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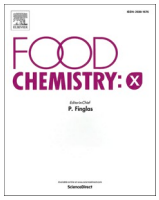

Effect of *Lactiplantibacillus plantarum*-mediated lactic fermentation on the characteristic flavor of sea buckthorn juice by volatolomics and metabolomics analysis

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ABSTRACT

Lactic fermentation enhances sensory quality and nutritional properties of fruit juice, though its comprehensive impact on sea buckthorn through *Lactiplantibacillus plantarum* fermentation (LPF) remains unreported. This study used volatolomics and metabolomics to explore mechanism of lactic fermentation improving flavor. LPF reduced total acidity (from 24.01 g/L to 15.79 g/L), increased total flavonoid by 20.35% and polysaccharide contents by 55.64%. It also increased the quantity of volatile compounds (from 36 to 41). *β*-Damascenone and ethyl isovalerate were key aroma compounds, while the increase of phenylethyl alcohol and phenylacetaldehyde improved sweet, fruity, and floral aroma. The rise of adenosine, hypoxanthine, and ornithine through purine metabolism pathways enhanced umami, the enlargement of pyridoxine, pyridoxamine, and tyramine through Vitamin B6 and tyrosine metabolism pathways increased richness, and the elevated glycyrrhizin, melezitose, and maltotetraose enhanced sweetness. This study provides insight into improving sea buckthorn flavor and direction to produce high quality products.

1. Introduction

Sea buckthorn (*Hippophae rhamnoides* L.) is deciduous perennial shrub of the *Elaeagnaceae* family, native to the Eurasian continent. Sea buckthorn is rich in multiple nutrients and contains numerous biologically active components, such as polyphenols, carotenoids, fatty acids and phytosterols (Ciesarová et al., 2020), which are beneficial to human health, including antioxidant, anti-inflammatory and anti-aging functions (Suomela et al., 2006). As medicinal and food resource, sea buckthorn rots quickly at room temperature due to its thin peel and juicy properties, so it is often processed into juice to preserve the degradation of nutrients (Ao et al., 2022). However, the high acidity and astringency of the sea buckthorn pulp (SBP) led to low sensory quality and are not easily accepted by customers. Currently, to increase the consumption of sea buckthorn, several innovative processing methods have been adopted to overcome its negative features. These methods include adding sugar, combining it with other berries or fruits, and applying heat treatment and high-pressure processing (Liu et al., 2022; Xia et al. 2023). Compared with physical methods and preservatives, fermentation is considered one of the simplest and most valuable biotechnological methods to maintain and improve the nutritional value and sensory quality.

Lactic fermentation facilitated by lactic acid bacteria offers a promising strategy to augment the sensory quality, nutritional value, and shelf-life properties of vegetables and fruits. This process not only preserves food but also transforms its flavor profile by reducing malic acid, breaking down carbohydrates and proteins, and producing organic acids and amino acids that contribute to sour and umami tastes (Liu et al.,

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2024; Marrero et al., 2019; Shah et al., 2024). Moreover, lactic fermentation generates new flavor substances including alcohols, acids and esters (Fuente et al., 2021), improving the taste and aroma properties of the food products. Numerous studies have indicated that fermentation by lactic acid bacteria significantly modifies the metabolite profiles in fruits and vegetables. Ji et al. (2023) verified *Lactobacillus reuteri* affected the overall aroma of apple juice by changing the type and content of volatile substances, improved the taste and flavor by increasing the contents of polyphenols and organic acids, and enhanced the antioxidant capacity and functionality. Zhao et al. (2025) discovered that lactic fermentation enhanced the quality of spicy cabbage, leading to higher levels of free sugar content, total titratable acidity, free amino acids, and volatile flavor compounds in the fermented spicy cabbage. Cagno et al. (2017) found lactic fermentation enhanced the flavor profile of pomegranate juice by increasing desired compounds such as alcohols, ketones, and terpenes, while decreasing non-desired aldehydes.

Lactic fermentation endows novel value to fruit and vegetable-based products due to the presence of probiotics and metabolites. Previous studies reported that lactic acid bacteria completely converted malic acid into lactic acid and significantly increased the total phenolic content, thereby enhancing the sensory qualities of sea buckthorn juice (Liu et al., 2022; Markkinen et al., 2019; Markkinen et al., 2021). They also revealed differential metabolites of sea buckthorn fermented by different *Lactobacillus* strains and provided optimum fermenting conditions of *Lactiplantibacillus plantarum (L.plantarum)* in sea buckthorn juice (Markkinen et al., 2022). *L. plantarum* is a lactic acid bacterium commonly used in plant-derived fermentation. It is well-known for its capacity to reduce acidity through the malolactic fermentation process (Yuan et al., 2024). While prior studies have demonstrated the efficacy of L. *plantarum* in fermenting sea buckthorn juice—effectively reducing acidity, nutritional enhancement, altering general metabolite profiles, and optimizing process conditions. However, a detailed mechanistic understanding of how L. *plantarum* fermentation induced metabolic changes drive the formation of complex flavor profiles remains largely unexplored. Specifically, the key aroma compounds, the contribution of volatile compounds to sea buckthorn's odor, and the material basis for sensory and flavor quality changes have not been reported.

Therefore, to bridge this gap, the present study employs an integrated volatilomic and non-targeted metabolomic approach, explicitly designed to correlate metabolic pathway activity with detailed sensory attributes. The key novel aspects of this work are: the identification of key aroma-active compounds and their direct contribution to sensory improvement; the elucidation of specific taste-modulating metabolic pathways; and most importantly, the comprehensive correlation of this multi-omics data with sensory properties to construct a mechanistic model of flavor formation. This study comprehensively studied the modification of lactic fermentation on components and flavor of SBP, aiming to provide guidance for improving the quality and consumer acceptance, thereby expanding the market potential of sea buckthorn-based products.

2. Materials and methods

2.1. Chemicals and reagents

Analytical regents including methanol, acetonitrile, ammonium acetate, and acetic acid were purchased from Merck Company (Darmstadt, Hesse, Germany) and ultrapure water was purchased from Wahaha Group Co., Ltd. (Hangzhou, China). The 1,1-Diphenyl-2-picrylhydrazyl radical (DPPH) and 2,2-azinobis-3-ethylbenzothiazoline-6-sulfonic acid (ABTS) kits were obtained from J&K Scientific Technology Co., Ltd. (Beijing, China). All other chemicals and standards of metabolites were purchased from Sigma-Aldrich (St. Louis, MO, USA).

2.2. Sample preparation

Sea buckthorn (*Hippophae rhamnoides* L. *subsp. sinensis*) was harvested from Jianping County, Chaoyang City, Liaoning Province, China, in December 2021. Frozen berry was gathered and sent to the juice processing company (Liaoning Shengshi Tianyuan Biotechnology Co., LTD) promptly. The berry was cleaned and pressed by screw presser (CTYZ-200, Weifang Weichang Environmental Technology Co., Ltd., Weifang, China) followed by clarification using centrifuges (LD-1500, Suzhou Batuo Centrifuge Manufacturing Co., Ltd., Suzhou, China). The juice yield of the berries was about 55%. The SBP (20 L, 5 L per tinfoil bag) was transported to the institute laboratory under 0 °C condition. The juice was sterilized by the ultra-high pressure sterilizer (5 L HPP, Jinan Zhitu Machinery Technology Co., LTD) at 500 MPa for 6 min for subsequent processing. The L. *plantarum* seed solution (SYAU23121) provided by the College of Food Science of Shenyang Agricultural University which was isolated from sauerkraut and commercialized in Shenyang Yuyuan Food Co., LTD (Shan et al., 2025). An adapted inoculum of L. *plantarum* was first prepared by culturing the activated bacteria at 37 °C for 24 h in a medium supplemented with 10% sea buckthorn juice, using a 1% (*v*/v) inoculation ratio. This adapted inoculum (10^8 CFU/mL viable cells) were then inoculated at 10% (v/v) to the SBP (2 L) and fermented in an incubator at 37 °C for 72 h with slow stirs under anaerobic conditions, a duration previously shown to be sufficient for complete metabolic activity and pH stabilization in this matrix (Gao et al., 2022). The fermentation products were cooled to 4 °C to terminate the fermentation, and then centrifuged (6000 ×*g*, 15 min) at 4 °C. The middle part of the clear liquid was chosen and put in a 50 mL centrifuge tube and then placed in a − 80 °C refrigerator as L. *plantarum*-led lactic fermenting sea buckthorn juice (LPF) for further analysis. The control sample was prepared by treating SBP with 10% pure water, incubating at 37 °C for 72 h, cooling to 4 °C, and finally centrifuging the mixture. All samples with three replicates were collected.

2.3. Determination of the main physicochemical parameters

2.3.1. Color properties

The chromatic value was measured by a reflector-mode colorimeter (NH310, Shenzhen 3NH Technology Co., Ltd., Shenzhen, China) with the L*, a*, and b* parameters. Calculate the total color difference (ΔE) with the following formula:

$$\Delta E^{*} = \sqrt{(\Delta L^{*})^{2} + (\Delta a^{*})^{2} + (\Delta b^{*})^{2}}$$

2.3.2. The pH value, the titratable acid content (TAC), the soluble solid content (TSSC) and the total polysaccharide contents (TPSC)

A handheld pH meter (PHB4, Shanghai Leici Technology Co., Shanghai, China) was used to measure the pH value. TAC was titrated with 0.05 mol/L sodium hydroxide, and it was converted to the concentration of citric acid equivalents according to the method of Liu et al. (2022). A digital refractometer (BM-04, Tianjin Lookout Photoelectric Technology Co., Ltd., Tianjin, China) was used to measure TSSC. TPSC was measured by phenol-sulfuric acid colorimetry according to the China Standard SN/T 4260–2015.

2.3.3. Measurement of total flavonoid contents (TFC)

According to the method of Zou et al. (2004), the $NaNO_2$-$AlCl_3$-NaOH method was used to determine TFC with minor modifications. The centrifuged sea buckthorn juice was diluted tenfold, and the measured wavelength was at 510 nm. Results were shown by the rutin equivalents (mg/mL) in triplicate.

2.3.4. In vitro antioxidant activity

Some modifications of DPPH radicals scavenging activity method were made based on the Cristina et al. (2018) report. Briefly, a mixture

was created by combining 1 mL sea buckthorn juice (diluted for 20 folds with ultrapure water) with 1 mL DPPH solution (prepared by dissolving 0.08 g/L in 95% ethanol). The mixture was reacted in 25 °C water bath in dark conditions for 30 min and measured absorbance at 517 nm. The ultrapure water served as the blank control. Formula for DPPH radical scavenging activity was as follows:

$$\text{DPPH radical scavenging activity (\%)} = [(1 - (A_x - A_{x0})/A_0)] \times 100$$

A_x refers to the sample absorbance; A_0 refers to the blank; A_{x0} refers to the control.

The method for $ABTS^+$ radical scavenging activity was performed as previously reported by Wang and Xiong (2005) with some modifications. Briefly, sea buckthorn sample and $ABTS^+$ working solution were added into the test tube at a volume ratio of 1:4, mixed well and reacted for 6 min, and the absorption was measured at 734 nm. Formula for ABTS radical scavenging activity was as follows:

ABTS radical scavenging activity (%) = $(A_0\text{-}A)/A_0 \times 100$.

A refers to the sea buckthorn sample absorbance; A_0 refers to the blank.

2.4. Determination of volatile compounds

The extraction and identification of volatiles were analyzed by the headspace solid-phase microextraction coupled with gas chromatography–mass spectrometry (HS-SPME/GC–MS) method, following the protocol of Shi et al. (2024) with minor adjustments. A total of 5 g sample was added in a 15 mL glass vial equipped with silica gel septum, and then 2 g NaCL was added. The volatile profiles of the sea buckthorn were extracted by a manual SPME sampler with a divinylbenzene/carboxen/polydimethylsiloxane (DVB/CAR/PDMS) fiber (75 μm CAR/PDMS, Supelco Corporation, USA). The fiber was activated at 250 °C in the GC–MS inlet for 30 min and then placed in the headspace of glass bottle. After equilibrating at 60 °C for 5 min, headspace extraction was carried out for 40 min. The injector was immediately inserted into the GC injection port and thermally desorbed at 250 °C for 5 min before being removed. The chemical analysis was carried out using a GC–MS system (Agilent 5975C-7890 A, Supelco Corporation, USA).

Compounds were separated using an SH-RXI-17SIL MS column (30 m × 0.25 mm × 0.25 μm, Restek, PA, USA). The carrier gas was helium, flowing at a rate of 1.78 mL/min during splitless injection at 250 °C inlet temperature. The column temperature program was as follows: starting at 40 °C, holding for 2 min, increasing to 100 °C with a 10 °C/min ramp rate, further increasing to 180 °C at a rate of 8 °C/min, and holding for 1 min. Finally, it was raised to 240 °C at a rate of 15 °C/min and maintained for 5 min. Mass spectra were acquired in full scan mode using an electron ionization (EI) ion source with electron energy of 70 eV. The ion source temperature was set at 230 °C, and the mass scan range was m/z 29–500 amu. Solvent delay was 3 min.

2.5. The ROAV analysis of volatile compounds

The comprehensive aroma evaluation of volatile compound can be analyzed based on relative percentage content using the ROAV. The ROAV value was the ratio of relative content of volatile components to their odor threshold. The component with the greatest contribution to the overall aroma (compound with the greatest odor activity value (OAV)) was defined as the standard, given a $ROAV_{stan}$ of 100. The ROAV values of other compounds were calculated by the relative content and sensory threshold. The larger ROAV value indicates the greater contribution to the overall aroma. Compounds with ROAV values $\geq$1 are key aroma components, 0.01 $\leq$ ROAV <1.00 are modified aroma components, ROAV values <0.01 are potential aroma components (Wang et al., 2024). Threshold value source refers to Zheng et al. (2025) result.

2.6. The aroma sensory evaluation

The comprehensive aroma of the sea buckthorn was evaluated by sensory group to complement the limitation of instrumental methods. The aroma attributes mainly included sea buckthorn odor, irritant, green, sweet, fruity, and overall aroma. The higher score indicated the more intense aroma. The sensory group was made up of 15 well-trained personnel from the College of Food Science of Shenyang Agricultural University (Shenyang, China). The sensory panelists were from our research group mainly aged from 18 to 22 years old, they gave their consent to participate in the sensory evaluation, and this work was approved by the ethics committee in the research of Shenyang Medical College under protocol number 2025–35. The descriptive olfactory analysis of sea buckthorn was performed as the standard GB/T 15549–2022/ISO 5496:2006 with slight modifications. The members of the panel were trained to evaluate the property and intensity of the aroma before formal evaluation. The training occurred twice weekly over a two-week period, with each session extending for 1 h. The evaluation was conducted on a 10-point scale, where 0 indicated no perception and 10 indicated extremely strong perception (The odor intensity value: 8–10 indicates intense aroma, 6–7 indicates medium aroma, 3–5 indicates faint aroma, 0–2 indicates no aroma). The assessors underwent training across three sessions with these solutions until they could accurately identify and differentiate the taste profiles of randomly provided sample solutions.

2.7. Metabolite analysis of taste-related compounds

Metabolite extraction was slightly modified based on the reported method (Xiao et al., 2021). Sea buckthorn sample (100 μL) was mixed with 400 μL 80% methanol in water and centrifuged at 15000 ×g and 4 °C for 20 min. The supernatant was further diluted with chromatographically pure water to yield 53% methanol concentration and then centrifuged again under same conditions. The supernatant was filtered through a 0.22 μm membrane before ultra-high performance liquid chromatography-electrospray tandem triple quadrupole mass spectrometry (UPLC-ESI-TQMS) detection. For the reproducibility of the mass spectrometry data, quality control samples were obtained with equal amounts of SBP (SBP1, SBP2 and SBP3) and LPF (LPF1, LPF2 and LPF3) extracts. One quality control (QC) sample was inserted in three test sample intervals.

The UPLC-ESI-TQMS analysis was carried out at Novogene Co., Ltd. (Beijing, China) with a Vanquish UPLC system (Thermo Fisher, Germany) coupled with Orbitrap Q Exactive™ HF-X mass spectrometer (Thermo Fisher, Germany). The samples were loaded in a Hypesil Gold column (100 × 2.1 mm, 1.9 μm) and were eluted by a 12-min linear gradient at 0.2 mL/min flow rate. For positive polarity mode, eluent A (0.1% FA in water) and eluent B (methanol) were used, while for negative polarity mode, eluent A (5 mM ammonium acetate, pH 9.0) and eluent B (methanol) were used. The solvent gradient conditions were as follows: 2% B for 1.5 min, 2–85% B for 3 min, 85–100% B for 10 min, 100–2% B for 10.1 min, and 2% B for 12 min. The Q Exactive™ HF-X mass spectrometer was operated with 3.5 kV spray voltage, 320 °C capillary temperature, 35 psi sheath gas flow rate and 10 L/min aux gas flow rate, the S-lens RF level was set to 60, and the aux gas heater temperature was set to 350 °C. The selected m/z range was 100–1500 in both positive and negative modes.

2.8. The taste evaluation by electronic tongue (E- tongue)

The taste characteristics of sea buckthorn samples were collected using an E-tongue (SA402B, Intelligent Sensor Technology, Inc., Japan). The validity of the E-tongue lies in its ability to simulate the adsorption of molecules on the human tongue using a “Double-Measurement” (CPA - Change of Membrane Potential caused by Adsorption) method. The basic taste attributes represented by the initial responses of the

sensors—such as sweetness, sourness, umami, saltiness, bitterness, and astringency. The system also provides information on attributes representing aftertaste, such as aftertaste bitterness (aftertaste-A), aftertaste astringency (aftertaste-B), and richness, by measuring the change in membrane potential caused by adsorption. The sensor was cleaned with a clean solution for 90 s, then rinsed with a reference solution for 120 s, and the data collection time was 90 s. Data collection was repeated four times, and the average of the last three sets of data was taken as the raw data for each group sample.

2.9. Statistics analysis

Principal component analysis (PCA), data transformation, and partial least squares discriminant analysis (PLS-DA) were performed using the Meta X software (Umetrics, Umea, Sweden) to obtain variable importance in the projection (VIP) values for metabolites. Statistical significance (*P*-value) was calculated using a *t*-test for each metabolite between groups, and the fold change (FC) for each metabolite was determined. Differential metabolite screening criteria were as follows: VIP $>$ 1, *P*-value $<$0.05, FC $\geq$ 2 (up-regulated) or FC $\leq$ 0.5 (down-regulated).

R software (www.r-project.org) was used to carry out volcano plot (VP), hierarchical clustering analysis (HCA), bubble plot mapping (BPM) and correlation analysis (Pearson correlation coefficient) of the different metabolites. The Kyoto Encyclopedia of Genes and Genomes (KEGG) database (https://www.genome.jp/kegg/pathway.html) was applied to elucidate the function of metabolites and metabolic pathways.

The mass spectrometric data of the detected compounds was matched with the NIST 14 Library database and the compounds with matching degree greater than 85% were retained. Data for SBP and LPF samples were collected in triplicate. The mean $\pm$ standard deviation (S.D.) was used to express the results. Statistical significance at $P < 0.05$ was considered.

3. Results and discussion

3.1. Effect of LPF on the main physicochemical properties

3.1.1. Effect of LPF on color properties

As Table 1 showed, the initial SBP appeared as a bright yellow liquid, with relatively high L* and b* values (36.45 $\pm$ 0.15 and 9.13 $\pm$ 0.09), and a low a* value (5.11 $\pm$ 0.06). After fermentation, the pulp became lighter and redder. The redness enhanced, as indicated by an increase in the a* value by 0.87, resulting a faint color difference (ΔE value 1.01 $\pm$ 0.03). This color shift is primarily attributed to the transformation of natural pigments in sea buckthorn, particularly carotenoids and flavonoids. The observed increase in redness may be linked to an overall rise in TFC or a potential increase in anthocyanin and carotenoid concentrations Zhang et al., 2024, which is consistent with previous findings (Liu et al., 2022).

3.1.2. Effect of LPF on pH, TAC, TSSC and TPSC

The physicochemical properties of SBP also varied along with the alteration of its component. As shown in Table 1, the pH value of the LPF sample rose from 3.22 $\pm$ 0.03 to 3.31 $\pm$ 0.05. The TAC decreased from 24.01 $\pm$ 0.03 g/L to 15.79 $\pm$ 0.07 g/L, and the TSSC decreased to 11.24 $\pm$ 0.25%. The small pH shift is buffered by the system, where weak organic acids and their conjugate bases stabilize hydrogen ion concentration even as the total acid content declines substantially. Moreover, when the pH value is 4.00 or below, to avoid excessive acidification of environmental conditions, sugar is scarcely used as a fermentation substrate. In this case, the glucose and fructose transport system of L. *plantarum* is restrained or downregulated, resulting in very low sugar utilization. Nevertheless, deprotonated malic acid can diffuse into cells and be converted into lactic acid, thereby completing the metabolic activity (Markkinen et al., 2022). TPSC, on the other hand, increased from 3.81 $\pm$ 0.14 to 5.93 $\pm$ 0.09 mg/g in LPF sample, probably not only due to the conversion of small molecule carbohydrates into active polysaccharides or degradation from the pomace (Zhang et al., 2022), but could also reflect contributions from bacterial cell-wall polysaccharides or exopolysaccharides produced by L. *plantarum* during the fermenting process. Further structural and compositional analyses would be required to clarify the specific sources and structural modifications of polysaccharides after fermentation.

3.1.3. Effect of LPF on the TFC

During the fermentation process, *Lactobacillus* produces new metabolites, which in turn influence the nutritional composition of sea buckthorn juice (Ji et al., 2023). In LPF sample, TFC exhibited an upward trend from 2.67 $\pm$ 0.12 to 3.24 $\pm$ 0.11 mg/mL (Table 1). The TFC was determined colorimetrically using rutin as the standard. It should be noted that this method provides an approximate measure of total flavonoids and primarily reflects overall trends in flavonoid variation. The increase in flavonoid content can be ascribed to multiple factors. During the fermenting process, specific hydrolytic enzymes, such as pectinase, β-glucosidase, amylase, and cellulase become activated (Dorjee et al., 2024). These enzymes can converse the combined flavonoids to soluble forms that can be determined. Microbial action also disrupts cell integrity, releasing flavonoids, while the reduction of flavonoids in the discarded residue elevates their relative content (Zhao et al., 2025).

3.1.4. Effect of LPF on antioxidant activity

Biological activity serves as one of the crucial indicators for evaluating the positive progress of fermentation. As shown in Table 1, the LPF exhibited enhanced antioxidant capacity. Compared with SBP samples, LPF demonstrated higher DPPH and $ABTS^{+}$ free radicals scavenging, rising from 93.24 $\pm$ 0.62% to 95.53 $\pm$ 0.54% for DPPH, and from 85.13 $\pm$ 0.59% to 90.38 $\pm$ 0.45% for $ABTS^{+}$, respectively. The minor differences in antioxidant activity were statistically significant, their practical relevance for human nutrition or functional food applications requires further investigation. The rise in antioxidant activities exhibited a trend consistent with those of TFC and functional polysaccharides, potentially attributed to the augmented presence of free phenolic compounds or depolymerization during microbial hydrolysis reactions (Ahmed et al., 2019).

Table 1
The main physicochemical parameters of SBP and LPF.

parameter	L*	a*	b*	pH	TAC (g/L)	TSSC (%)	TPSC (mg/mL)	TFC (mg/mL)	DPPH (%)	ABTS (%)
SBP	36. 45 $\pm$ 0.15	5.11 $\pm$ 0.06	9.13 $\pm$ 0.09	3.22 $\pm$ 0.03	24.01 $\pm$ 0.03	13.72 $\pm$ 0.29	3.81 $\pm$ 0.14	2.67 $\pm$ 0.12	93.24 $\pm$ 0.62	85.13 $\pm$ 0.59
LPF	36. 96 $\pm$ 0.04	5.98 $\pm$ 0.17†	9.20 $\pm$ 0.31	3.31 $\pm$ 0.05	15.79 $\pm$ 0.07†	11.24 $\pm$ 0.25†	5.93 $\pm$ 0.09†	3.24 $\pm$ 0.11†	95.53 $\pm$ 0.54†	90.38 $\pm$ 0.45†

Note: Data is reported as the mean $\pm$ standard deviation of 3 replicates. The † means significant differences based on Duncan's multiple range tests at $P < 0.05$. TAC was the citric acid equivalents concentration.

3.2. Volatile components and aroma analysis

3.2.1. Effect of LPF on volatile compounds

The content of the volatile compounds in sea buckthorn varied obviously after lactic fermentation, and the variations in their proportions exert a substantial influence on the aroma of sea buckthorn (Ma et al., 2021). A summary of the detected volatile compounds and their classifications in sea buckthorn was shown in **Supplementary Table S1**. A total of 48 volatile compounds were detected in the samples, mainly composed of esters, alcohols, and ketones, which are important

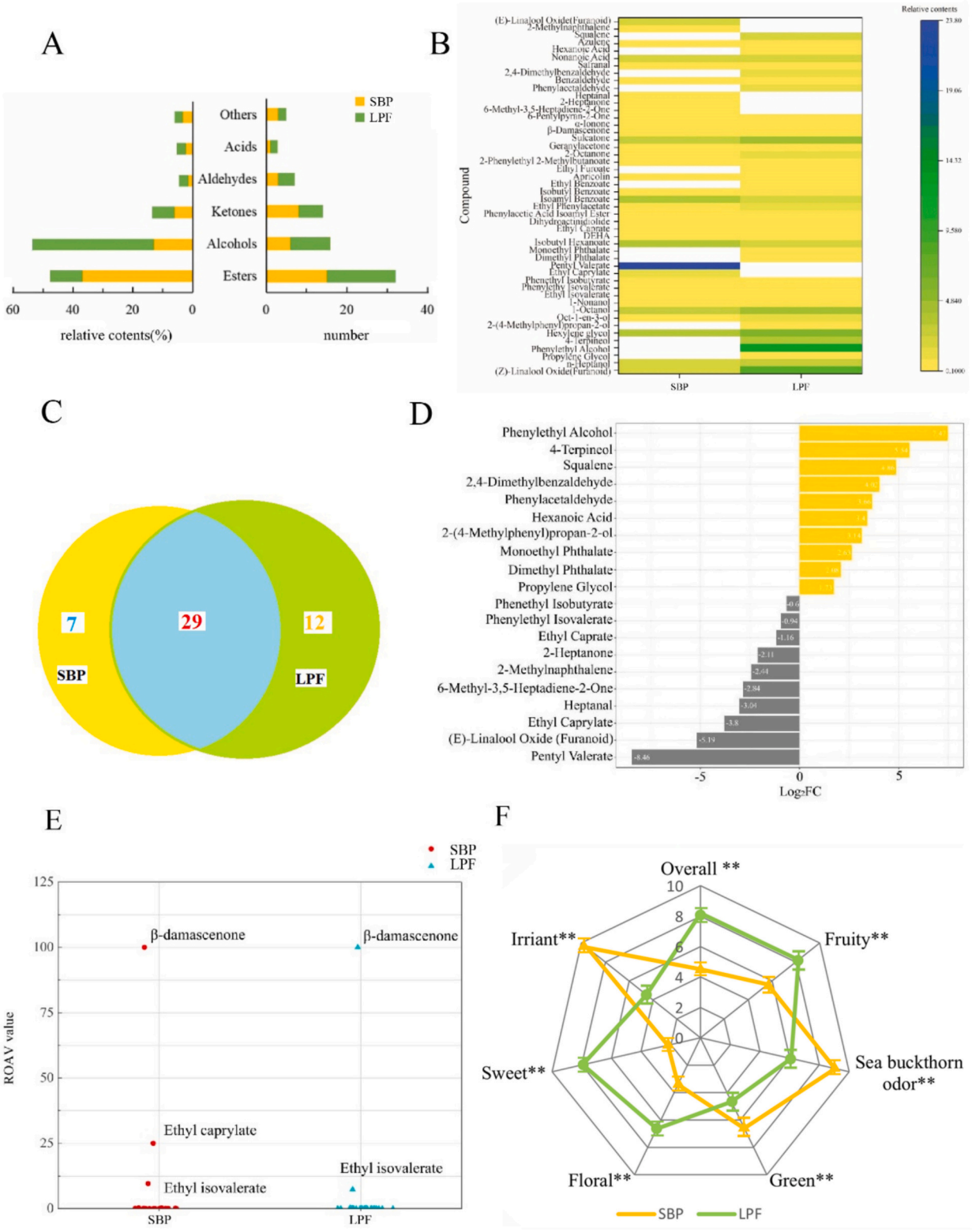

Fig. 1. (A) The quantity and relative concentration of different categories of volatile compounds. (B) The relative concentration heatmap of the detected volatile compounds. (C) The Venn diagram of the volatile compounds. (D) The differential analysis bar chart of the main volatile compounds. (E) The ROAV values of the main volatile compounds. (F) The radar diagram of the aroma sensory evaluation. Note: The ** means significant differences ($P < 0.01$).

components of the sea buckthorn characteristic aroma. There was also a small quantity of acids, aldehydes, terpenes, and naphthalenes. The bar stack diagram of the relative content and quantity was shown in Fig. 1A. Among them, the quantity of esters was the largest (15 in SBP and 17 LPF samples), and the relative content of esters in SBP was the highest (36.87%), while the relative content of alcohols was highest (40.56%) in LPF. The relative content of esters decreased to 10.87%, while the relative content of alcohols increased to 40.56% from 12.89% after fermentation. The lactic fermentation process produces multiple alcohols (quantity from 6 to 10) and esters (quantity from 15 to 17) obviously. The increase in alcohols content is mainly ascribed to the generation of various higher alcohols such as butanol, pentanol, and hexanol (Markkinen et al., 2022). Meanwhile, some alcohols also can undergo esterification reactions, leading to an increase in the variety of esters. These transforming processes are completed by microbial metabolism and are closely related to fermentation conditions (Liu et al., 2022).

The heatmap of the detected volatile compounds and their relative content was shown in Fig. 1B **and Supplementary Table S1**, and the Venn diagram of the volatile compounds was shown in Fig. 1C. In SBP, the quantity of volatile compounds was 36, and the most abundant compounds were pentyl valerate (23.76%), hexylene glycol (3.72%), and isobutyl hexanoate (3.36%). After lactic fermentation, the number of volatile compounds reached 41, and the most abundant compounds were phenylethyl alcohol (13.15%), (*Z*)-linalool oxide (8.11%), and hexylene glycol (5.94%). Lactic fermentation increased the quantity of volatile compounds, and a total of 29 compounds overlapped in both samples. After fermentation, totally 30 volatile compounds increased, and 18 compounds decreased. The differential substances in relative content (top 10) were shown in Fig. 1D. After lactic fermentation, the compounds that showed the most significant changes in relative content were newly generated compounds. The notably increased volatile compounds were phenylethyl alcohol, *4*-terpineol, squalene, *2,4*-dimethylbenzaldehyde, and phenylacetaldehyde, while the significantly decreased compounds included pentyl valerate, (*E*)-linalool oxide (furanoid), ethyl caprylate, and heptanal.

After lactic fermentation, alcohols became the predominant volatile group. This shift may be attributed to the generation of new alcohols such as phenylethyl alcohol and *4*-terpineol coupled with the volatilization or degradation of certain esters, including pentyl valerate and ethyl caprylate. Lactic acid bacteria primarily convert sugars into lactic acid as the main fermentation product, but they are also capable of producing alcohols, ketones, aldehydes, and esters (Ji et al., 2022). In a related study, Fuente et al. (2021) reported that alcohols accounted for 70.6% of total volatiles in raw pomegranate juice, and after lactic fermentation, they remained the dominant class, comprising 51.0–62.7% of volatiles. Similarly, Gao et al. (2018) observed that L. *plantarum* enhanced the aroma profile of *Momordica charantia* juice by reducing aldehyde and ketone contents while increasing the levels of alcohols and acids.

3.2.2. Analysis of key volatile compounds in SBP and LPF samples

The contribution of volatile compounds to the overall fragrance depends on both their concentration and odor thresholds. ROAV was used to evaluate the influence of volatile components on the aroma of sea buckthorn samples, offering an objective assessment of each compound's aroma contribution (Li et al., 2024). The ROAV values and odor thresholds of volatile compounds in sea buckthorn were shown in Fig. 1E **and supplementary Table S2**. The SBP sample contained three key aroma components, namely β-damascenone (ROAV = 100.000), ethyl caprylate (ROAV = 25.025), and ethyl isovalerate (ROAV = 9.594). In addition, 11 modified aroma components ($0.01 \leq$ ROAV <1.00) with fruity and woody aromas were identified. Notably, ethyl caprylate is an important stable aroma compound in sea buckthorn wine, as demonstrated by Meng et al. (2024). The LPF sample contained two key aroma components, β-damascenone (ROAV = 100.000) and ethyl isovalerate (ROAV = 7.329), along with 8 modified aroma components ($0.01 \leq$ ROAV <1.00), which showed fruity, floral, and honey aromas overall. The β-damascenone and ethyl isovalerate were identified as key aroma compounds in both SBP and LPF samples. Although the relative content of β-damascenone in SBP was only 0.52%, its exceptionally low odor threshold made it the most important aroma compound. After lactic acid fermentation, its content increased slightly to 0.68% in the LPF sample, where it remained the dominant odorant. Thus, β-damascenone was identified as the key aroma contributor in sea buckthorn in this study. β-damascenone, a C-13 norisoprenoid compound, is usually presented as an impact odorant in red wines (Pineau et al., 2007). However, few studies have investigated β-damascenone in sea buckthorn, despite its significant contribution to aroma. The biosynthesis of β-damascenone has been shown to occur via the methylerythritol *4*-phosphate pathway. *Lactobacillus* species possess β-glucosidase, which plays a key role in the release of β-damascenone Zhang et al., 2024. The high content of this compound in sea buckthorn might be attributed to the abundance of carotenoids, as β-damascenone is formed through the biodegradation of carotenoid precursors (Bai et al., 2025; Black et al., 2015).

3.2.3. Effect of LPF on aroma sensory evaluation

When the volatile compound analysis was correlated with aroma properties, the common limitation is the significant variability in odor threshold among compounds, which is heavily influenced by the sample matrix (Mahanti et al., 2024). Therefore, aroma sensory analysis by human assessors is ultimately required to complement chemical analysis. The aroma attributes were shown in Fig. 1F. After fermentation, the characteristic sea buckthorn odor, along with irritant and green aroma significantly decreased, while sweet, fruity and floral aroma increased significantly, enhancing the overall aroma ($P < 0.01$). The LPF sample was more preferred by panelists. According to the evaluators' descriptions, the SBP sample exhibited strong green, irritant and sea buckthorn-like odor, with medium fruity and floral aroma. This might be attributed to the key aroma compound (β-damascenone, ethyl caprylate, and ethyl isovalerate) and the modified aroma compounds such as heptanal, 2-methylnaphthalene, and 1-nonanol, which has fat, irritant, rancid, and green aromas. The strong correlation of these aldehydes and esters with the irritant and green attributes was confirmed by correlation analysis (**Supplementary Table S3**). In contrast, the LPF sample featured strong floral, fruity, and sweet aromas. This might be attributed to the key aroma compounds (β-damascenone and ethyl isovalerate) and the modified aroma compounds for example oct-1-en-3-ol and phenylacetaldehyde with floral, fruity, and sweet aromas (**Supplementary Table S3**). This also could be related to the significant increase in relative contents of phenylethyl alcohol and phenylacetaldehyde and the decrease of heptanal after fermentation. Phenylethyl alcohol as potential aroma compound endows strong spice, rose, and lilac aroma to fermented food. Although its odor activity value is less than 1.00, and its contribution to the LPF sample cannot be ignored. Beyond its direct aromatic contribution, it exerts harmonizing and synergistic effects on other aroma compounds and may play a pivotal role in sustaining postnasal aroma persistence (Li et al., 2025). Research suggests that the degree of interaction among odorants depends on their intensity and pleasantness; when these factors are comparable, synergistic or additive effects become more pronounced (Li et al., 2023). Accordingly, its enhancing effect on sweet and floral notes was further supported by aroma sensory evaluation. Phenylacetaldehyde has a strong hawthorn, honey, and sweet aroma, while *4*-terpineol contributes to a pepper, light earth, and woody odor. The increase of these substances enhances the sweet, fruity and floral aroma of LPF sample, likely making it more appealing. Heptanal in SBP was completely transformed in fermentation, playing a crucial role in altering the sea buckthorn aroma (Xia et al., 2023). A fermentation strategy can be modulated by target regulation of the key aroma compounds, such as β-damascenone and ethyl isovalerate, to achieve desirable aroma characteristics in juices.

3.3. Widely targeted metabolomics analysis of taste-related compounds

Analysis of taste-related compounds is based on widely targeted metabolomics approach by UPLC-ESI-TQMS and high-resolution mass spectrometry. A total of 736 metabolites were detected in positive ion mode among all sea buckthorn samples. The metabolites were classified and quantified as follows: 101 lipids and lipid-like molecules (19.54%), 97 organic acids and derivatives (18.76%), 93 heterocyclic compounds (17.99%), 78 phenylpropanoids and polyketides (15.09%), 49 benzenoids (9.48%), 44 organic oxygen compounds (8.51%), 17 nucleosides and analogues (3.29%), 12 alkaloids and derivatives (2.32%), 11 organic nitrogen compounds (2.13%), 7 none (1.35%), 6 lignans, neolignans and related compounds (1.16%), 1 homogeneous non-metal compounds (0.19%), and 1 organosulfur compounds (0.19%) (Fig. 2A). It verified that the sea buckthorn contains abundant lipid and organic acid compounds.

High correlation of QC samples ($R^2 > 0.99$) indicates superior stabilization of the entire assay process (Cao et al., 2024). In Fig. 2B, PC1 and PC2 contributed 76.39% and 9.57%, respectively after PCA. The SBP, LPF, and QC samples were effectively distinguished, indicating that fermentation significantly changed the taste-related compounds of SBP, and the intensive distribution of QC samples indicated that the results were highly reproducible and reliable (Zhang et al., 2022). The score scatter plot of the PLS-DA model was depicted in Fig. 2C. Model evaluation parameters R^2 and Q^2 came from 7-fold cross-validation. With R^2Y exceeding 1.00 and the Q^2Y at 0.82, it indicated that the model was appropriate with a high explanatory rate and predictive power. The $R^2 > Q^2$ and the Y-axis intercept of the Q^2 regression line <0, it proved that the model is excellent and can describe the sample well. Hence, the established experimental PLS-DA model is reliable for further screening of differential metabolites. Despite the valuable insights into volatile compound trends, the statistical power is constrained by the small sample size ($n = 3$), potentially leading to PLS-DA overfitting and less reliable *t*-test results. Thus, this work is preliminary and hypothesis-generating, necessitating future validation with expanded sample sets.

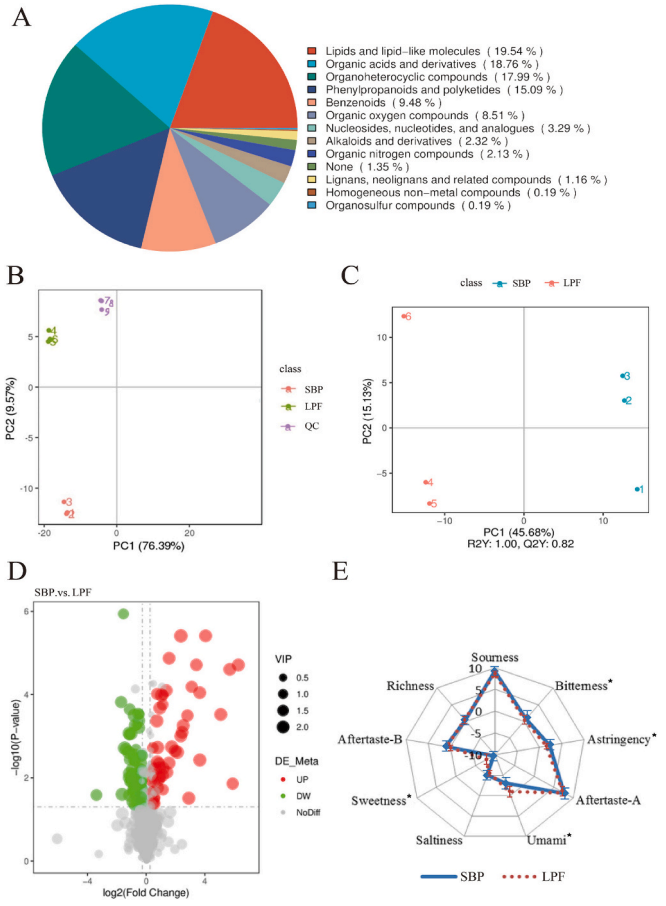

Fig. 2. (A) Classification of all the detected non-volatile compounds of sea buckthorn samples. (B) Principal component analysis (PCA) of SBP, LPF and QC samples. (C) The score plots of PLS-DA pairwise comparisons of differential metabolites in SBP vs. LPF samples. (D) Volcano plot of the differential non-volatile metabolites. (E) The radar diagram of the taste evaluation by electronic tongue. Note: The * means significant differences ($P < 0.05$).

In the PLS-DA model, the SBP and LPF groups were separated, and significant metabolite differences existed between the two treatments. Differentiated metabolites were screened according to VIP, FC, and *P*-value. The following thresholds were set: *P*-value <0.05, FC > 2 or FC < 0.5, and VIP > 1.0 (Heischmann et al., 2016). The metabolite comparison analysis is presented in **Supplementary Table S4**. Volcano plots (Fig. 2D) illustrate the up and down-regulation of metabolites, and the results showed that the number of down - regulated metabolites exceeds that of up - regulated ones. In particular, 115 differential metabolites between SBP and LPF (51 up-regulated, 64 down-regulated) were notably regulated. According to the value of –log10 (*P*-value), the prime up-regulated metabolites included tyramine, *2*-[(*2*-chlorobenzyl) sulfanyl]-*4,6*-dimethylnicotinonitrile, maltotetraose, pyridoxine, *3*-amino-*4*-(propylamino) cyclobut-3-ene-1,2-dione, GLY-GLY-PH*E*-LEU-NH_2 (FNK), acetophenone, desthiobiotin, ornithine, esculetin. While the important down-regulated metabolites mainly included neosaxitoxin, ribulose-5-phosphate, H-Trp-NH2.HCl, diaminopimelic acid, malic acid. Markkinen et al. (2022) investigated the impact of lactic fermentation on the metabolomic profile of sea buckthorn juice. Malic acid, essential amino acids and nucleosides were consumed early during fermentation. Obviously, lactic fermentation can affect the chemical composition of the sea buckthorn, especially increasing the organic oxygen, nucleoside and analogue compounds, decreasing the organic acids and derivatives compounds.

3.4. Effect of LPF on taste properties

The E-tongue was used for taste evaluation, and the fermentation effect on the taste characteristics was shown in Fig. 2E After lactic fermentation, sweetness (from −9.54 ± 0.03 to −7.89 ± 0.02), and umami (from −3.01 ± 0.01 to −0.95 ± 0.04) significantly increased, while the astringency (from 2.34 ± 0.01 to 1.53 ± 0.01) and bitterness (from 0.72 ± 0.01 to 0.28 ± 0.01) decreased notably ($P < 0.05$). The sourness of the LPF sample evaluated by the sensory panel significantly dropped, but the difference of the electronic tongue data (from 9.15 ± 0.01 to 8.63 ± 0.04) was not significant ($P < 0.05$). In overall taste evaluation, the LPF sample has a higher score. The SBP is a product with high acidity and astringency. Most evaluators found that the fermented sea buckthorn had a milder aroma and lower acidity, but the sensory panel did not score the different taste in detail, this needs to supplement in future study. Lactic fermentation reduced acidity, bitterness, and astringency, while increasing richness, sweetness, and umami, making the taste more palatable and well-rounded, thus enhancing consumer acceptance. The change in taste after lactic fermentation, influenced by taste-related metabolites in sea buckthorn, verified significant changes in these metabolites. High contents of ethyl isovalerate and phenethyl isobutyrate were detected in sea buckthorn. These esters ethyl isovalerate and phenethyl isobutyrate are known to enhance the perception of “sweetness” or “fruitiness” through aroma-taste interactions, which may explain their contribution to the sweetness of the SBP (Tong et al., 2025). Additionally, phenylethyl alcohol and phenylacetaldehyde were found to be positively associated with increased sweetness. Their relatively high content in the LPF sample suggests they contribute to its overall sweet taste, potentially through stable binding to the sweet taste receptor, which may explain their role in sweetness modulation (Cao et al., 2026).

3.5. Differential taste-related metabolite analysis

Hierarchical clustering analysis (HCA) was performed to regularize and cluster the relative quantitative values among the comparison pairs for the differential metabolites. As shown in Fig. 3A, the 115 metabolites in SBP and LPF samples distributed in distinctly different profiles. The concentrations had obvious differences in different treatments, and the consistency of the samples in same treatment was high, so they were differential metabolites. Lactic fermentation significantly influenced taste-related metabolites of sea buckthorn. The differential metabolites mainly consisted of organic acids, amino acids, nucleosides, and flavonoids. In SBP, high contents of amino acids such as *L*-hisidine, tyrosine, proline, and organic acids such as xanthurenic acid, salicylic acid, vitamin C, and *L*-malic acid provided the basis for the sour and astringent taste. After lactic fermentation, the level of amino acids such as D-glutamine, and tyramine and nucleosides such as 5′-adenylic acid, adenosine, *4*-pyridoxate, and xanthine increased dramatically. In LPF sample, nucleosides, energy and free amino acids (especially phenylalanine and branched-chain amino acids), are indispensable for cellular function and the growth of L. *plantarum*. Thus, they are rapidly consumed in the early fermentation stage. This explains the presence of numerous differential metabolites participating in the amino acid synthesis pathway (Ma et al., 2016). Moreover, during fermentation, amino acid analogs were involved in metabolic pathways such as signal transduction, redox regulation and energy homeostasis during fermentation, contributing to the flavor formation of sea buckthorn juice (Yu & Yang, 2020).

To clearly express the compounds with high variance multiples in the metabolites, the FC values of the differential metabolites were logarithmically transformed. The top 20 up-regulated metabolites by FC value were shown in Fig. 3B. After lactic fermentation, the key up-regulated taste-related metabolites included *3*-amino-*4*-(propylamino) cyclobut-*3*-ene-*1,2*-dione, MET-SER-SER-ARG-NH_2 (RMH), FNK, *2*-oxopiperidine-*3*-carbohydrazide, tyramine, adenosine, ornithine, pyridoxine, acetophenone, D-glutamine, glycyrrhizin, hypoxanthine, and melezitose (FC > 2.5). They were primarily nucleotide, peptide, and amino acid compounds. The nucleotides of adenosine, ornithine, and hypoxanthine were the main compounds enhancing the umami, while acetophenone, lycyrrhizin, and melezitose were the main compounds increasing the sweetness. Glycyrrhizin is a natural sweetener with high sweetness (80–300 specific sweetness), low thermal energy, and multiple pharmacological activities (Su et al., 2017).

The down-regulated metabolites calculated by FC value in LPF sample were shown in Fig. 3C. The top 10 down-regulated metabolites were *6*-phosphogluconate, ribulose-*5*-phosphate, adenosine *5*′-monophosphate, neosaxitoxin, *L*-histidine, trigonelline, vitamin C, murrangatin, *1*-methyladenine, carbadox (FC < −1). The *6*-phosphogluconate, ribulose-*5*-phosphate, adenosine *5*′-monophosphate, and vitamin C with sour and astringent tastes were down-regulated, so it was the main cause of reducing the acidity and astringency. Neosaxitoxin, *L*-histidine, and trigonelline have bitter taste, and they were down-regulated, so the bitterness of the LPF sample decreased. Additionally, L-histidine is a precursor to histamine—a compound known for its cytotoxicity at high concentrations, which can induce adverse effects such as respiratory and blood pressure disorders. The significant decrease in *L*-histidine content suggests that lactic acid bacteria fermentation may enhance the product's safety profile by limiting the potential formation of histamine. Trigonelline is the main bitter compound and a vital precursor substance in the formation of the aroma of coffee beverages (Zhou et al., 2024). Murrangatin is an aroma compound, which also contributes to the aromatic profile of fermenting beverages (Luo et al., 2011). All these metabolic differences suggested that lactic fermentation was an attractive method to enhance the taste quality of sea buckthorn. Future studies should include a broader selection of L. *plantarum* strains to determine whether the flavor profile observed here represents a conserved trait within the species or a unique metabolic signature of this particular isolate.

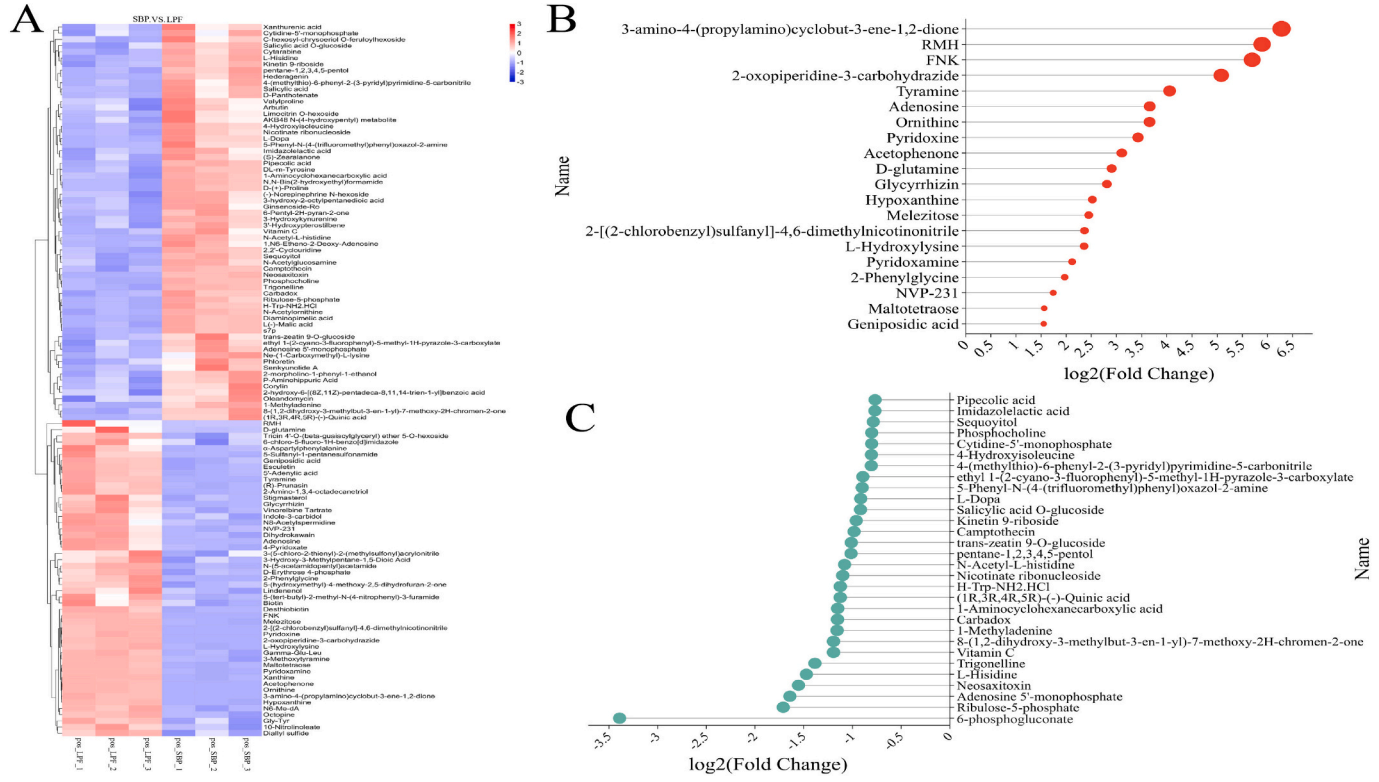

Fig. 3. (A) The HCA diagram of the differential non-volatile metabolites in SBP vs. LPF samples. (B) Matchstick diagram of the main up-regulated differential metabolites. (C) Matchstick diagram of the main down-regulated differential metabolites.

3.6. Correlating analysis of the taste-related compounds and taste property

The taste property originates mainly from the taste-related compounds, so the variation in the taste sensory properties chiefly ascribes to the differential taste-related compounds. The Pearson's coefficients between the 115 main taste-related compounds in sea buckthorn are presented in **Supplementary Table S5**, revealing significant correlations among nearly all the differential taste-related compounds. The main differential non-volatiles compounds with high correlation and FC values are presented in Fig. 4A. The negative correlation compounds include neosaxitoxin, ribulose-*5*-phosphate, H-Trp-NH_2.HCl, diaminopimelic acid, and *L*-malic acid. On the other hand, the positively correlation compounds consist of tyramine, *2*-[(*2*-chlorobenzyl) sulfanyl]-*4,6*-dimethylnicotinonitrile, maltotetraose, pyridoxine, *3*-amino-*4*-(propylamino) cyclobut-*3*-ene-*1,2*-dione, FNK, acetophenone, desthiobiotin, ornithine, esculetin, xanthine, gamma-Glu-Leu, *5′*-adenylic acid, *N*-(*5*-acetamidopentyl) acetamide, and *2*-oxopiperidine-*3*-carbohydrazide. Notably, after LPF, the compounds that experienced an increase in concentration predominantly comprised nucleosides, peptides, vitamins, and oligosaccharides. Among them, peptides such as FNK and gamma-Glu-Leu, as well as nucleotides including ornithine, xanthine, and 5′-adenylic acid, are known to impart umami taste. When present together in solution, these components may exhibit synergistic effects that collectively enhance the overall umami flavor profile. Conversely, while the compounds that reduced content were mainly organic acids and basic peptides.

Compared to the result of taste sensory property evaluation, after

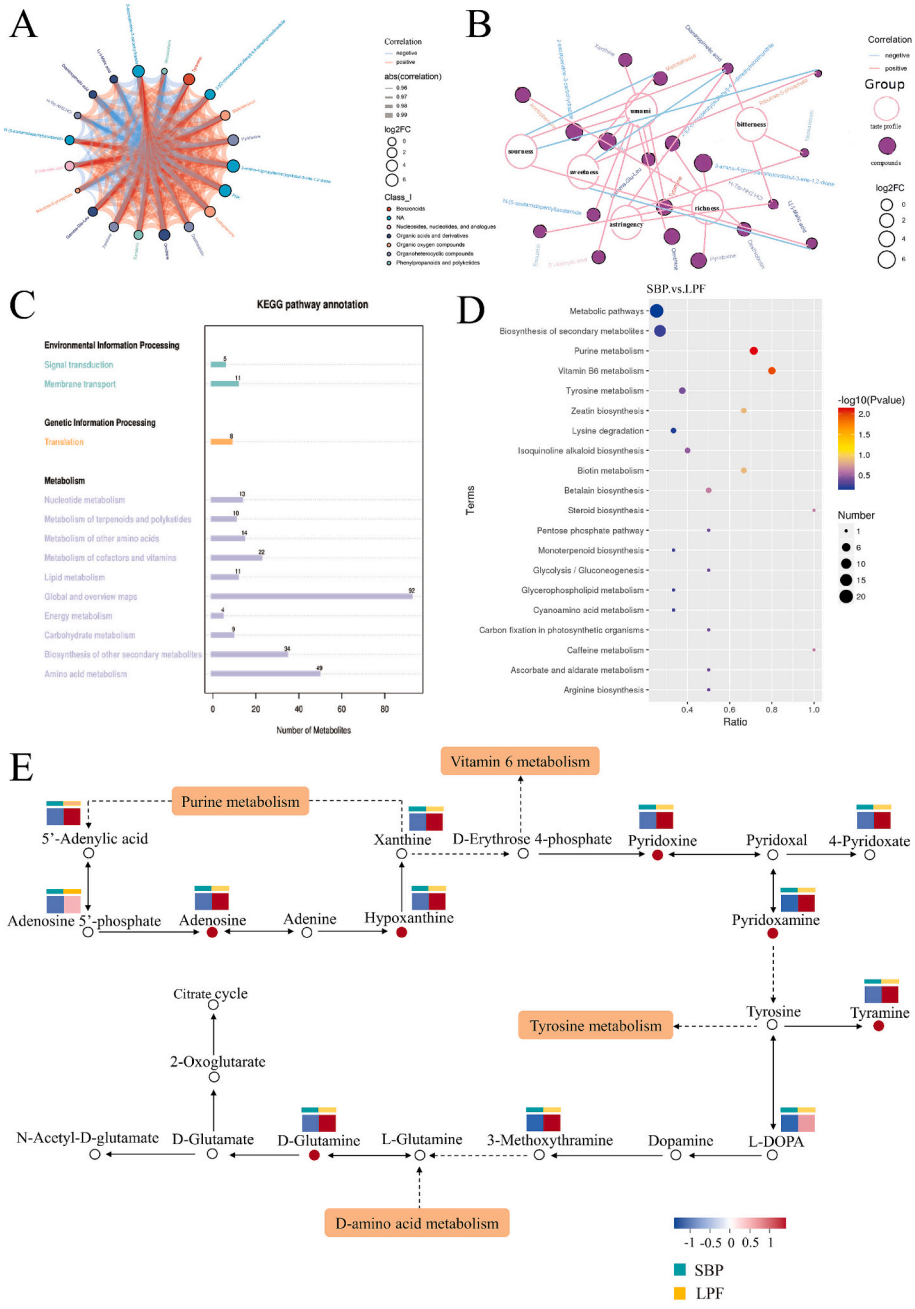

Fig. 4. (A) The correlating cord diagram of the main differential non-volatiles. (B) The correlating network diagram of taste sensory properties and main taste compounds. (C) KEGG pathway annotation for all non-volatile metabolites. (D) KEGG enrichment bubble plot of differential metabolites. (E) The main differential metabolites and their associated metabolic pathway according to the KEGG database.

lactic fermentation, it became evident that lactic fermentation led to a significant upsurge in sweetness, umami, and richness. Conversely, there was a notable reduction in sourness, aftertaste A, astringency, bitterness, and aftertaste B. Subsequently, these results were utilized to construct a correlation network in Fig. 4B, which delineated the relationships between the main taste-related compounds and taste sensory properties. As depicted in the network, compounds such as FNK, ornithine, xanthine, gamma-Glu-Leu, *5′*-adenylic acid, *N*-(*5*-acetamidopentyl) acetamide, and *2*-oxopiperidine-*3*-carbohydrazide exhibited a highly positive correlation with the umami taste ($P < 0.001$). Meanwhile, tyramine, *2*-[(*2*-chlorobenzyl) sulfanyl]-*4,6*-dimethylnicotinonitrile, acetophenone, desthiobiotin, esculetin, pyridoxine, and *3*-amino-*4*-(propylamino) cyclobut-*3*-ene-*1,2*-dione exhibited a highly positive correlation with the richness taste ($P < 0.001$), and maltotetraose showed a strong positive correlation with the sweet taste ($P < 0.001$). These correlations strongly suggested the elevated sweetness, umami, and richness values in LPF samples. In contrast, neosaxitoxin and H-Trp-NH_2.HCl were found a markedly positive correlation with the bitterness and astringency taste ($P < 0.001$), while ribulose-*5*-phosphate, diaminopimelic acid, and *L*-malic acid exhibited a highly positive correlation with the sourness ($P < 0.001$). These results imply the relatively high sourness, bitterness, and astringency values present in the SBP samples. The sensory quality of the sea buckthorn juice can be improved by standardizing the fermentation process by leveraging the synergy between malolactic fermentation and volatile composition. While correlations between volatile profiles and *E*-tongue were derived from different matrices, where viscosity and sugar content could affect volatile release, the consistent trends across all samples confirm their relevance to the overall flavor profile.

3.7. KEGG pathway annotation and enrichment analysis

The KEGG database was used to analyze enriching pathway of the differential taste-related metabolites. A total of 282 metabolites were annotated based on KEGG pathways. As illustrated in Fig. 4C, the pathways with a higher number of metabolites were prominently featured in global and overview maps, amino acid metabolism, and biosynthesis of other secondary metabolites. These pathways contained 92, 49, and 34 metabolites respectively, constituting 32.62%, 17.37% and 12.06% of total annotated metabolites. The metabolic pathways related to cofactors and vitamins, other amino acids, and nucleotides had 22, 14, and 13 metabolites annotated within them, respectively. The analysis revealed that lactic fermentation had a significant impact on metabolic pathways evidenced by Fig. 4D. A total of 30 differential metabolites were mainly distributed in 24 pathways, accounting for 26.09% of all the differential metabolites identified. When ranked by *P*-value, the top pathways with the highest enrichment were purine metabolism and Vitamin B6 metabolism (**Supplementary Table S6**).

The main metabolic pathways of differential metabolites according to the KEGG database are presented in Fig. 4E. Adenosine has a strong umami and can improve the food taste and flavor (Sato et al., 2005). The upregulation of purine metabolism significantly enhanced the levels of adenosine and hypoxanthine. However, this accumulation may be attributed to the degradation of intrinsic nucleotides, or a synergistic effect of synthesis and secretion by L. *plantarum* combined with the degradation of nucleotides within the fermented samples. These nucleotide metabolites are intermediate metabolites of energy metabolism and can enhance the umami taste of sea buckthorn. Furthermore, *L. plantarum* possesses more precursors for Vitamin B6 biosynthesis and a greater potential for Vitamin B6 convertase expression from *D*-erythrose-*4*-phosphate and the *L*-glutamine pathway for synthesis. This aligns with established findings that lactic acid fermentation increases Vitamin B6 content in products such as chickpea milk (Fan et al., 2025) and a sweet Japanese beverage (Oguro et al., 2017). Our analysis revealed, for the first time, an upregulation of pyridoxine and pyridoxamine in sea buckthorn. This upregulation is significant as these compounds enhance umami and richness and facilitate the synthesis of nucleic acids and amino acids in sea buckthorn (Li et al., 2018).

We observed that the tyrosine metabolic pathway was upregulated during fermentation, leading to elevated tyramine biosynthesis from tyrosine. Tyramine widely presents in fermented foods. It is formed by decarboxylation of the precursor amino acid, tyrosine, catalyzed by bacterial decarboxylase. A number of lactic acid bacteria have been characterized as producing excessive amounts of tyramine in fermented foods, like cheese, beer, kimchi and soy sauce. Although tyramine is associated with hypertensive crises, neurological disorders and abnormal levels are criteria for food spoilage and food safety. Few studies suggest the importance of tyramine in olfactory associative and in appetite regulation by experiences of food flavors (Nisimura et al., 2005). Glutamate is an important umami amino acid, the increase of glutamate can improve the umami taste quality of sea buckthorn (Yu & Yang, 2020). Glutamine with light sweet and umami tastes also showed an up-regulation trend in amino acid metabolism pathway Leke and Schousboe, 2016. All of these metabolites contribute to improving the taste and nutrition of sea buckthorns after lactic fermentation. The taste characteristic was mainly improved by the increase of the amino acid and nucleotide metabolites through purine, tyrosine, and vitamin metabolism pathways. Sea buckthorn juice provides a rich source of specific precursors, including tyrosine and nucleotides, which supply the material basis for activating related metabolic pathways. Building on this substrate availability and considering the established enzymatic properties of L. *plantarum*, such as its tyrosine decarboxylase activity. We propose that microbial bioconversion of native juice components constitutes the key pathway responsible for the accumulation of associated metabolites. While this study establishes these associations, future work employing precursor feeding experiments, metabolic inhibitors, or engineered strains will be essential to actively steer these fluxes, quantify their contribution, and translate these mechanistic insights into precise fermentation control strategies.

4. Conclusion

Lactic fermentation (*Lactiplantibacillus plantarum*) enhanced remarkably the nutritional value and antioxidant capacity by decreasing the acidity, while increasing the active ingredients such as flavonoids and polysaccharides significantly. It also improved the aroma by increasing the variety and quantity of volatile compounds. The β-damascenone and ethyl isovalerate were key aroma compounds, and the rise in phenylethyl alcohol and phenylacetaldehyde enhanced the sweet, fruity, floral aroma. The umami taste was increased by the rise of adenosine, ornithine, xanthine, and hypoxanthine through purine metabolism pathways. Meanwhile, the richness taste was improved by the enlargement of pyridoxine, pyridoxamine, and tyramine through Vitamin B6 and tyrosine metabolism pathways, and the sweetness taste was enhanced by the increase of glycyrrhizin, melezitose, and maltotetraose concomitant degradation of malic acid. This sensory transition was further intensified by increases in specific amino acids and volatile esters, which may act synergistically to intensify sweetness perception through taste-aroma interactions. The decrease of bitterness was ascribed to the reduce of neosaxitoxin. This study provides a foundational understanding of flavor enhancement achieved by 72-h lactic fermentation, although the full dynamic profile of metabolite changes prior to this timepoint warrants further investigation. In conclusion, lactic fermentation can improve sea buckthorn product quality. This study elucidates the mechanisms of flavor transformation during lactic acid fermentation and establishes a foundation for improving the sensory profile of sea buckthorn by supplementing key precursors and modulating relevant metabolic pathways. It further emphasizes that dynamic monitoring of critical metabolic and sensory markers represents a crucial next step in optimization research, ultimately providing a practical basis for developing high-quality, functional sea buckthorn beverages in the food industry.

CRediT authorship contribution statement

Tingcai Yan: Writing – original draft, Visualization, Supervision, Conceptualization. **Xiying Qin:** Validation, Formal analysis, Data curation. **Helu Sun:** Methodology, Investigation, Formal analysis. **Yuanyue Gao:** Writing – review & editing, Visualization, Validation, Software. **Le Chu:** Visualization, Validation, Software. **Mingyue Wang:** Visualization, Validation, Software. **Xianjun Meng:** Supervision, Resources, Project administration. **Bin Li:** Supervision, Resources, Project administration. **Yingchun Han:** Validation, Software, Resources. **Baoru Yang:** Writing – review & editing, Supervision, Conceptualization. **Chi-Tang Ho:** Writing – review & editing, Supervision, Conceptualization. **Hui Tan:** Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fochx.2026.103921.

Data availability

Data will be made available on request.

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