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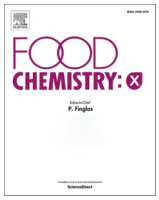

Innovative enhancement of flavor profiles and functional metabolites composition in *Pandanus amaryllifolius* through lactic acid bacteria fermentation

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ABSTRACT

Pandanus amaryllifolius, known as Pandan, serves as a coloring agent and spice in food. The effects of lactic acid bacteria (LAB) on Pandan are underexplored. This study aimed to investigate changes in physicochemical properties, antioxidant activity, volatile compounds and metabolites of Pandan fermented with *Lactobacillus acidophilus*, *Levilactobacillus brevis* and *Lacticaseibacillus rhamnosus*. Fermented Pandan showed increased total phenol (13 %–21 %) and flavonoid (33 %–53 %) content. Pandan fermented with L. *rhamnosus* exhibited significantly higher antioxidant activity, followed by those fermented with *L. brevis* and L. *acidophilus*. Key components like naringenin and volatile compounds such as α-ionone significantly increased after fermentation, with the production of new compounds, including damascenone and linalool. These compounds enhance the flavor and functional properties of fermented Pandan. This research lays a foundation for developing novel LAB-fermented Pandan products.

1. Introduction

Pandanus amaryllifolius (Pandan) is a perennial herb and the only aromatic plant in the Pandanaceae family (Routray & Rayaguru, 2010). It is widely distributed in South Asian and Southeast Asian countries, including India, Sri Lanka, Malaysia and Singapore. Often used as food colorants and spices, pandan can be applied fresh or as juice and has become popular in Asian cuisines for its green hue and flavor. Furthermore, it is an important medicinal plant that has anti-inflammatory, antioxidant, antiproliferative, hepatoprotective, antidiabetic, antibacterial and antiviral activities (Tan et al., 2022). The volatile flavor components of Pandan are hexan-2-one, 3-methyl-2(5H)-furanone, nonan-2-one, benzaldehyde and linalool. Additionally, Pandan contain essential oils, carotenoids, tocopherols, tocotrienols, alkaloids, fatty acids and esters (Routray & Rayaguru, 2010). Pandan is also rich in functional compounds such as polyphenols, alkaloids, flavonoids, saponins and tannins (Nguyen et al., 2021). These components contribute significantly to the distinctive fragrance and potential health benefits of Pandan.

Lactic acid bacteria (LAB) fermentation enhances the bioactive components, functional properties, antimicrobial activity, flavor and bioavailability of fermented food. Fermented plant products are functional liquids or solids produced by probiotics via fermentation of one or more fresh vegetables, fruits, mushrooms, herbs, etc. The preparation of fermented plant-based beverages presents great potential in the development of new functional products. Fermented plant products possess many functional properties, such as antioxidation, bacteriostasis, improved intestinal function and immunity, antialcohol and liver protection (Zhang et al., 2021). The antioxidant activity and total phenol content increased in mixed vegetable juice from cabbage, broccoli, carrot and beetroot fermented by *Companilactobacillus allii* WiKim39 and *Lactococcus lactis* WiKim0124 (Lee et al., 2021). The antioxidant activity

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increased in Cerasus humilis juice fermented with *Lactobacillus acidophilus* and *Lactobacillus plantarum*. Moreover, the abundance of probiotics increased in the gut microbiota after in vitro digestion (Li et al., 2023). The contents of total phenols, total flavonoids, free amino acids and flavor nucleotides increased in rose shiitake mushroom beverages fermented by *Lactobacillus plantarum* 90, *Lactobacillus plantarum* N13, *Lactobacillus plantarum* CN2018, *Lactobacillus rhamnosus* 05 and *Lactobacillus paracasei* 86 (Qiu et al., 2023). Additionally, the total phenol content and antioxidant activity significantly increased in honeysuckle extracts fermented with *L. plantarum* and L. *acidophilus* (Ran et al., 2024). Fermentation is also used to increase shelf-life and nutritional and organoleptic qualities and removes undesirable compounds from primary food substrates. Research on the effects of specific LAB fermentation methods on the quality of Pandan is limited. On the basis of our previous research, *Lactobacillus. acidophilus* CCTCC CB 20081799, *Levilactobacillus. brevis* CICC 20014, and *Lacticaseibacillus. rhamnosus* Gorbach Goldin ATCC 53103 were selected for fermentation of Pandan.

The aims of this study were to reveal the changes in the physicochemical properties, antioxidant activity, volatile flavor compounds and metabolites of Pandan fermented by these three lactic acid bacteria., prepare mixed starter cultures and develop high-quality fermented Pandan products with unique characteristics.

2. Materials and methods

2.1. Experimental raw materials and strains

The freeze-dried Pandan powder was obtained from Xingke Company (Wanning, Hainan, China). *Lactobacillus. acidophilus* CCTCC CB 20081799 and *Levilactobacillus*. *brevis* CICC 20014 were obtained from the China National Microbiology Resource Center (Beijing, China). *Lacticaseibacillus. rhamnosus* Gorbach Goldin ATCC 53103 was obtained from Christian Hansen. For activation, MRS was used to culture L. *acidophilus*, L. *brevis* and *L. rhamnosus*. The MRS broths were incubated at 37 °C for 16 h. For the preparation of the inoculum, the cultures were centrifuged (6000 ×*g*, 4 °C, 10 min) and washed twice with sterilized PBS (0.03 mol/L, 7.2). Each culture was suspended in PBS (0.03 mol/L, 7.2) to a final concentration of 5 log CFU/mL.

2.2. Fermentation of the Pandan liquid

Pandan liquid was prepared with freeze-dried Pandan powder (20 g) and distilled water (100 mL). The mixture was sterilized at 95 °C for 15 min. L. *acidophilus*, *L. brevis*, and L. *rhamnosus* were inoculated into three groups of identical Pandan liquid, each with an inoculum volume of 2 % (*v*/v), thoroughly mixed and subsequently incubated at 37 °C for 24 h. Samples collected at 0 h and 24 h of fermentation were subjected to subsequent analysis.

2.3. Analysis of physiochemical properties

The pH was measured via a pH meter (Metrohm, Herisau, Switzerland). The reducing sugar content was deter-mined by the 3,5-dinitrosalicylic acid colorimetric method. The total phenolic content (TPC) and total flavonoid content (TFC) were determined according to the methods of Wu et al. (2020). The TPC was expressed as mg of gallic acid equivalents per gram (mg GAE/g). TFC was expressed as mg rutin equivalents per gram (mg RE/g). Viable cell counts were determined via the standard plate count method (Fu et al., 2023).

2.4. Antioxidant activity assay

The determination of DPPH radical scavenging activity was conducted following the method of Sun, Zhang, et al. (2022). The results are expressed as mg of ascorbic acid equivalents per gram (mg AAE/g). The ABTS radical scavenging activity was determined according to a modified method described Sun, Zhang, et al. (2022) previously. The sample (200 μL) was mixed with ABTS solution (800 μL) and reacted in the dark at 25 °C for 30 min. Absorbance was measured at 734 nm. The results are expressed as mg of ascorbic acid equivalents per gram (mg AAE/g). The determination of FRAP followed a modified method of Gu et al. (2019). Acetate buffer (0.3 mol/L, pH 3.6), TPTZ (10 mmol/L) and $FeCl_3$ (20 mmol/L) were mixed at a ratio of 10:1:1 to prepare the FRAP solution, which was allowed to react at 37 °C for 30 min. Samples (20 μL) were mixed with the dye mixture (380 μL) and incubated at 37 °C for 20 min. The absorbance was measured at 593 nm. The results are reported as milligrams of ascorbic acid equivalents per gram (mg AAE/g).

2.5. Analysis of volatile flavor compounds

The volatile flavor compounds were analyzed via Agilent Technologies 7890/7000 A GC-QQQ-MS according to the methods of Hou et al. (2020). For the gas chromatographic system, an HP-5MS capillary column (30 m × 0.25 mm, 0.25 μm film thickness) was used. The inlet temperature was maintained at 250 °C. The flow rate of the carrier gas (He) was 1 mL/min. The split ratio was 5:1. The column temperature was maintained at 35 °C for 5 min and then increased to 60 °C at a rate of 6 °C/min for 1 min. Then, the column temperature was increased to 140 °C at a rate of 3 °C/min and maintained for 1 min. Finally, the column temperature was increased to 240 °C at a rate of 7 °C/min and maintained for 3 min. The triple quadrupole mass spectrometer was operated in full-scan mode. The temperature of the electron ionization source was 230 °C. The ionization voltage was 70 eV, and the solvent delay was 3 min. Data acquisition was set within a *m/z* range of 50–450.

2.6. Analysis of metabolites

The solid samples (10 mg) were extracted in a solution (400 μL) of methanol:water (4:1, *v*/v) with 0.02 mg/mL L-2-chlorophenylalanine as an internal standard. The extracts were subsequently centrifuged (13,000 ×*g*, 4 °C, 15 min). The supernatants were analyzed by LC–MS/MS via a UPLC system (Vanquish, Thermo Fisher Scientific). A 2 μL aliquot of each sample was injected onto a UPLC HSS T3 column (2.1 mm × 100 mm, 1.8 μm) with the sample tray maintained at 4 °C.

The Orbitrap Exploris 120 mass spectrometer was chosen for its information-dependent acquisition (IDA) mode governed by the acquisition software (Xcalibur, Thermo). The acquisition software continuously evaluated the full-scan MS spectrum in this mode. The mobile phases consisted of water with 0.1 % formic acid: acetonitrile (95:5, *v*/v) (solvent A) and acetonitrile with 0.1 % formic acid: isopropanol: water (47.5:47.5:5.0, v/v) (solvent B). The solvent gradient changed according to the following conditions: 0–3.5 min, 0–24.5 % B; 3.5–5 min, 24.5–65 % B; 5–5.5 min, 65 %–100 % B; 5.5–7.4 min, 100 %–100 % B; 7.4–7.6 min, 100 %–51.5 % B; 7.6–7.8 min, 51.5–0 % B; 7.8–10 min, 0 %–0 % B. The sample injection volume was 2 μL and the flow rate was set to 0.4 mL/min. The column temperature was maintained at 40 °C. The ESI source conditions were set as follows: sheath gas flow rate of 50 Arb, aux gas flow rate of 13 Arb, capillary temperature of 320 °C, full MS resolution of 60,000, MS/MS resolution of 7500, collision energy of 20/40/60 in NCE mode, and spray voltage of 3.5 kV (positive) or − 3.5 kV (negative). An in-house MS2 database (BiotreeDB) was used for metabolite annotation.

2.7. Data analysis

All the experiments were conducted three times, and the data are expressed as the means ± standard deviations. The differences in the mean values among all samples were determined via one-way analysis of variance (ANOVA) followed by Duncan's test, where $P < 0.05$ indicated significance. Principal component analysis (PCA) and partial least squares-discriminant analysis (PLS-DA) were performed to visualize the discrimination among samples via SIMCA 14.1. Other data and

visualizations were processed via Origin software (OriginLab Corporation, Northampton, MA, USA).

3. Results

3.1. Physicochemical properties

The physicochemical properties of fermented Pandan (FP) and unfermented Pandan (UFP) were assessed (Table 1). The pH significantly decreased in FP ($P < 0.05$), ranging from 3.73 to 3.85, with the most significant decrease in FP by L. *acidophilus*. The viable cell counts of L. *acidophilus*, L. *brevis* and *L. rhamnosus* were 8.18 ± 0.03 log CFU/mL, 8.64 ± 0.02 log CFU/mL and 8.68 ± 0.02 log CFU/mL, respectively, in FP. The reducing sugar content significantly decreased in FP, particularly in FP by L. *acidophilus*, at 6.75 ± 0.09 mg/g, indicating a 71 % decrease compared with that in the UFP.

3.2. Changes in volatile flavor compounds

Thirty-three volatile flavor compounds were detected in the UFP. Furthermore, 39, 39 and 45 volatile flavor compounds were detected in FP by L. *acidophilus*, *L. brevis* and *L. rhamnosus*, respectively. Compared with UFP, 17 new volatile flavor compounds were detected in FP by *L. acidophilus*, including 3,4-dimethyl-benzaldehyde, 2-methoxy-4-vinylphenol and butylated hydroxytoluene; 15 new volatile flavor compounds were detected in FP by L. *brevis*, such as linalool, 9,12,15-octadecatrienoic acid ethyl ester and benzylalkohol; and 19 new volatile flavor compounds, such as ethyl caprate, hexadecanoic acid ethyl ester and n-decanoic acid, were detected in FP by L. *rhamnosus*. The relative abundance of volatile flavor compounds changed significantly in UFP and FP (Fig. 1A). Compared with UFP, ketones were notably predominant in FP, comprising approximately 30 % of the volatile flavor compounds. The relative abundance of ester components increased markedly, ranging from 10 % to 18 %. Conversely, the relative abundance of aldehydes significantly decreased, with the most obvious decrease in FP caused by L. *acidophilus*. The relative abundances of alcohols and phenols remained relatively stable, with alcohols accounting for approximately 6 % of the volatile flavor compounds.

To analyze the differences in metabolites among the four groups of samples, a PLS-DA model was established for comparisons (Fig. 1B). Compared with those in UPF, the profiles of volatile flavor compounds in FP were significantly different. On the basis of the results of PLS-DA model analysis, compounds with VIP > 1 and $P < 0.05$ were identified as differential volatile flavor compounds. A total of 25 differential volatile flavor compounds were identified in FP, comprising 7 aldehydes, 7 ketones, 1 alcohol, 2 acids, 5 esters, 1 phenol and 2 other compounds. Hierarchical clustering on the basis of concentration changes clearly distinguished between different sample groups (Fig. 1C).

Ketones emerged as the primary differential volatile flavor compounds generated in FP, constituting the highest proportion (26.32 %) of the total volatile flavor compounds. Among the ketones, 3-methyl-2-(5H)-furanone was the most prominent, accounting for 38.03 % of the total ketones. (E, E)-3,5-Octadien-2-one, 3-methyl-2(5H)-furanone and α-ionone were detected in FP and UFP. The relative abundances of (E, E)-3,5-octadien-2-one and α-ionone increased in FP treatment compared with those in the UFP treatment, whereas the relative abundance of isophorone decreased. Moreover, new ketone compounds, such as 6-methyl-5-hepten-2-one, are produced in FP by L. *acidophilus*, L. *brevis* and L. *rhamnosus*.

Among the aldehydes, (E)-2-hexenal and benzaldehyde were detected in the UFP and FP. Compared with those in UPF, the relative abundances of these two volatile flavor compounds were lower in FP caused by L. *acidophilus*, *L. brevis* and *L. rhamnosus*. Hexanal, octanal and nonanal were exclusively detected in the UFP. 3,4-Dimethylbenzaldehyde was newly generated in FP by L. *acidophilus*. Furfural was absent in FP of L. *acidophilus,* but it was present in the UFP and FP of L. *brevis* and *L. rhamnosus*. Benzaldehyde and (E)-2-hexenal were the predominant aldehydes in FP, accounting for 31.76 % and 29.22 % of the total aldehydes, respectively.

Among esters, dihydroactinidiolide can be detected in both FP and UFP. Ethyl 2-(5-methyl-5-vinyltetrahydrofuran-2-yl) propan-2-yl carbonate was a newly generated volatile flavor compound in FP. Ethyl 2-(5-methyl-5-vinyltetrahydrofuran-2-yl) propan-2-yl carbonate is a significant volatile ester, comprising 75.65 % of the total ester compounds. Ethyl caprate and hexadecanoic acid ethyl ester were exclusively detected in FP by L. *rhamnosus*.

(E)-3-hexenoic acid and n-decanoic acid were newly generated in FP. Linalool was also newly generated in FP. The abundance of phenolic volatile flavor compounds was relatively low. Phenol was present in FP and UFP, and its relative abundance increased in FP by L. *acidophilus*, L. *brevis* and *L. rhamnosus*. Notably, 3,4,4a,5,6,8a-hexahydro-2,5,5,8a-tetramethyl-2H-1-benzopyran accounted for 79.81 % of the total other volatile flavor compounds.

3.3. Changes in metabolites

A total of 4528 kinds of metabolites were identified in UFP. A total of 4520, 4522 and 4529 metabolites were identified in FP by L. *acidophilus*, *L. brevis* and *L. rhamnosus*, respectively. Compared with UFP, L. *acidophilus* and *L. brevis* generated 73 new metabolites in FP, and 77 new metabolites were generated in FP by L. *rhamnosus*. Lipids and lipid-like molecules, as well as organic acids and their derivatives, were the most significant metabolites in FP, accounting for 25.75 % and 17.60 % of the total metabolites, respectively (Fig. 2A).

Metabolites in different fermentation groups were further analyzed via PCA. The results revealed that the first two principal compounds accounted for 70.3 % of the total variance (PC1, 59.5 %; PC2, 10.8 %) (Fig. 2B). Furthermore, PLS-DA can better achieve effective separation of samples between groups (Fig. 2C). PC1 and PC2 explained 76.3 % and 8.62 % of the total variance, respectively. These results indicated that there were significant differences in metabolites among the four groups.

On the basis of the results from PLS-DA, differentially abundant metabolites were further selected with the criteria of VIP > 1.00, $P < 0.05$ and FC > 1.50. Fifty key metabolites (either with greater relative abundance or greater differences) were screened in FP, and hierarchical clustering was performed on each sample group on the basis of changes in relative abundance (Fig. 2D). Organic acids and their derivatives were the most abundant metabolites in FP. Malic acid, succinic acid and citric acid were the major organic acids. Compared with that of UFP, the relative abundance of succinic acid was significantly greater in FP by L. *acidophilus*, L. *brevis* and *L. rhamnosus*, with the highest relative abundance in FP by L. *brevis*. However, the relative abundance of citric acid was lower in FP than in the UFP, with a decrease of approximately 20 %. The relative abundance of most amino acids, including L-leucine and L-tyrosine, decreased in FP by L. *acidophilus*, *L. brevis* and *L. rhamnosus*.

Table 1
Physicochemical properties in different groups.

Physicochemical properties	pH	Viable count (log CFU/mL)	Reducing sugar (mg/g)
LA	3.73 ± 0.09^{b}	8.18 ± 0.03^{b}	6.75 ± 0.09^{b}
LB	3.83 ± 0.02^{b}	8.64 ± 0.02^{a}	7.32 ± 0.11^{b}
LGG	3.85 ± 0.04^{b}	8.68 ± 0.02^{a}	7.79 ± 0.15^{b}
UFP	5.44 ± 0.10^{a}	–	23.87 ± 1.28^{a}

The different superscripts in the same column mean significant differences ($P < 0.05$). Pandan fermented by *L.acidophilus* (LA), *L. brevis* (LB), *L. rhamnosus* (LGG) and unfermented pandan (UFP).

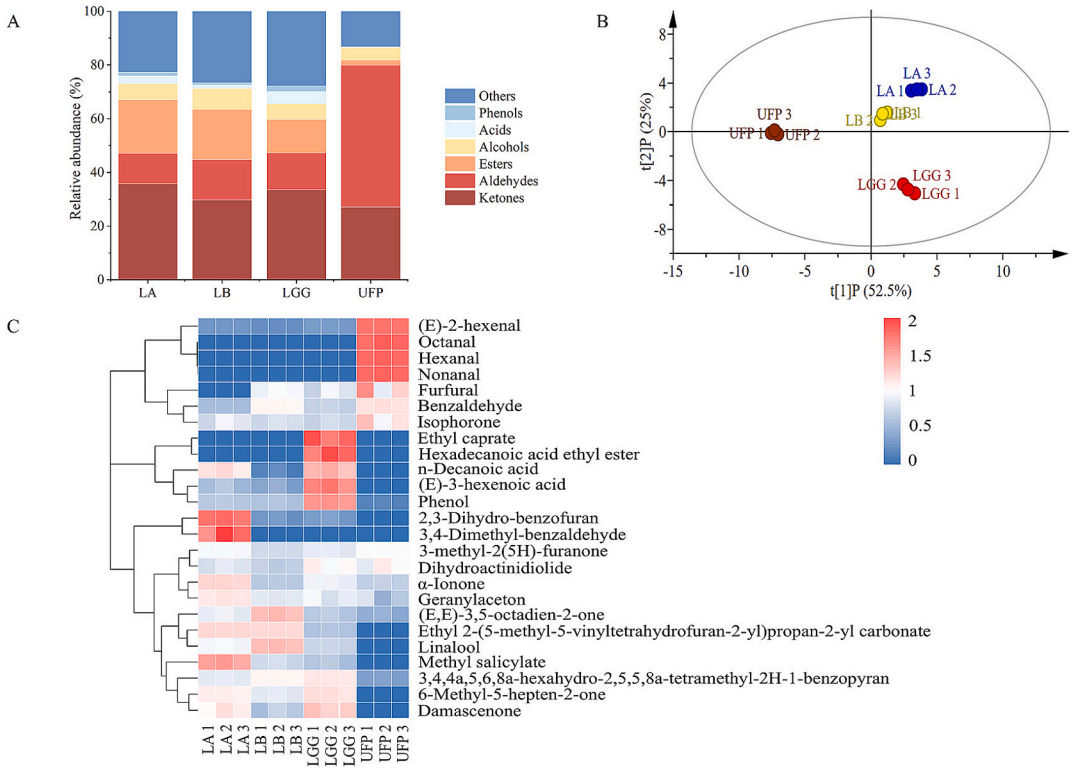

Fig. 1. Relative abundance of each type of volatile flavor metabolite (A). Partial least squares-discriminant analysis (PLS-DA) score plots of volatile flavor metabolites (B). Heatmap of clustering analysis of volatile flavor metabolites (C). Pandan fermented by L. *acidophilus* (LA), *L. brevis* (LB), *L. rhamnosus* (LGG) and unfermented pandan (UFP).

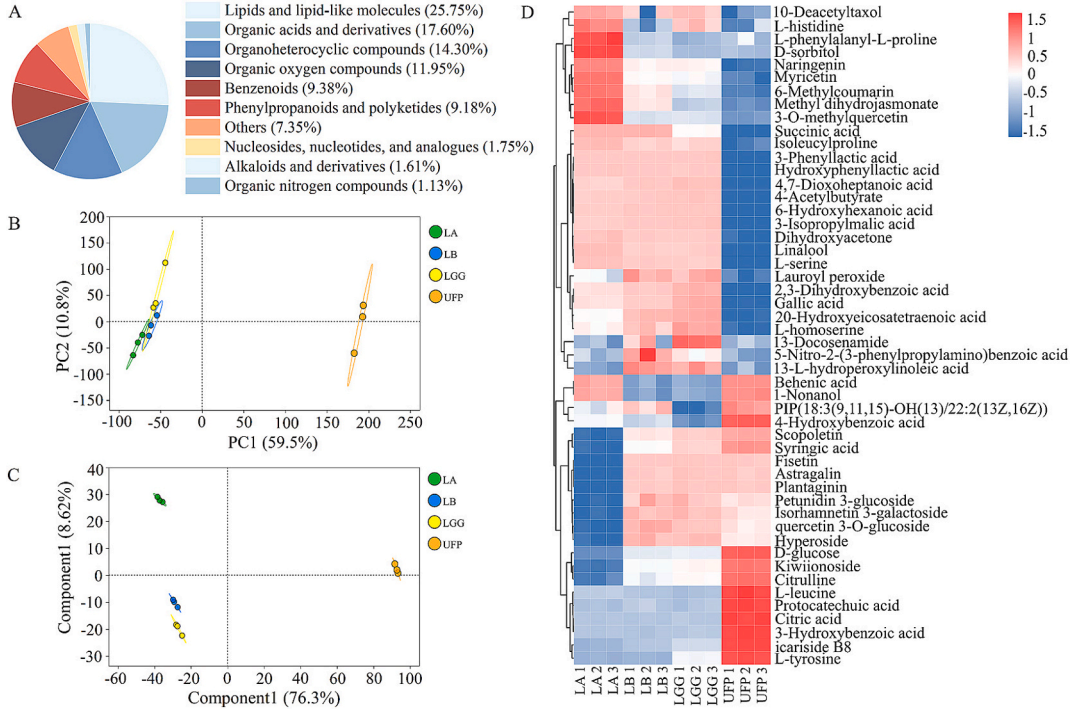

Fig. 2. Metabolite classification (A). Principal component analysis (PCA) and partial least squares-discriminant analysis (PLS-DA) score plots of the metabolites (B: PCA, C: PLS-DA). Heatmap of the results of the clustering analysis of the metabolites (D). Pandan fermented by *L. acidophilus* (LA), *L. brevis* (LB), *L. rhamnosus* (LGG) and unfermented pandan (UFP).

Conversely, the relative abundances of L-histidine and L-serine increased in FP.

The phenylpropanoids and polyketides included 8 flavonoids, 2 phenylpropanoic acids and 2 coumarins and their derivatives. Flavonoids include mainly myricetin, naringenin, hyperoside, 3-*O*-methylquercetin and astragalin. 6-Methylcoumarin and scopoletin are coumarins, whereas 3-phenyllactic acid and hydroxyphenyllactic acid are phenylpropanoid acids. The relative abundance of scopoletin decreased in FP by L. *acidophilus*, L. *brevis* and *L. rhamnosus*. The relative abundances of 3-phenyllactic acid, myricetin, 3-*O*-methylquercetin, naringenin and 6-methylcoumarin increased in FP. Specifically, the relative abundance of 3-phenyllactic acid increased by approximately 50 % on average. The relative abundances of myricetin, 3-*O*-methylquercetin, naringenin and 6-methylcoumarin were the highest in FP caused by L. *acidophilus*, whereas the relative abundance of astragalin decreased in FP by *L. acidophilus*. There was no significant change in the relative abundance of hyperoside in the UFP and FP.

The key metabolites of the benzene compounds included gallic acid, protocatechuic acid, syringic acid and 3-hydroxybenzoic acid. The relative abundance of most of these metabolites decreased in FP. The relative abundance of gallic acid increased in FP by L. *acidophilus*, L. *brevis* and *L. rhamnosus*, with the highest relative abundance in FP by L. *rhamnosus*.

The key metabolites of lipids and lipid-like compounds included 4-acetylbutyrate, 13-l-hydroperoxylinoleic acid, 3-isopropylmalic acid, linalool, behenic acid, 1-nonanol and methyl dihydrojasmonate. Compared with those of the other metabolites, the relative abundances of 4-acetylbutyrate, 13-l-hydroperoxylinoleic acid and 3-isopropylmalic acid increased in FP by *L. acidophilus*, L. *brevis* and *L. rhamnosus*. The relative abundance of 3-isopropylmalate was the highest in FP by L. *rhamnosus*, with a relative increase in abundance of 119 %.

3.4. Phenolic profile and antioxidant activities

Twenty phenolic compounds (VIP > 1.00, $P < 0.05$), including 10 phenolic compounds and 10 flavonoid compounds, were screened from the metabolites. Hierarchical clustering was performed on each sample group on the basis of changes in relative abundance (Fig. 3A). The relative abundances of hesperidin, 3,4-dihydroxymandelic acid, 2-(2-amino-3-methoxyphenyl)-4H-1-benzopyran-4-one and coniferyl aldehyde decreased in FP by L. *acidophilus*, L. *brevis* and *L. rhamnosus*. However, the relative abundances of peonidin-3-glucoside, luteolin, myricetin, 3-*O*-methylquercetin, naringenin, sinapyl alcohol, coniferyl alcohol and oleacein were the highest in FP by L. *acidophilus*. The relative abundance of quercetin 3-O-glucoside was the highest in FP by L. *brevis*, and the relative abundance of hydroquinone was the highest in FP with L. *rhamnosus*.

TPC and TFC were greater in FP than in the UFP (Fig. 3B). The TPC was 11.07 ± 0.00, 10.32 ± 0.16 and 10.46 ± 0.09 mg GAE/g in FP by *L. acidophilus*, L. *brevis* and *L. rhamnosus*, respectively. Compared with that of UFP, the TPC of FP caused by L. *acidophilus* was the highest, increasing by 1.94 mg GAE/g. The TFC were 9.57 ± 0.26, 9.90 ± 0.22 and 10.97 ± 0.30 mg RE/g in FP by *L. acidophilus*, *L. brevis* and *L. rhamnosus*, respectively. The TFC was the highest in FP by L. *rhamnosus*, increasing by 53 % compared with the UFP.

Compared with that of UFP, the ABTS radical scavenging activity of FP was greater (Fig. 3C). The ABTS radical scavenging activity was 18.11 ± 0.08, 18.20 ± 0.20 and 18.11 ± 0.33 mg AAE/g in FP by *L. acidophilus*, L. *brevis* and *L. rhamnosus*, respectively. The results showed that the ABTS radical scavenging activity increased by approximately 15 % on average in FP. Correlation analysis indicated that the ABTS radical scavenging activity was highly correlated with the TPC ($R^2 = 0.894$, $P < 0.01$) and TFC ($R^2 = 0.912$, $P < 0.01$) (Fig. 3D). Moreover, the DPPH radical scavenging activity and FRAP were correlated with the TFC ($R^2 = 0.704$, $P < 0.05$; $R^2 = 0.694$, $P < 0.05$). Compared with those of UFP, the DPPH radical scavenging activity and FRAP were greater in FP. The DPPH radical scavenging activity was the highest in FP by L. *rhamnosus* (5.04 ± 0.15 mg AAE/g), followed by those of L. *acidophilus* and L. *brevis*. FRAP was the highest in FP by L. *brevis* (5.24 ± 0.06 mg AAE/g), while it was the lowest in FP by L.

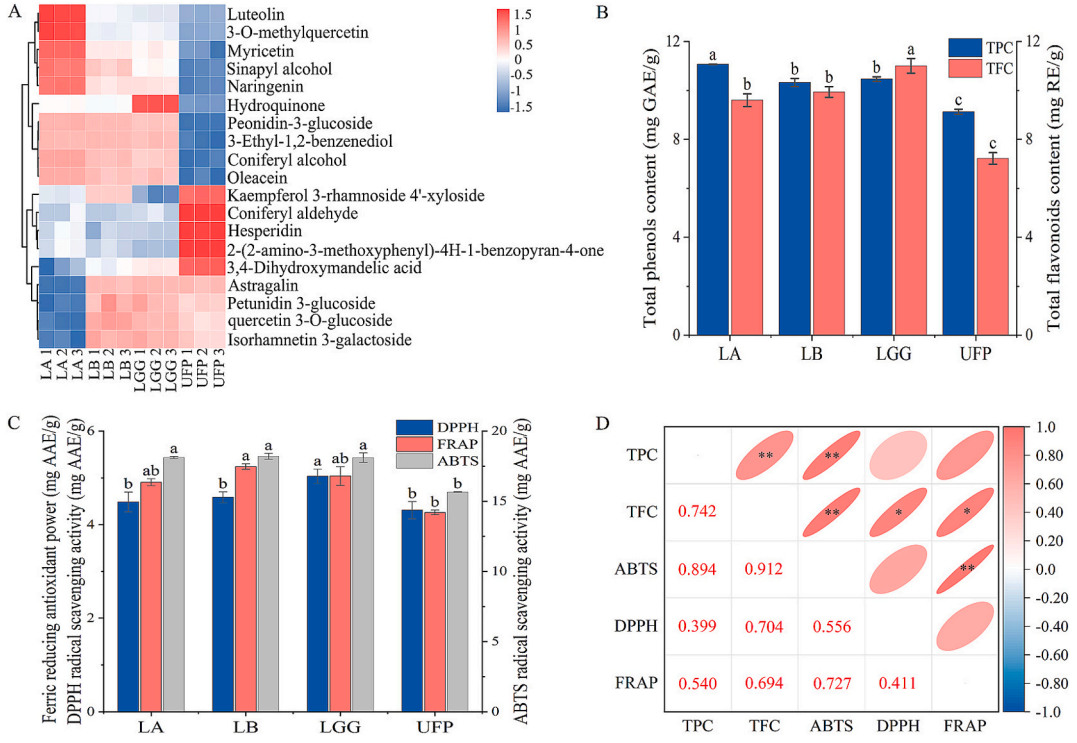

Fig. 3. Heatmap of clustering analysis of phenolic compounds (A). TPC and TFC contents (B). Antioxidant activity (C). Pearson correlation of phytochemical concentration and antioxidant activity (D). Pandan fermented by *L. acidophilus* (LA), *L. brevis* (LB), *L. rhamnosus* (LGG) and unfermented pandan (UFP).

acidophilus (4.91 ± 0.07 mg AAE/g). In general, the antioxidant activity of FP with L. *acidophilus*, *L. brevis* and *L. rhamnosus* improved. The antioxidant activity was the highest in FP by *L. rhamnosus*.

3.5. KEGG pathway enrichment

On the basis of the KEGG database, different metabolites were associated with specific metabolic pathways, and enrichment analysis identified essential metabolic pathways of differentially abundant metabolites. Most enriched KEGG pathways were related to amino acid metabolism. Unlike UFP, the fermentation process of L. *acidophilus* involves primarily tyrosine metabolism, galactose metabolism, phenylpropanoid biosynthesis, niacin and niacinamide metabolism, the biosynthesis of various plant secondary metabolites and tryptophan metabolism (Fig. 4A). The key metabolites in FP by L. *brevis* were involved in tyrosine metabolism; cysteine and methionine metabolism; folate biosynthesis; phenylpropanoid biosynthesis; tryptophan metabolism; valine, leucine and isoleucine biosynthesis; and phenylalanine metabolism (Fig. 4B). The most relevant metabolic pathways in L. *rhamnosus* fermentation included tyrosine metabolism; plant hormone signal transduction; arginine and proline metabolism; phenylalanine metabolism; valine, leucine and isoleucine biosynthesis; niacin and niacinamide metabolism; and galactose metabolism (Fig. 4C). A detailed analysis of the metabolic pathway enrichment of metabolites was conducted (Fig. 4D). The results revealed that tyrosine metabolism was the most differentiated pathway. LAB fermentation primarily affects amino acid metabolism, cofactor and vitamin metabolism, phenylpropanoid biosynthesis and the biosynthesis of other secondary metabolites in FP and UFP.

The metabolic profiles of the key metabolites were constructed via the KEGG database (Fig. 5). Galactose metabolism, tyrosine metabolism, the biosynthesis of various plant secondary metabolites and phenylpropanoid biosynthesis were the principal differential metabolic pathways. Galactitol is converted into sorbitol and sucrose, with sucrose further metabolized into D-glucose in the galactose metabolism pathway. Phosphoenolpyruvate synthesizes *L*-phenylalanine and pyruvate. *L*-phenylalanine can be converted into L-tyrosine, which further converts into 4-hydroxyphenylacetic acid and gentisic acid. In the biosynthesis of secondary metabolites, L-tyrosine generates 7-hydroxycoumarin and scopoletin.

4. Discussion

The viable cell counts of LAB reflect their growth status in pandan (Peng et al., 2021). The present study indicated that pandan is an ideal culture medium for the growth of L. *acidophilus*, L. *brevis* and *L. rhamnosus*. Compared with the UFP, the relative abundances of most volatile flavor compounds increased in FP, especially in FP by L. *acidophilus*. Octanal, hexanal and nonanal were not present in FP. Benzaldehyde and furfural emerged as the predominant volatile flavor components in FP. Benzaldehyde contributes to a pleasant, fruity aroma, and furfural imparts a sweet and almond-like aroma (Yang et al., 2022). Similarly, fewer aldehydes are present in fermented apricot juice (Sun, Zhao, et al. 2022). This result may be attributed to the instability of aldehyde compounds during LAB fermentation. Aldehyde compounds are readily reduced to alcohols or oxidized to acids in the food matrix (Di Cagno et al., 2017). Excessive aldehyde compounds negatively impact the overall aroma of food. The occurrence of beany off-aroma diminished in the soybean-based products fermented by *Lycoperdon pyriforme*. This was due to the degradation of aldehydes with high OAV values, such as hexanal and heptaldehyde, into alcohols or the synthesis of nonvolatile compounds (Nedele et al., 2022). In the present study, the

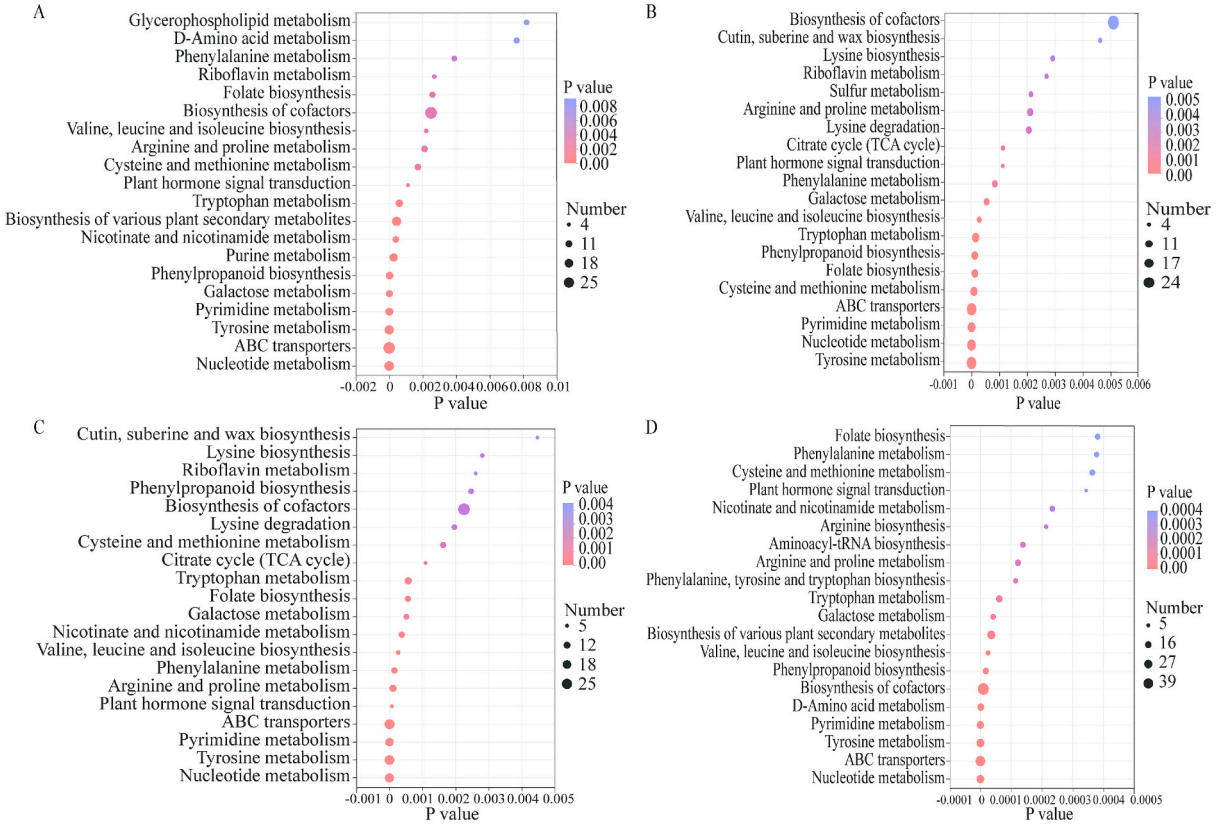

Fig. 4. Metabolic pathway enrichment analysis of differentially abundant metabolites between LA and UFP (A), between LB and UFP (B), and between LGG and UFP (C). Metabolic pathway enrichment analysis of the 4 groups of differentially abundant metabolites (D). The color and size of each circle are based on the *p* value and the pathway impact value, respectively. Pandan fermented by *L. acidophilus* (LA), *L. brevis* (LB), *L. rhamnosus* (LGG) and unfermented pandan (UFP).

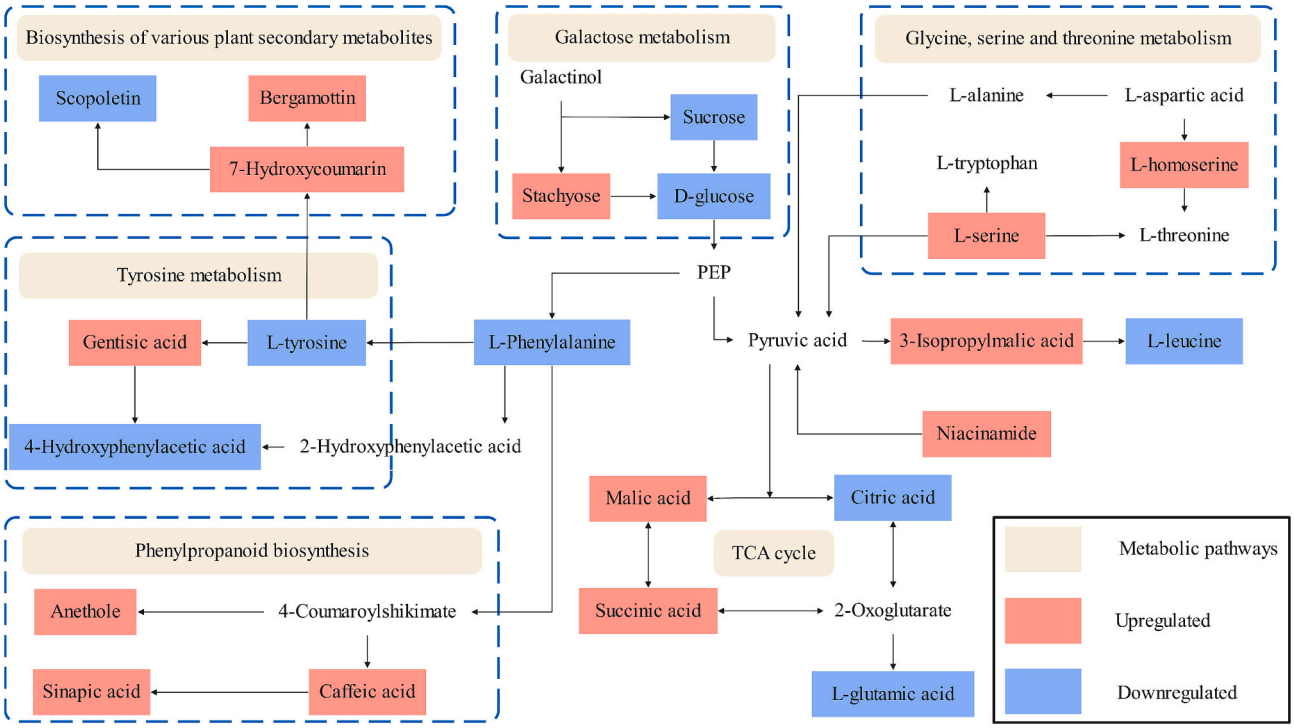

Fig. 5. The metabolic map of key metabolites during fermentation. The substances with frames are the differentially abundant metabolites, whereas the substances without frames are the intermediate metabolites in the metabolic pathway.

relative abundance of aldehydes was reduced in FP by L. *acidophilus*, *L. brevis* and *L. rhamnosus*. It potentially mitigated off-flavors and enhanced the overall flavor quality of FP.

The relative abundance of alcohol compounds significantly increased in FP, especially the newly generated linalool. Its relative abundance was the highest in FP by L. *brevis*. Alcohols are formed through ketone reduction, amino acid metabolism and fatty acid degradation (Bezerra et al., 2017). Linalool is an aromatic monoterpene alcohol with anti-cancer, antimicrobial, and anti-inflammatory properties and has potential as a safe alternative therapy (An et al., 2021). Methyl salicylate is an aromatic compound with medicinal properties and a wintergreen aroma in plants (Frick et al., 2023). Dihydroactinidiolide has been found to be responsible for the aroma of black tea and tobacco (Das et al., 2018). The sensory threshold values of the esters were low. These compounds are important for imparting pleasant flavors in fermented products (Reyes-Díaz et al., 2020). Many esters with fruity and floral aromas hid bitter and unpleasant odors caused by fatty acids and amines. In addition, the relative abundance of ketone flavor compounds, including 6-methyl-5-hepten-2-one, geranylaceton, damascenone and α-ionone, increased in FP. These flavor compounds with floral, fruity, rose-like and violet-like aromas potentially enhanced the pleasant aroma profile in FP.

Organic acids were significant components of the microbial metabolites in FP. The major organic acids included malic acid, succinic acid and citric acid in FP. The relative abundances of malic acid and succinic acid increased, whereas that of citric acid decreased. Succinic acid and citric acid are the main organic acids in Shenheling fermented by L. *fermentum* and exhibit similar patterns of upregulation and downregulation (Yan et al., 2023). Amino acids enhance the flavor characteristics of foods. A high level of amino acids contributed significantly to the taste of FP. L-serine, a sweet-tasting amino acid, is an important precursor for phospholipid synthesis. It can be used as a food additive to supplement essential nutrients in food and functional beverages (Teng et al., 2024). The relative abundance of L-serine increased by 1.26 times in FP in response to L. *acidophilus*. The relative abundance of L-histidine was the highest in FP treated with L. *acidophilus*. L-histidine is an essential proteinogenic amino acid in food. It plays significant roles in the food and pharmaceutical industries (Kim et al., 2024). Gentisic acid is associated with anti-inflammatory, hepatoprotective and antioxidant activities (Abedi et al., 2020). The relative abundance of gentisic acid increased by approximately 52 % in FP.

Most key metabolites exhibited diverse biological activities in FP. In this study, the relative abundance of 3-phenyllactic acid increased by approximately 56 % in FP due to L. *rhamnosus*. A study showed that 3-phenyllactic acid has efficient broad-spectrum antibacterial and antifungal activity. Researchers evaluated the ability of 13 strains of LAB to produce 3-phenyllactic acid and found that L. *rhamnosus* produced it at a higher level (Cortés-Zavaleta et al., 2014). Naringenin, one of the most well-known plant flavonoids with antioxidant properties, has been demonstrated to be produced by L. *acidophilus* through the degradation of naringenin-7-O-rutinoside (Guo et al., 2021). The relative abundance of naringenin increased by 1.28 times in FP in response to *L. acidophilus*. Gallic acid exhibits a variety of biological activities including antioxidant, anti-tumor, anti-inflammatory, and anti-bacterial properties. A study evaluated the fermentation performance of *Lactobacillus* spp. in strawberry puree and found that L. *brevis* increased the gallic acid content by 11.67 % (Yang et al., 2023). This finding aligns with the results of this study, which indicated that the relative abundance of gallic acid in FP increased by 14.09 % after fermentation with L. *brevis*. Quercetin, which also has powerful antioxidant activity, saw its relative abundance increased by 14 % as a result of FP with L. *acidophilus*. Another study employed L. *plantarum* and L. *acidophilus* to ferment Huyou peel and pomace, resulting in an increase of quercetin content by over 100 % (He et al., 2023). Additionally, myricetin, hyperoside and 6-methylcoumarin exhibited antioxidant and anti-inflammatory properties, with their relative abundance increasing in FP. These findings indicate that FP can be beneficial to human health.

The relative abundance of most of the phenolic compounds, such as myricetin, naringenin and 3-*O*-methylquercetin, which have antioxidant activity, increased in FP. The TPC and TFC significantly increased in FP. Compared with UFP, TPC was greater in FP caused by L. *acidophilus*, with an increase of 21.25 %. The TFC was the highest in FP by L.

rhamnosus, with an increase of 52.57 %. The TFC increased nearly 37 % in loquat juice fermented by L. *acidophilus* (Meng et al., 2022). The TFC increased 33.1 % in FP by L. *acidophilus* in this study. The breakdown of plant cell walls led to the release of various phenolic and flavonoid compounds during LAB fermentation (Meng et al., 2022). Furthermore, organic acids help mitigate the oxidative degradation of phenolic compounds. The TPC decreased by 15 % and 24 %, and the TFC decreased by 15.7 % and 23.9 % in cabbage juice fermented by L. *brevis* and L. *rhamnosus*, respectively (Jaiswal & Abu-Ghannam, 2013). Increases or decreases in TPC and TFC could depend on the type of starter culture strain and fermentation substrate. Therefore, the impact of LAB on the composition and contents of phenolic and flavonoid compounds should be considered comprehensively.

Phenolic compounds exhibit significant antioxidant activity as reducing agents, radical scavengers and singlet oxygen quenchers, this activity is mainly attributed to their ability to transfer hydrogen atoms or electrons to radicals (Verón et al., 2019). The antioxidant activity significantly increased in FP. Compared with that of UFP, the DPPH radical scavenging activity increased by 1.17 times in FP by L. *rhamnosus*. The DPPH radical scavenging activity increased by 1.04 times in walnut flowers fermented by L. *rhamnosus* (Ru et al., 2021). The DPPH radical scavenging activity increased by 1.62 times in mulberry juice fermented by L. *brevis* (Gong et al., 2023). The increase in DPPH radical scavenging activity suggested that LAB enhanced the availability of polyphenolic compounds with proton-supplying properties (Gulcin & Alwasel, 2023). The difference in ABTS radical scavenging activity may be related to the antioxidant content in UFP and FP. DPPH and ABTS radical scavenging activities are based on the electron transfer mechanism and hydrogen atom transfer mechanism, respectively. The ABTS radical scavenging activity significantly increased by 16.22 % in FP by L. *brevis*, followed by L. *acidophilus* and *L. rhamnosus,* with increases of 15.64 %. Therefore, LAB had a considerable positive effect on the ABTS radical scavenging activity of FP. ABTS free radical scavenging activity increased by 14.31 % and 13.83 % in black chokeberry fermented with L. *acidophilus* and *L. rhamnosus*, respectively (Wang et al., 2024). FRAP significantly increased in FP, with the most notable increase of 23 % in FP by *L. brevis*. FRAP increased by 11.76 % in apple juice fermented by L. *acidophilus* (Wu et al., 2020). This was attributed to the production of certain reducing agents during LAB fermentation, such as myricetin, hyperoside, 3-*O*-methylquercetin and 6-methylcoumarin. In one study, the antioxidant activity of 18 structurally different flavonoids was investigated, and quercetin and myricetin showed the highest FRAP values (Firuzi et al., 2005). Therefore, LAB fermentation is an important strategy for producing functional plant-based beverages.

5. Conclusion

Pandan is an excellent substrate for the growth of L. *acidophilus*, L. *brevis* and *L. rhamnosus,* with viable cell counts exceeding 8 log CFU/mL. The volatile flavor compounds primarily consisted of ketones and aldehydes. The most desirable volatile flavor compounds presented in FP by L. *rhamnosus*. The relative abundance of 6 compounds with better flavors, mainly α-ionone, dihydroactinidiolide and geranylaceton, was increased in FP by L. *rhamnosus*. Furthermore, 11 volatile flavor compounds, predominantly linalool, damascenone, and methyl salicylate, were newly detected. Lipids and lipid-like molecules as well as organic acids and their derivatives were the most significant metabolites in FP. L. *acidophilus* had the greatest effect on metabolites in FP. The relative abundance of 14 functional metabolites, including 3-phenyllactic acid, myricetin, 3-*O*-methylquercetin, naringenin and 6-methylcoumarin, increased in FP of L. *acidophilus*. DPPH and ABTS radical scavenging activities, as well as FRAP, in FP significantly increased with higher polyphenol and flavonoid content. The TFC and TPC were the highest in FP by L. *rhamnosus* and L. *acidophilus*, respectively. Tyrosine metabolism was the most significantly enriched pathway. The flavor profiles and functional metabolites were reconstructed in FP. The present study provides theoretical support for the preparation of mixed starter cultures and the development of fermented pandan products with unique characteristics.

CRediT authorship contribution statement

Junping Zhou: Writing – original draft, Software, Methodology, Investigation, Formal analysis, Data curation. **Zhen Feng:** Writing – original draft, Software, Methodology, Formal analysis, Data curation. **Mingzhe Yue:** Software, Data curation. **Ziqing Chang:** Resources, Investigation, Formal analysis. **Junxia Chen:** Software, Methodology. **Mengrui Wang:** Formal analysis, Data curation. **Fei Liu:** Writing – review & editing, Visualization. **Chunhe Gu:** Writing – review & editing, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declared that they have no conflicts of interest to this work. We declare that we do not have any commercial or associative interest that represents a conflict of interest in connection with the work submitted in *FOOD CHEMISTRY: X*.

Data availability

Data will be made available on request.

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