009, 2015; Jung et al., 2015, 2016b).

BAs are low-molecular-weight amine-containing compounds that are generally produced by the decarboxylation of their corresponding amino acids or nitrogen compounds by microbial enzymes during food fermentation. For instance, putrescine, cadaverine, histamine, tyramine, and β-phenylethylamine are produced by the decarboxylation of ornithine, lysine, histidine, tyrosine, and phenylalanine, respectively. However, spermidine, a polyamine, is formed by spermidine synthase, not by decarboxylation, from putrescine. The excessive uptake of BAs may cause adverse health effects, such as headache, nausea, hot flushes, localized inflammation, heart palpitations, and hypertension and thus the concentration of BAs is often an important indicator for the evaluation of safety and quality of fermented foods (Bulushi et al., 2009; Suzzi and Torriani, 2015). To develop a strategy to prevent or reduce the formation of BAs during food fermentation, several biological control methods have been considered (Shukla et al., 2014; Zaman et al., 2011; Lorenzo et al., 2017; Renes et al., 2014; Ranucci et al., 2016; Saelao et al., 2018). The use of a starter culture with no BA-producing ability may be a good means to produce fermented foods without BAs. The use of starter cultures can also contribute to the economical production of high quality standardized fermented foods (Shukla et al., 2015; Yongsawatdigul et al., 2007).

Members of the genus *Tetragenococcus* are moderately halophilic homofermentative lactic acid bacteria (LAB) that grow in 18% NaCl or greater and are frequently found in salted fermented foods such as fish sauce and soy sauce (Justé et al., 2012; Lee et al., 2015; Jung et al., 2016a, 2016b; Jeong et al., 2017; An et al., 2010). It was reported that they may play important roles for amino acid production by aminopeptidases and flavor improvement during salted fish fermentation (Fukami et al., 2004; Udomsil et al., 2010). Therefore, the use of *T.*

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halophilus as a starter culture may improve flavoring, taste characteristics, and safety of salted fermented fish products (Udomsil et al., 2011, 2016; Kuda et al., 2014). In addition, some *T. halophilus* strains have the ability to reduce the formation of biogenic amines, especially histamine, during fermentation (Jeong et al., 2017; Lee et al., 2018; Kuda et al., 2012). However, the extent of the reduction of BA formation by *T. halophilus* is so far tenuous or mainly limited to histamine (Udomsil et al., 2011; Lee et al., 2018). In addition, it has been reported that *Tetragenococcus* strains can be causative agents in the production of biogenic amines during salted food fermentation (Sitdhipol et al., 2013; Satomi et al., 2008, 2011, 2014; Kobayashi et al., 2016; Jung et al., 2016a). Therefore, further development of a *Tetragenococcus* strain that can prevent or reduce the formation of BAs during salted food fermentation is necessary to produce fermented fish products with high standards of quality and safety.

In this study, we isolated a *T. halophilus* strain (MJ4) with no BA-producing ability from a salted fish sauce (anchovy sauce). We investigated the BA-producing ability of strain MJ4 by genomic analysis and an *in vitro* BA production test. In addition, we tested the hypothesis that strain MJ4 may successfully be used as a starter culture to reduce BA formation during salted fish fermentation.

2. Materials and methods

2.1. Isolation and phylogenetic analysis of strain MJ4

A myeolchi-aekjeot (a Korean traditional fermented anchovy sauce) sample was previously fermented for 200 days at 25 °C and determined to be BA-free with a predominance of *Tetragenococcus* species (Lee et al., 2015). The sample was serially diluted in De Man-Rogosa-Sharpe (MRS; BD, USA) broth supplemented with 5% (w/v) NaCl and aliquots of each serial dilution were spread on MRS agar supplemented with 5% NaCl. The agar plates were sealed with parafilm and incubated at 30 °C for 3 days. Colonies grown on agar plates were analyzed based on their 16S rRNA gene sequences as described previously (Choi et al., 2014) and a representative *Tetragenococcus* strain, designated strain MJ4, was selected for further analysis. A phylogenetic analysis of strain MJ4 based on 16S rRNA gene sequences was performed using the neighbor-joining algorithm with bootstrap values (1000 replications) within the MEGA 7 software (Kumar et al., 2016). Average nucleotide identity (ANI) and *in silico* DNA-DNA hybridization (DDH) values between strain MJ4 and closely related *Tetragenococcus* strains using whole genomes were calculated using a stand-alone software (http://www.ezbiocloud.net/sw/oat; Lee et al., 2016) and the server-based genome-to-genome distance calculator ver. 2.1 (http://ggdc.dsmz.de/distcalc2.php; Meier-Kolthoff et al., 2013), respectively, as described previously (Kim et al., 2018).

2.2. Genome analysis of strain MJ4

The genome of strain MJ4 was analyzed as described previously, with some modifications (Kim et al., 2018). In brief, the whole genomic DNA of strain MJ4 was extracted using phenol-chloroform and ethanol precipitation and sequenced using a hybrid approach combining PacBio RS single-molecule real-time (SMRT) sequencing with a 10-kb library and Illumina Hiseq 2500 paired-end sequencing (101 bp) at Macrogen (Seoul, Korea). De novo assembly of the sequencing reads derived from the PacBio SMRT sequencing was performed using HGAP (v3.0) in SMRT Portal v2.3.0 and PacBio SMRT sequencing errors were corrected by mapping Illumina sequencing reads on the complete genome of strain MJ4 obtained from the PacBio SMRT sequencing using Pilon (v1.21). Automated annotation and cluster of orthologous groups (COG) analysis of the genome were performed using the NCBI Prokaryotic Genome Annotation Pipeline (PGAP) and the Function Category comparisons tool at IMG/ER (http://img.jgi.doe.gov/cgi-bin/er/main.cgi), respectively. Genomic islands (GIs) and clustered regularly interspaced short palindromic repeats (CRISPR) were identified using Island Viewer 4 (http://www.pathogenomics.sfu.ca/islandviewer/) and a web-based analysis (http://crispr.i2bc.paris-saclay.fr/Server/), respectively.

2.3. In vitro BA production test of strain MJ4

The BA-producing ability of strain MJ4 was assessed according to a procedure described previously, with some modification (Kim et al., 2017). The type strain of *Tetragenococcus muriaticus* (KCTC 21008^T), a known producer of BA, was used as a positive control. In brief, strains MJ4 and KCTC 21008^T were inoculated into MRS broth supplemented with 5% (w/v) NaCl, 0.005% (w/v) pyridoxal-5-phosphate-HCl (Sigma-Aldrich, USA), and a 0.25% (w/v) BA precursor (L-tyrosine, L-histidine hydrochloride, L-lysine hydrochloride, or L-ornithine hydrochloride; Sigma-Aldrich, USA) and cultivated at 30 °C for 2 days. One milliliter of each culture broth was syringe-filtered through a 0.2 μm filter (Biofact, Korea) and the resulting filtrates were derivatized with 9-fluorenylmethoxy carbonyl (FMOC). For the FMOC derivatization, 20 μL of the filtrates or standards (5, 10, and 20 μM of cadaverine dihydrochloride, histamine dihydrochloride, putrescine, and tyramine hydrochloride in 0.1 N HCl) and 200 μL of 1.5 mM FMOC (in acetone) were added to 200 μL of 0.5 M sodium borate buffer (pH 8.5) containing 20 μM norvaline as an internal standard, and then vigorously mixed. After 3 min at room temperature, 50 μL of 10 mM glycine in 0.5 M sodium borate buffer was added to the mixture to scavenge excess FMOC. The FMOC-derivatized biogenic amines were analyzed by HPLC (Shimadzu, Japan) equipped with a reverse-phased Hypersil ODS C_{18} Column (250 × 4.6 mm; Thermo Fisher Scientific, USA) and a fluorescence detector (RF-10AXL; Shimadzu, Japan) using the conditions described by Brückner et al. (2012).

2.4. Fish fermentation starter culture experiment using strain MJ4

2.4.1. Preparation of starter culture

Strain MJ4 cells were cultured to a concentration of $\sim 10^9$ cells/ml in MRS broth (BD, USA) supplemented with 5% (w/v) NaCl at 30 °C for 2 days and harvested by centrifugation at 7000 × *g* and 4 °C for 10 min. The harvested cells were washed with 25% (w/v) solar salt (Shinan, Korea) solution and resuspended in 25% solar salt solution to a concentration of 10^{10} cells/mL for starter inoculation.

2.4.2. Preparation of saeu-jeot and sampling

The effects of *T. halophilus* MJ4 as a starter culture on the reduction of BA formation during salted fish fermentation were investigated by applying it to the fermentation of saeu-jeot (fermented salted shrimp sauce). Three sets of triplicate saeu-jeot samples were prepared according to the procedure described previously (Lee et al., 2014a). In brief, fresh shrimp (*Acetes japonicus*) approximately 4–6 cm in length that were caught from the Yellow Sea in South Korea and solar salt (Shinan, Korea) were equally dispensed into nine plastic containers to include 1.5 kg of shrimps and 450 g of solar salts, respectively. Next, 600 mL of 25% solar salt solution, 600 mL of 25% solar salt solution containing 10^7 strain MJ4 cells/mL, and 600 mL of 25% solar salt solution containing 10^7 strain MJ4 cells/mL and 1% (w/v) glucose were poured into three containers each, mixed well, and stored at 20 °C.

Four milliliters of liquid from the saeu-jeot broths were sampled from each container and their pH values were immediately measured. Viable cells in saeu-jeot samples were enumerated by the standard plate-counting method. The saeu-jeot broth samples were serially diluted in MRS broth and the diluted samples were spread on MRS agar supplemented with 5% NaCl. The agar plates were sealed with parafilm and incubated at 30 °C for 3 days. The numbers of viable microorganisms in the saeu-jeot samples were calculated as colony forming units (CFU) per milliliter.

The sampled saeu-jeot broths were filtered through four layers of sterile coarse gauze (Daehan, Korea) to remove large particles, and

1 mL of the saeu-jeot filtrates was centrifuged at 13400 × *g* and 4 °C for 5 min to separate microorganisms and supernatants. The harvested microorganisms from three replicate containers were combined and stored at −80 °C for bacterial community analysis. The supernatants were separately stored at −80 °C for triplicate metabolite analysis.

2.4.3. Bacterial community analysis using barcode pyrosequencing

Genomic DNA from the combined pellets of the triplicate samples was extracted using a FastDNA SPIN Kit (MP Biomedicals, USA), according to the instructions of the manufacturer. Bacterial 16S rRNA genes of the extracted genomic DNA were amplified and their PCR products were sequenced using barcode pyrosequencing, as described previously (Jung et al., 2013).

Pyrosequencing reads were processed using the Ribosomal Database Project (RDP) Release 11 (http://pyro.cme.msu.edu/) (Cole et al., 2014), according to the procedure described previously (Lee et al., 2014a). The pyrosequencing reads were sorted to each saeu-jeot sample based on their barcode sequences, and then the barcodes were removed. Sequencing reads with more than two ambiguous 'N' (nucleotides), shorter than 300 bases, and with an average quality score below 20 (error rate 0.01) were excluded from further analysis. Putative chimeric sequences were additionally removed by USEARCH 6.0 in RDPipeline (Edgar et al., 2011). The resulting sequencing reads in each samples were normalized to the smallest sequencing read number (583 reads) by randomly removing sequencing reads from the fasta data using the MOTHUR program (v. 1.39.1) (Schloss et al., 2009). From the normalized sequencing reads, the generation of rarefaction curves and the calculation of operational taxonomic units (OTU), Shannon-Weaver, and Chao1 richness indices, and evenness were performed at a 3% dissimilarity level using RDPipeline. The normalized sequencing reads were taxonomically classified at the genus using the RDP naïve Bayesian Classifier within the 16S rRNA training set 16 at an 80% confidence threshold (Wang et al., 2007). Sequencing reads classified as *Tetragenococcus* at the genus level were further classified at the species level based on the best match against 16S rRNA gene sequences of *Tetragenococcus* type strains in the RDP database using the SeqMatch algorithm.

2.4.4. Metabolite analysis using ^{1}H NMR and multivariate statistical analysis

Fermentative metabolites in saeu-jeot samples were analyzed using a Varian Inova 600 MHz ^{1}H NMR spectrometer, according to the procedure described previously (Jung et al., 2013). For a multivariate statistical analysis of metabolite change during saeu-jeot fermentation, all ^{1}H NMR peaks were manually phased and baseline-corrected using MestReNova software (ver. 8.1, Mestrelab Research SL, Spain). The ^{1}H NMR spectra of 0.5–10.0 ppm were reduced into 0.001 ppm spectral buckets and the water regions of 4.6–4.8 ppm were removed using MestReNova. The resulting ^{1}H NMR spectra were normalized to the total spectral area and then converted to ASCII format using MestReNova. The data files were imported into MATLAB (ver. 9.4, Mathworks, USA), and all spectra data were aligned using the icoshift algorithm (Savorani et al., 2010) and mean-centered without scaling. Principal component analysis (PCA) was performed using the vegan package in the R programming environment (http://cran.r-project.org/; Oksanen et al., 2011) at a confidence level of 95%. The identification and quantification of amino acids, nitrogen compounds, free sugars, organic acids, and amines from the ^{1}H NMR spectra were performed using the Chenomx NMR suite software (ver. 8.2, Chenomx Inc., Canada) based on the NMR peak intensity of 2,2-dimethyl-2-silapentane-5-sulfonate (DSS), used as an internal standard.

2.5. Data availability

The genome sequence of strain MJ4 was deposited to GenBank/EMBL/DDBJ under the accession number CP012047.1. The pyrosequencing data of 16S rRNA genes from this study are also publicly available in the NCBI Short Read Archive under accession no. SRX2992827 (NCBI BioProject PRJNA393597).

3. Results

3.1. Isolation and phylogenetic analysis of strain MJ4

We isolated a strain of *T. halophilus* (MJ4) that had no BA-producing ability from a Korean fermented anchovy sauce, in which *Tetragenococcus* was predominant, but no BAs were detected (Lee et al., 2015). A phylogenetic analysis based on 16S rRNA gene sequences showed that strain MJ4 formed a tight phyletic lineage with the type strains of *T. halophilus* subsp. *flandriensis* and *T. halophilus* subsp. *halophilus* (Supplementary Fig. S1) and was most closely related to these two strains, showing high 16S rRNA gene sequence similarities (99.5 and 99.3%, respectively). ANI and *in silico* DDH values between strain MJ4 and the type strains of *T. halophilus* subsp. *halophilus* and *T. halophilus* subsp. *flandriensis* were 97.5 and 79.7% and 97.0 and 76.0%, respectively— higher than the ANI and DDH cutoff values, 95–96 and 70%, respectively, for prokaryotic species delineation (Rosselló-Mora and Amann, 2015). These results clearly suggest that strain MJ4 is a member of *T. halophilus*.

3.2. Genomic features of strain MJ4

The genome of strain MJ4 consisted of only one single circular chromosome of 2389470 bp with a G + C content of 36 mol%; no plasmid was found. A total of 2399 genes including 2260 protein-coding sequences, 62 tRNA genes, and 5 rRNA operons (16S, 23S, and 5S) were identified (Table 1). No amino acid decarboxylase and spermidine synthase genes for BA production were identified from the genome of strain MJ4.

3.3. In vitro BA production test for strain MJ4

The BA production test showed that the formation of cadaverine, histamine, putrescine, and tyramine by strain MJ4 in MRS (supplemented with 5% NaCl) containing their corresponding BA precursors was negligible, whereas high amounts of BAs, except for putrescine, were formed by the *T. muriaticus* type strain (KCTC 21008^T), a known BA producer (Satomi et al., 1997) (Fig. 1.). In particular, histamine, a representative BA compound found from fermented salted fish sauces, was barely detected from the cultures inoculated with strain MJ4, whereas approximately 584.8 μmol/L of histamine was formed in the cultures inoculated with *T. muriaticus* KCTC 21008^T.

3.4. Strain MJ4 as a starter culture for saeu-jeot fermentation

3.4.1. pH and microbial cell counts during saeu-jeot fermentation

The pH profiles during saeu-jeot fermentation in this study were

Table 1
General features of the genome of strain MJ4.

Feature	Value
Status (no. of contigs)	Complete (1)
Size (bp)	2,389,470
G + C content (%)	36.0
No. of total genes	2399
No. of protein coding sequences	2260
Protein assigned to COG (%)	72.7
No. of rRNA gene operon (16S, 23S, and 5S)	5 (5, 5, 5)
No. of tRNA genes	62
No. of confirmed CRISPRs	3
No. of genomic islands	12

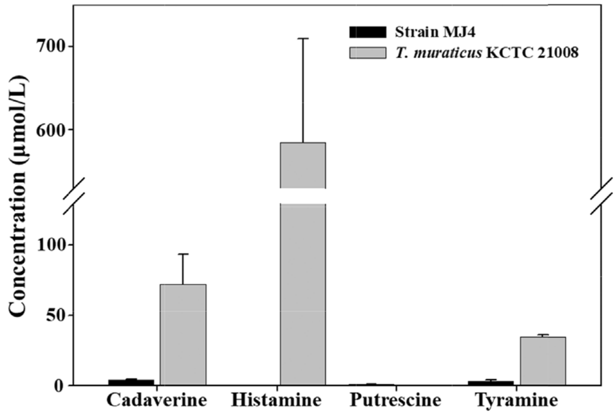

Fig. 1. Biogenic amine production by *Tetragenococcus halophilus* MJ4 and the type strain of *T. muriaticus* (KCTC 21008^T) in MRS broth supplemented with 5% (w/v) NaCl and a 0.25% (w/v) biogenic amine precursor (lysine, histidine, ornithine, or tyrosine for cadaverine, histamine, putrescine, and tyramine, respectively).

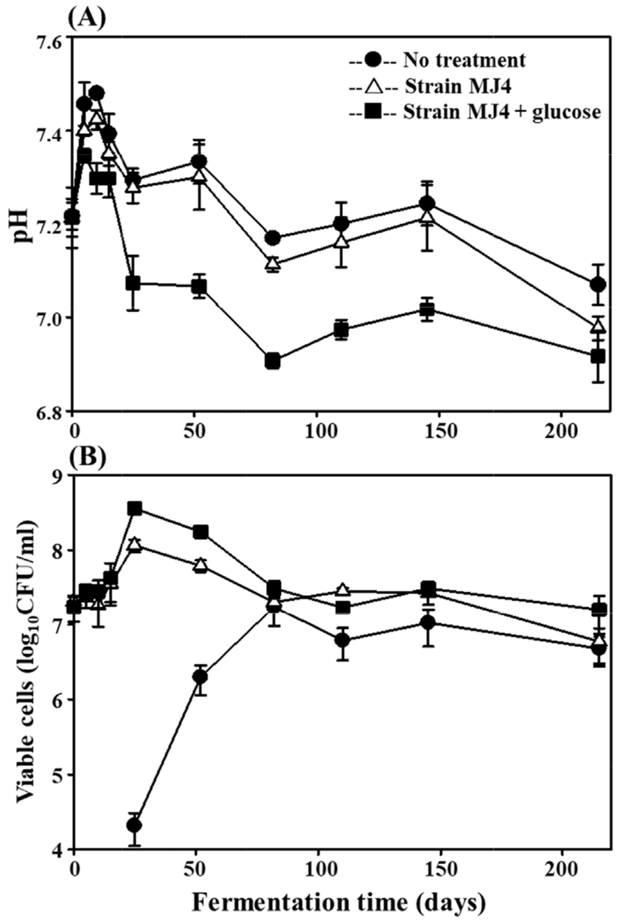

Fig. 2. Changes in pH values (A) and viable cell counts (CFU/ml) (B) of microbial cells during saeu-jeot fermentation with/without *T. halophilus* MJ4 and with/without glucose supplementation. Measurements of pH and CFU were performed in triplicate, and the error bars represent their standard deviations.

generally similar to those of previous studies (Jung et al., 2013; Lee et al., 2014a, 2014b) (Fig. 2A). The initial pH values of saeu-jeot were approximately 7.2. After a slight initial increase, the pH values gradually decreased to approximately pH 7.0–7.1 in all saeu-jeot samples at the end of fermentation. The pH profiles of saeu-jeot inoculated with strain MJ4 (no glucose addition) were relatively similar to those of non-treated saeu-jeot (no MJ4 inoculation and no glucose addition). However, the pH values of saeu-jeot with both MJ4 inoculation and glucose addition decreased more quickly and to a greater extent than saeu-jeot without glucose addition.

Viable halophilic bacteria including *Tetragenococcus*, present in saeu-jeot samples were enumerated on MRS agar supplemented with 5% NaCl. The halophilic bacteria in saeu-jeot without MJ4 inoculation were below detection level until 10 days of fermentation, but increased to approximately 2.1×10^4 CFU/mL at 25 days of fermentation and gradually increased further to approximately 1.7×10^7 CFU/mL at 82 days of fermentation (Fig. 2B). After 82 days of fermentation, the levels of viable halophilic bacteria became relatively constant. Halophilic bacteria in saeu-jeot that was inoculated with approximately 10^7 cells/mL increased during the early fermentation period, but after 15 days of fermentation, they decreased similarly to the cell numbers in saeu-jeot without MJ4 inoculation at 82 days of fermentation. The increase of halophilic bacteria in saeu-jeot with both MJ4 inoculation and glucose addition during the early fermentation period was significantly higher than that in saeu-jeot with MJ4 inoculation alone, suggesting that strain MJ4 grew by glucose metabolism.

3.4.2. Bacterial successions and changes in bacterial diversity during saeu-jeot fermentation

The analysis of rarefaction curves and diversity indices including OTU, Shannon-Weaver, and Chao1 richness showed that bacterial diversities generally decreased in all saeu-jeot samples as the fermentation progressed regardless of the inoculation of strain MJ4 and glucose addition (Supplementary Fig. S2 and Table S1). The bacterial diversities decreased rapidly in saeu-jeot inoculated with strain MJ4 and in particular, they decreased faster with MJ4 inoculation and glucose addition, suggesting that strain MJ4 may well adapt to saeu-jeot fermentation conditions for its growth. The rarefaction curve analysis showed that approximately 600 sequencing reads in saeu-jeot with MJ4 inoculation were almost sufficient to describe the entire bacterial communities of the saeu-jeot, that is, the slopes neared the zero values in the rarefaction curves (Supplementary Fig. S2).

To compare the bacterial community in saeu-jeot according to MJ4 inoculation and glucose addition, the pyrosequencing reads of bacterial 16S rRNA genes were classified at the genus level (Fig. 3A). We were not able to analyze bacterial communities of 0 day-samples because PCR amplification of non-treated samples at 0 day failed, probably due to too few bacterial cells present. In the non-treated samples, the genera *Bacillus* and *Psychrobacter* were dominant during the early fermentation period. As the fermentation progressed, the initially dominant genera gradually diminished and the genera *Staphylococcus*, *Salimicrobium*, and *Alkalibacillus* became dominant after 25 days of fermentation, in agreement with the results of previous studies (Jung et al., 2013; Lee et al., 2014a, 2014b). After 82 days of fermentation, *Tetragenococcus* became dominant and *Dolosigranulum* became dominant at 215 days. On the other hand, in saeu-jeot inoculated with strain MJ4 as a starter culture, members of *Tetragenococcus* predominated, regardless of glucose addition, after 5 days of fermentation (Fig. 3A). In particular, in saeu-jeot with both MJ4 inoculation and glucose addition, *Tetragenococcus* constituted more than 80% of the total community at just 5 days of fermentation. In saeu-jeot with MJ4 inoculation, but without glucose addition, *Staphylococcus* appeared as one of dominant genera at 10 days of fermentation, but eventually *Tetragenococcus* members became predominant to almost 100% relative abundance. After 52 days of fermentation, the relative abundance of *Tetragenococcus* gradually and slightly decreased and the genera *Salimicrobium* and *Dolosigranulum* appeared as dominant genera, although their relative abundance was not particularly high. However, in saeu-jeot with both MJ4 inoculation and glucose addition, *Tetragenococcus* members predominated without the appearance of *Staphylococcus* and *Salimicrobium* until the end of fermentation.

The sequencing reads that were classified as *Tetragenococcus* at the

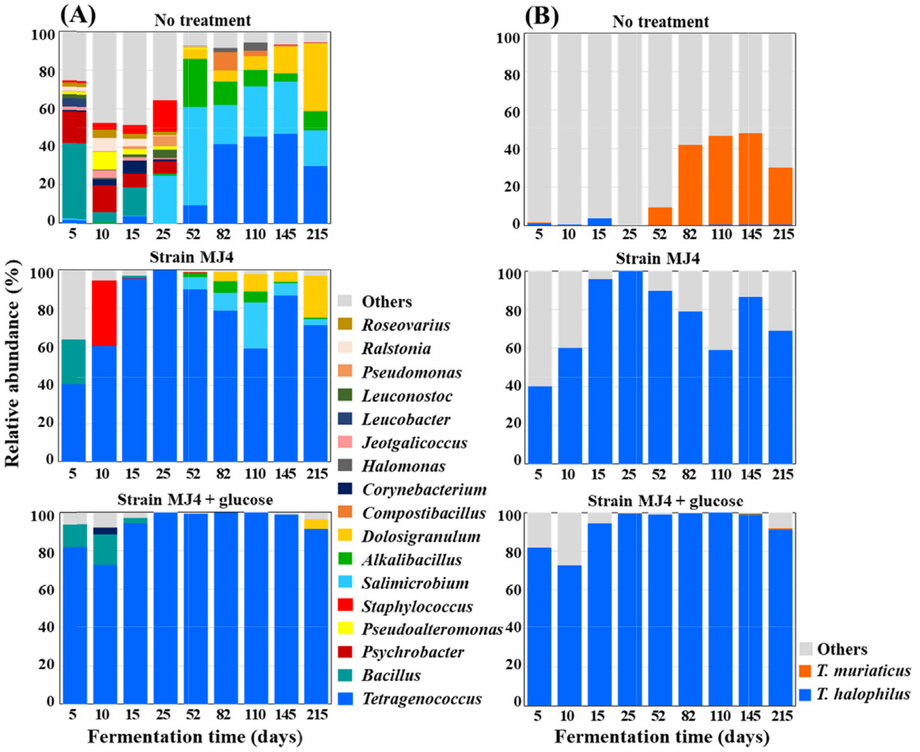

Fig. 3. Bacterial taxonomic compositions at the genus (A) and species (B) levels showing bacterial community changes of saeu-jeot samples during the fermentation period under different conditions. The term “Others” in panel (A) comprises genera with less than 3.0% of the total reads in all samples and “Others” in panel (B) comprises genera except *Tetragenococcus*.

genus level were further classified at the species level to differentiate *Tetragenococcus* members in saeu-jeot more finely (Fig. 3B). Almost all sequencing reads classified as *Tetragenococcus* in non-treated saeu-jeot were classified as *T. muriaticus*, while almost all *Tetragenococcus* sequencing reads in saeu-jeot inoculated with strain MJ4 as a starter culture were classified as *T. halophilus* regardless of glucose addition, which suggests that *Tetragenococcus* members in non-treated saeu-jeot and in saeu-jeot with strain MJ4 inoculation were phylogenetically different. Only a few sequencing reads classified as *T. muriaticus* were identified from saeu-jeot with strain MJ4 inoculation.

3.4.3. Metabolite changes in saeu-jeot samples during fermentation

For the comparison of metabolite changes in saeu-jeot fermented under three different conditions, a multivariate PCA was performed using all ^{1}H NMR spectra peaks (Fig. 4). The PCA biplots showed that metabolite changes in saeu-jeot with both, inoculation with strain MJ4 and glucose addition, were clearly differentiated from those in saeu-jeot without glucose addition, especially after 25 days of fermentation, which suggests that glucose addition greatly altered the metabolites of saeu-jeot products. However, the analysis showed that the metabolite profiles in saeu-jeot inoculated with strain MJ4, but without glucose addition, were relatively similar with those in non-treated saeu-jeot.

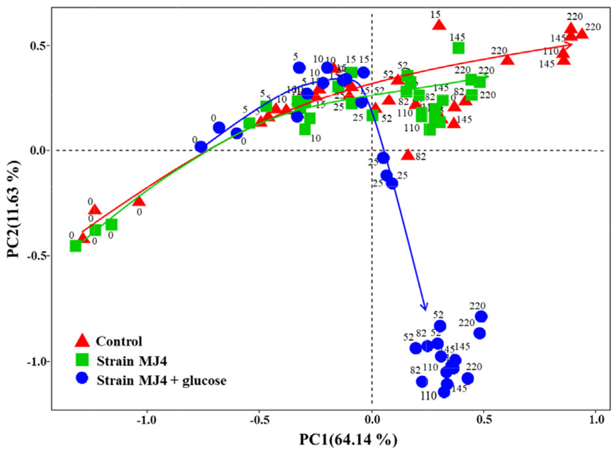

Fig. 4. PCA biplots based on all ^{1}H NMR spectra showing metabolite changes in saeu-jeot samples fermented under three different conditions. The curved arrows indicate the directions of metabolite changes on the biplots during saeu-jeot fermentation. Numbers beside data points on the biplots represent the fermentation time (days) of triplicate saeu-jeot samples.

Amino acids, nitrogen compounds, carbohydrates, and organic acids of saeu-jeot fermented under different conditions were identified and quantified (Figs. 5 and 6). The profiles of amino acids were relatively similar in all saeu-jeot regardless of strain MJ4 inoculation and glucose addition during the entire fermentation period (Fig. 5).

Free sugars were rarely detected in saeu-jeot and only glucose was detected in saeu-jeot samples with glucose addition (Fig. 6A). The glucose decrease occurred rapidly in saeu-jeot with glucose addition during the early fermentation period, which was stoichiometrically associated with lactate increase (Fig. 6B). Glycerol level increased rapidly in all saeu-jeot samples regardless of MJ4 inoculation and glucose addition during the early fermentation period (Fig. 6C). The glycerol levels gradually decreased as the fermentation progressed and at the same time the acetate levels gradually increased. The glycerol decrease was stoichiometrically correlated with the acetate increase (Fig. 6D), which suggests that acetate may be produced from glycerol during saeu-jeot fermentation.

Methylamines, including trimethylamine (TMA) and dimethylamine (DMA), which are an important cause of the unique odors of fermented fish products, are subsequently generated by the reduction and demethylation of trimethylamine *N*-oxide (TMAO). TMAO gradually decreased with an increase of TMA and DMA in all saeu-jeot, regardless of strain MJ4 inoculation and glucose addition, as the fermentation progressed (Fig. 6E, F, and G). However, the production of TMA and DMA from TMAO in saeu-jeot with strain MJ4 inoculation was a little lower than those in non-treated saeu-jeot, which suggests that strain MJ4 can to some extent repress the conversion of TMAO to TMA and DMA.

Cadaverine, produced by microbial decarboxylation of lysine, was identified from non-treated saeu-jeot as a dominant BA and its level gradually increased as the fermentation progressed (Fig. 6H). However,

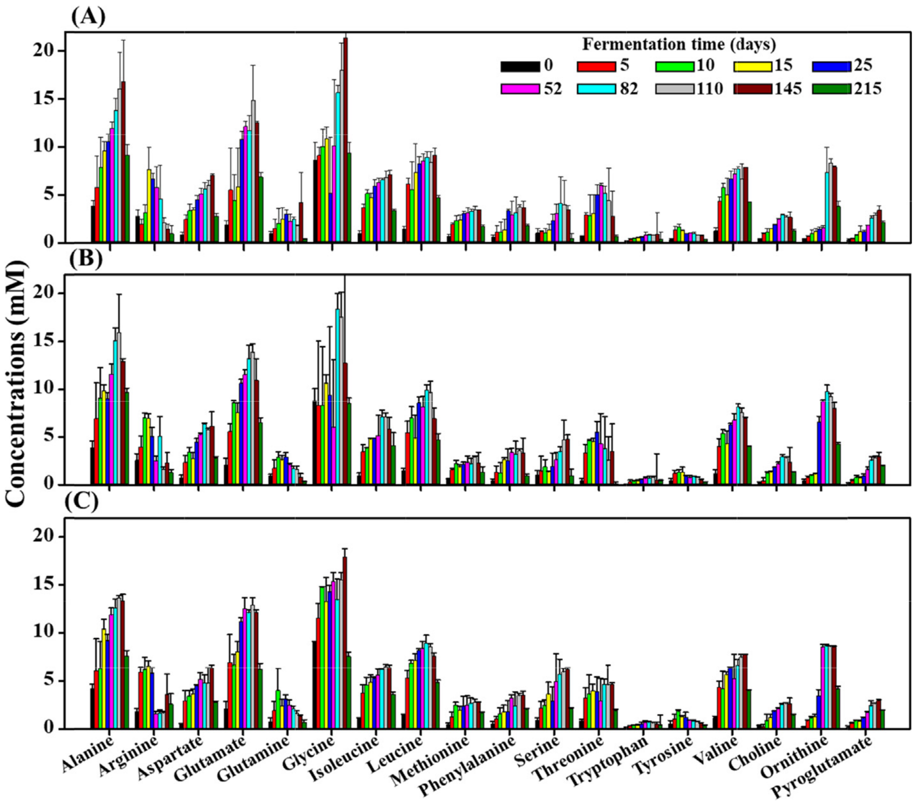

Fig. 5. Changes in amino acids and major nitrogen compound concentrations identified from saeu-jeot samples with no treatment (A), strain MJ4 inoculation (B), and strain MJ4 inoculation and glucose addition (C). Data are indicated as mean values ± standard deviations, measured in triplicate. The concentrations were quantified using Chenomx NMR suite (ver. 6.1) with 2,2-dimethyl-2-silapentane-5-sulfonate (DSS) as an internal standard.

only small amount of cadaverine was detected from saeu-jeot with strain MJ4 inoculation, which suggests that the formation of cadaverine during saeu-jeot fermentation can be repressed by strain MJ4 inoculation as a starter culture.

4. Discussion

Korean traditional fermented salted foods, such as doenjang, ganjang and jeot, are generally prepared through spontaneous fermentation by various microorganisms, mainly derived from raw materials or solar salts. The uncontrolled nature of the fermentation process makes it difficult to produce traditional fermented salted foods commercially due to issues with standardization. In addition, the generation of BAs or toxins during food fermentation by the growth of undesirable microorganisms also prevents the commercialization of Korean traditional fermented salted foods (Lee et al., 2009, 2015; Jung et al., 2015, 2016b). *Tetragenococcus* strains have been suggested as a starter culture for the production of high quality standardized fermented salted foods because they are frequently found to be dominant in fermented salted foods (Yongsawatdigul et al., 2007; Justé et al., 2012; Udomsil et al., 2011, 2016; Jung et al., 2016a, 2016b; Jeong et al., 2017; Kuda et al., 2012; An et al., 2010). However, their use in the commercial production of traditional fermented salted foods has been limited because some strains can be a major causative agent in the production of BAs during fermentation (Sitdhipol et al., 2013; Satomi et al., 2008, 2011; 2014; Kobayashi et al., 2016; Jung et al., 2016b). Therefore, it is necessary to isolate *Tetragenococcus* strains with no BA-producing ability and explore the effects of *Tetragenococcus* strains as a starter culture on microbial community, metabolites, and BA production during entire fermentation period for their safe use as a starter culture.

A strain of *T. halophilus* (MJ4) with no BA-producing ability was isolated from a fermented salted fish food (anchovy sauce) with no detectable BA formation, and its BA-producing capability was investigated through genome analysis. The genome of strain MJ4 did not harbor amino acid decarboxylase and spermidine synthase genes for BA production, which suggests that strain MJ4 may not genetically have the capability to produce BAs. In addition, we confirmed that strain MJ4 did not produce BAs with an *in vitro* BA production test (Fig. 1). The formation of BAs by strain MJ4 from their supplied precursors was negligible, but high amounts of BAs were produced by *T. muriaticus* KCTC 21008^T, a representative BA producer (Fig. 1). These results suggest that strain MJ4 may have no BA-producing ability during salted food fermentation.

To use strain MJ4 as a starter culture for salted food fermentation, its viability and adaptability under salted food fermentation conditions and its effects on microbial community and metabolites in fermented foods during fermentation should be investigated. In addition, the reduction of BA production by using strain MJ4 as a starter culture during salted food fermentation needs to be addressed, because BAs can be produced by other indigenous bacteria or other metabolic pathways. Therefore, strain MJ4 was tested as a starter culture for the fermentation of saeu-jeot (shrimp sauce), the most representative fermented salted fish sauce in Korea.

Viable cell counting of halophilic bacteria on MRS agar supplemented 5% NaCl showed that viable cells rapidly increased during the early fermentation period in saeu-jeot even without the addition of a sugar source (glucose) (Fig. 2B), which suggests that *Tetragenococcus*, including strain MJ4, can grow well under saeu-jeot fermentation conditions with nearly no free sugar. In particular, the abundance of halophilic bacteria in saeu-jeot with both MJ4 inoculation and glucose addition was significantly higher than that in saeu-jeot with only strain MJ4 inoculation, suggesting that strain MJ4 may be viable and metabolically active under saeu-jeot fermentation conditions.

Bacterial community analysis showed that in saeu-jeot without inoculation with strain MJ4, a bacterial succession of *Psychrobacter*, *Staphylococcus*, *Salimicrobium*, and *Alkalibacillus* occurred as the fermentation progressed and *Tetragenococcus* became a dominant genus member after 82 days of fermentation, while in saeu-jeot with strain MJ4 inoculation, *Tetragenococcus* predominated during the entire saeu-jeot fermentation period, although glucose was not supplied (Fig. 3A).

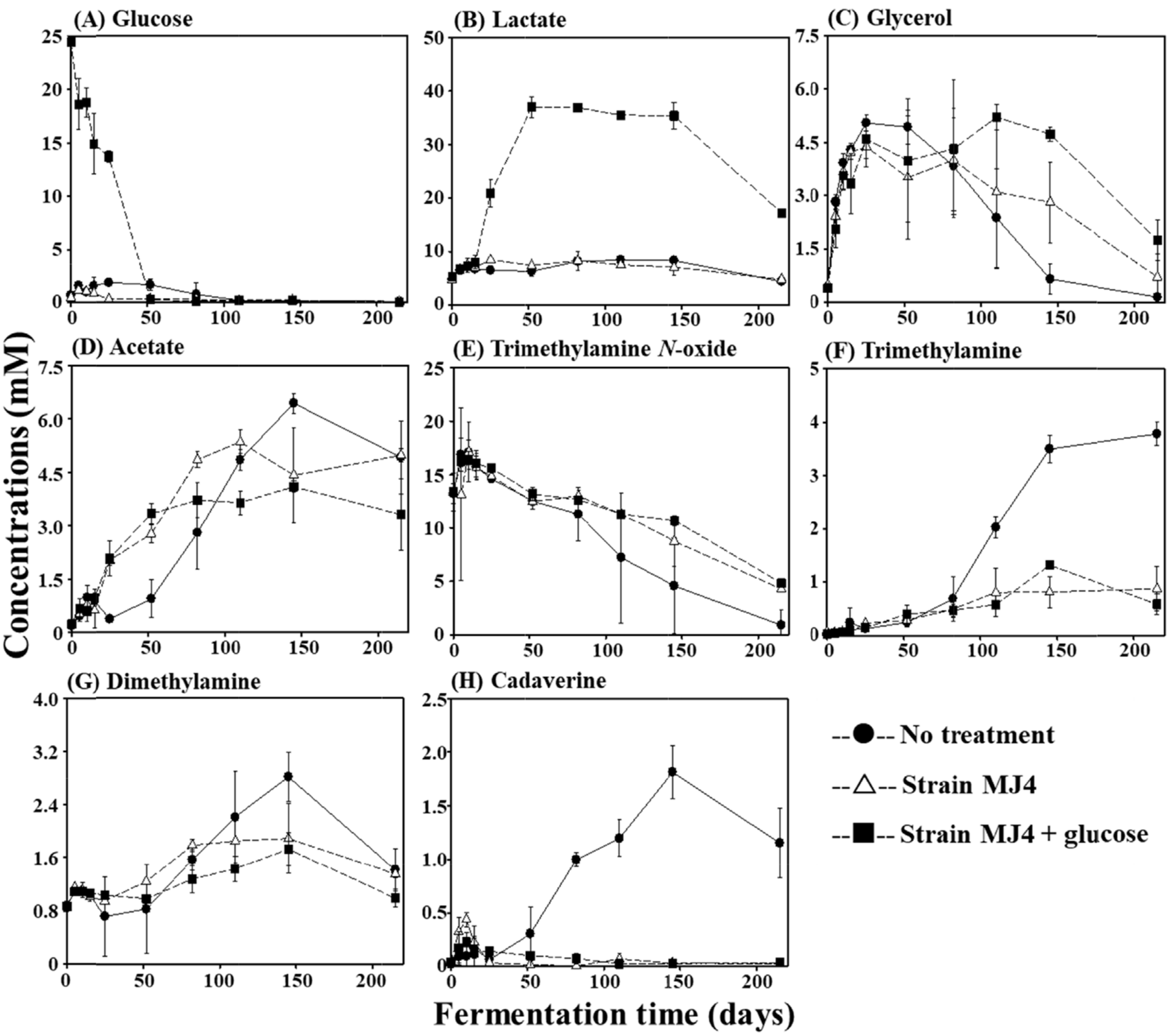

Fig. 6. Changes in major carbohydrate, organic acids, and amine concentrations identified from saeu-jeot samples fermented with/without *T. halophilus* MJ4 and with/without glucose supplementation. Data are indicated as mena values ± standard deviations, measured in triplicate. The concentrations were quantified using Chenomx NMR suite (ver. 6.1) with 2,2-dimethyl-2-silapentane-5-sulfonate (DSS) as an internal standard.

In particular, in saeu-jeot with MJ4 inoculation and glucose addition, *Tetragenococcus* was predominant in the bacterial community without the growth of *Staphylococcus* and *Salimicrobium*. Species level analysis of the *Tetragenococcus* members showed that in saeu-jeot without strain MJ4 inoculation, sequencing reads classified as *T. muriaticus* were dominant during the end of fermentation, while in saeu-jeot with strain MJ4 inoculation, sequencing reads classified as *T. halophilus* were predominant during the entire fermentation period and sequencing reads classified as *T. muriaticus* were rarely detected (Fig. 3B). These results suggest that the use of strain MJ4 as a starter culture can repress the growth of undesirable microorganisms including *T. muriaticus*, a known BA producer, during salted food fermentation.

The PCA of all ^{1}H NMR peaks representing total saeu-jeot metabolites showed that the metabolite profiles in saeu-jeot without glucose addition were relatively similar regardless of MJ4 inoculation as a starter culture during fermentation (Fig. 4). The pH profiles in saeu-jeot without glucose addition were also relatively similar regardless of strain MJ4 inoculation, probably indicating their similar metabolite profiles (Fig. 2A). These results suggest that the use of strain MJ4 as a starter culture does not make a big impact on saeu-jeot metabolites if an external carbon source is not supplied.

The generation of amino acids from proteins by proteolysis during food fermentation is important because amino acids influence the taste and flavor of fermented foods. It was previously reported that *Tetragenococcus* strains may be associated with amino acid production by aminopeptidases (Udomsil et al., 2010). However, other reports found that bacterial proteinases may not play an important role in amino acid production during salted fish fermentation (Lee et al., 2014a, 2014b; Jung et al., 2016a). In our study, metabolite analysis using ^{1}H NMR showed that amino acids were identified as the major metabolites of saeu-jeot in all fermentation conditions (Fig. 5). Interestingly, the profiles of amino acids were relatively similar during the entire saeu-jeot fermentation period regardless of MJ4 inoculation or glucose addition, although viable cell numbers were different (Fig. 2B), which suggests that *Tetragenococcus* strains may not be greatly involved in amino acid production during salted fish fermentation like previous studies (Lee et al., 2014a, 2104b; Jung et al., 2016a).

Carbon compound analysis showed that glucose decrease was stoichiometrically correlated with the increase in lactate in saeu-jeot with MJ4 inoculation and glucose addition (Fig. 6A and B), suggesting that *Tetragenococcus* metabolizes glucose to lactate through the homofermentative lactic acid pathway. Glycerol level increased rapidly and to similar levels regardless of MJ4 inoculation or glucose addition during the early fermentation period (Fig. 6C), which suggests that the glycerol increase may be not related to the presence of *Tetragenococcus*. The decrease in glycerol and increase in acetate levels in saeu-jeot without strain MJ4 inoculation were a little late compared to those in saeu-jeot with strain MJ4 inoculation and the acetate increases were relatively well associated with *Tetragenococcus* (Figs. 2B and 3A), suggesting that *Tetragenococcus* strains might play an important role in the production of acetate from glycerol. Because carbohydrates were rarely detected in saeu-jeot without glucose addition, it is assumed that glycerol may be a major carbon source for the growth of *Tetragenococcus* strains and acetate may be a major organic acid in saeu-jeot without an external carbon source addition. Cadaverine was identified as the dominant BA in saeu-jeot without strain MJ4 inoculation after 52 days of fermentation (Fig. 6H), which was generally well-associated with the profile of sequencing reads classified as *T. muriaticus* (Fig. 3B), suggesting that *T. muriaticus* might be a causative agent of cadaverine formation in saeu-jeot fermentation of this study. However, the production of TMA and cadaverine in saeu-jeot with strain MJ4 inoculation was significantly lower than that in non-treated saeu-jeot (Fig. 6F and H), which suggests that strain MJ4 can repress the formation of BAs during salted food fermentation.

5. Conclusion

A strain of *Tetragenococcus halophilus* was found to be non-BA producing and prevent the production of BAs by other *Tetragenococcus* strains. This study suggests confirms the hypothesis that the use of strain MJ4 as a starter culture in salted fish fermentation may be a good strategy to reduce BA formation during fermentation. However, further researches on the safety properties of strain MJ4 and the sensory (tastes and flavors) profile of salted foods fermented by strain MJ4 will be necessary for prior to its use as a starter culture.

Conflicts of interest

The authors have no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fm.2019.02.017.

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