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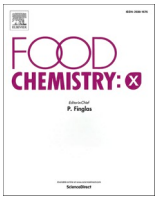

Comparative evaluation of the flavor characteristics and nutritional value of different varieties of *Gracilariopsis lemaneiformis* by sensory flavor chemistry

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ABSTRACT

Gracilariopsis lemaneiformis is an important edible marine alga, currently recognized as the second most productive seaweed in China. In this study, the flavor and nutritional components of three varieties of *G. lemaneiformis*—981, LuLong No. 1, and NB-18 were investigated using sensory flavor chemistry, emphasizing their potential flavor properties and health benefits. The e-tongue and e-nose profiles of *G. lemaneiformis* were analyzed for the first time, revealing significant differences between NB-18 and the other two varieties. Free amino acids, 5′-nucleotides, and volatile compounds (VOCs) were also evaluated. NB-18 exhibited significantly lower levels of VOCs and higher content of Glu, contributing to its superior sensory characteristics. Furthermore, it demonstrated a higher proportion of polyunsaturated fatty acids (PUFAs) and the lowest *trans*-fatty acid content. In conclusion, NB-18 stands out as a nutrient-rich, high-protein seaweed with excellent flavor and considerable market value, providing a strong basis for future large-scale promotion and cultivation.

1. Introduction

Seaweed is a kind of marine resource that has been consumed as a traditional food in Asian countries, particularly in China, Japan, and Korea, since ancient times. Recently, awareness of the benefits of seaweed has increased in Western countries, resulting in growing consumption in South America and Europe (Bakky et al., 2023). According to the latest data from the FAO, global seaweed production reached 37.8 million tons (fresh weight) in 2022 (FAO, 2024). Seaweeds are recognized as a rich source of protein, dietary fiber, vitamins, minerals, essential amino acids, and PUFAs (Chen et al., 2022; Illijas et al., 2023). These characteristics make seaweeds as a valuable component of daily diets and an effective nutritional supplement for alleviating malnutrition. In addition to their health benefits, people increasingly appreciate the taste and flavor of seaweed-based foods (Figueroa et al., 2023; Liang et al., 2023). The primary sensory attributes of algae as foods or supplements include their umami taste and marine aroma. These properties arise from two types of compounds: non-volatile taste-active compounds, which elicit gustatory reactions, and VOCs, which trigger olfactory responses. The former, mainly free amino acids and 5′-nucleotides, contribute to the umami taste of seaweed. In addition to enhancing flavor, umami contributes to reduce salt consumption, which is vital for a healthy diet (Milinovic et al., 2021). The latter consists of seaweed's VOCs, such as alkanes, aldehydes, alcohols, ketones, esters, and terpenes, imparting the distinctive aroma of seaweed (Francezon et al., 2021; Mirzayeva et al., 2021).

Gracilariopsis lemaneiformis (Rhodophyta) is recognized for its high content of proteins, dietary fiber, minerals, vitamins, and numerous bioactive compounds, such as PUFAs and polyphenols (Rocha et al., 2021). Given its considerable nutritional advantages and its contributions to environmental sustainability, *G. lemaneiformis* plays a significant role in the global seaweed aquaculture industry. In China, its production ranked second among all cultured seaweeds, reaching 550,000 tons dry mass in 2023, underscoring its substantial market potential. Seaweeds, particularly *Gracilaria* sp., are known for adding a crispy texture to foods and are often combined with raw fish in dishes such as "poke bowl" (Paull & Chen, 2008). However, as a food product, *G. lemaneiformis* is characterized by fishy and umami flavors typical of seaweed, which present challenges for its development and promotion in health foods, seasonings, and other products. Although research on *G. lemaneiformis* has increased, most studies have focused on its chemical or nutritional composition (Chan & Matanjun, 2017; Chen et al., 2017; Francavilla et al., 2013; Wang et al., 2019; Wen et al., 2006), while limited attention has been given to its flavor profiles and nutritional value (Liang et al.,

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2023; Nayyar & Skonberg, 2019). In particular, few studies have specifically analyzed the umami amino acid content of *G. lemaneiformis*, despite its importance in evaluating its potential as a food source. Investigating these characteristics is essential for enhancing product quality and tailoring flavor to meet the preferences of target consumers.

Considering the above results and the growing global interest in seaweed as a source of bioactive compounds and novel biomaterials, two red algae with significant market shares of *G. lemaneiformis*: 981, LuLong No. 1, and one new variety NB-18, developed by our group, were selected. This study conducted a comprehensive comparative analysis of their flavor profiles and nutritional values, with a particular focus on key indicators such as free amino acids, 5′-nucleotides, VOCs, and free fatty acids. This study aims to provide precise quantitative data on the chemical composition of *G. lemaneiformis*, combining with sensory evaluations to fully reveal the potential of this alga as a nutritious and tasty food source.

2. Materials and methods

2.1. Materials and experimental conditions

Fresh seaweed of *G. lemaneiformis* "981" was collected from Xiapu County, Ningde, Fujian Province, "LuLong No. 1" was from Lianjiang County, Fuzhou, Fujian Province, and "NB-18" was from Xiangshan County, Ningbo, Zhejiang Province. The fresh seaweed was rinsed with seawater to remove surface attachments and impurities and then transported to the laboratory under low temperature. Healthy seaweeds were selected and cultured in a pilot-scale cultivation system for one week (temperature: 23 °C, photoperiod: 12 L:12D, light intensity: 30 μmol/m^2/s). Samples were taken and stored at −80 °C for future use.

2.2. Flavor profile analysis

An e-nose (PEN3, AIRSENSE, Schwerin, Germany) was used to analyze the odors of the seaweed. A 0.3 g sample was weighed and transferred into a 20 mL headspace vial, sealed, and allowed to equilibrate at room temperature for 30 min. The headspace gas is then extracted for detection. The sample preparation time was 5 s, the sampling time was 60 s with a flow rate of 600 mL/min, and the analysis time was 120 s. The sensor self-cleaning time was 100 s. Each sample was measured five times in parallel, and the last three stable and reliable results were used.

A fresh sample of seaweed weighing 10 g was mixed with 100 mL of water and homogenized. It was then centrifuged at 10,000 rpm for 10 min, and the supernatant was used for e-tongue analysis. The taste analysis system (SA402B, INSENT, Japan) was used to measure aftertaste and the five basic tastes of the seaweed—sourness, bitterness, astringency, saltiness, and umami. Before testing, all sensors were activated and thoroughly cleaned. The electrical potential of the reference solution (Vr) and sample solution (Vs) were measured separately. Artificial saliva was used as the reference solution, which is tasteless.

2.3. Taste-related compounds determination

Free amino acids were detected using a high-performance liquid chromatography-mass spectrometer (HPLC-MS, QTRAP 6500+, SCIEX, USA). 30 mg of freeze-dried sample was mixed with 500 μL of methanol-water (*v*/v, 70 %) in a 2 mL centrifuge tube. After vertexing for 3 min, the mixture was centrifuged at 12,000 r/min for 10 min at 4 °C. The supernatant was collected and stored at −20 °C for 30 min, followed by an additional centrifugation. The supernatant was then filtered through a protein precipitation plate to eliminate proteins for analysis. The content of each free amino acid in the algae was determined using the peak area of standard compounds. LC conditions: an ACQUITY BEH Amide column (1.7 μm, 100 mm × 2.1 mm i.d.) was used. Mobile phase A was 2 mM ammonium acetate with 0.1 % formic acid, and mobile phase B was acetonitrile. The injection volume was 2 μL with a flow rate of 0.4 mL/min. MS conditions: ESI source, 550 °C, positive ion mode voltage 5500 V, negative ion mode voltage −4500 V.

The nucleotide analysis of selected water extracts was carried out according to (Moerdijk-Poortvliet et al., 2022). 30 mg of sample was weighed and mixed with 1 mL of water, then homogenized and left to equilibrate overnight at 4 °C. The mixture was homogenized again and centrifuged, and ethanol was added to the supernatant to remove proteins and polysaccharides. The remaining supernatant was dried under nitrogen and then reconstituted in 100 μL of ultrapure water, followed by filtration through a 0.45 μm filter. The content of umami substances in the supernatant was detected using high-performance liquid chromatography (HPLC, LC-20, SHIMADZU, Japan). The concentrations of adenosine monophosphate (AMP) and inosine monophosphate (IMP) were determined by comparing the retention time and peak area of the samples with those of standard compounds.

2.4. Volatile compounds determination

The pretreatment method for VOCs was modified based on the method described by Sun et al. (2012). Fresh samples were ground in liquid nitrogen, and 0.3 g was weighed and placed into a 20 mL headspace vial. 10 μL of internal standard solution and 2 mL of saturated NaCl solution were added, then sealed the vial with a polytetrafluoroethylene septum. The headspace vial was placed in a 60 °C water bath and allowed to equilibrate for 10 min with shaking. The VOCs were extracted from the headspace of the sample vial for 15 min by using a 65 μm Polydimethylsiloxane/Divinylbenzene-coated solid-phase microextraction (SPME) fiber.

The Agilent 8860/5977C system was used to analyze the VOCs in the algal samples. The adsorbed SPME fiber was inserted into the gas chromatography (GC) injection port and desorbed at 250 °C for 5 min. The Agilent DB-5 MS UI column was used, and the oven temperature program was as follows: started at 40 °C and held for 3.5 min, then rising at 10 °C/min to 100 °C, at 7 °C/min to 180 °C, and 25 °C/min to 280 °C, held for 5 min. The carrier gas was high-purity helium (He, >99.999 %) with a flow rate of 1.2 mL/min. The mass spectrometry was recorded under 70 eV electron ionization (EI) mode. The transfer line temperature was set to 280 °C and the ion source temperature was to 230 °C. Full scan mode was applied for the acquisition, with a mass range of 35–500 *m/z*.

The raw data were processed for qualitative analysis and peak area extraction using Mass Hunter Workstation 10.2. The missing values were filled by using the minimum value method. After obtaining the peak area for each volatile substance, a semi-quantitative analysis of the VOCs in the samples was conducted by the following formula:

$$VOC\left(\frac{\mu g}{g}\right) = \frac{V_s \times C_s}{M} \times \frac{I}{I_s} \times 10^{-3}$$

V_s means the volume of the internal standard (μL), V_s denotes the concentration of the standard (μg/mL), M is the mass of the sample (g), I_s indicates the peak area of the standard, and I is the peak area of the substance to be measured.

2.5. Free fatty acid determination

The sample preparation for free fatty acids determination followed the method described by Illijas et al. (2023). Firstly, 30 mg of freeze-dried seaweed powder was placed in a grinding tube and thoroughly ground. Then, 1 mL of a chloroform-methanol mixture (*v*/v, 2:1) was added, and the tube was subjected to ultrasonic oscillation for 30 min to promote lipid extraction. After oscillation, the supernatant was collected via centrifugation and transferred to a 15 mL centrifuge tube. The sediment was re-extracted 2–3 times by adding 1 mL of the chloroform-methanol mixture each time until the lipid extraction was complete. The collected supernatants were dried using a nitrogen evaporator. Next, 2

mL of sulfuric acid-methanol solution (v/v, 5:95) was added to the tube and heated in a 70 °C water bath for 4 h to convert the free fatty acids into fatty acid methyl esters. Finally, 2 mL of n-hexane and 2 mL of distilled water were added for extraction. After shaking and standing, the upper organic phase was filtered through a 0.22 μm organic filter. The filtered organic phase was then analyzed by using GC–MS (8860/5977C, Agilent, USA).

The GC system includes an Agilent DB-FATWAX UI column (30 m × 350 μm × 0.25 μm), and the injection port temperature was set at 260 °C with a split ratio of 20:1. He was used as the carrier gas with a flow rate of 1 mL/min. The temperature program started at 50 °C and was held for 3 min, then increased at a rate of 25 °C/min to 180 °C, where it was held for 3 min. Finally, the temperature was increased at 2 °C/min to 230 °C and held for 7 min.

Data in MS system was collected in selected ion monitoring (SIM) mode, with the quantification ions of *m/z* 55, 67, 74, and 79. The temperature of the quadrupole mass spectrometer, ion source and transfer line were 150, 200 and 240 °C, respectively. Data processing was performed using Mass Hunter software, with compound qualitative based on standard compounds (fatty acid methyl ester mix, FAME, Sigma Aldrich, Germany) and comparison with the NIST 20 database. Quantitative analysis was carried out using the external standard method (more details are provided in Table S1).

2.6. Nutritional value analysis

The total phenolic content (TPC) was determined following the method of Limiñana et al. (2023) with minor modifications. Specifically, 100 mg of sample was placed in a grinding tube, and 1 mL of 60 % ethanol solution was added. After homogenizing, ultrasonic extraction was performed at 40 °C for 30 min. Then, 100 μL of the supernatant was collected, and 125 μL of Folin-Ciocalteu reagent was added. After vertexing for 10 s, 400 μL of sodium carbonate solution (1 %, *w/v*) and 375 μL of distilled water were added to the mixture. The mixed solution was then left to react in the dark at 30 °C for 60 min. Afterward, the absorbance of both sample solution and gallic acid standard solution was measured at a wavelength of 760 nm using a spectrophotometer (TU-1810Plus, Xipu, China). The TPC was expressed as milligrams of gallic acid equivalent (GAE) per gram of dry weight. The flavonoid content was determined according to the method described by Nie et al. (2023). Total protein content was measured using the Coomassie brilliant blue G250 method, while total sugar and starch contents were determined using the Suzhou Keming ZT-1-Y total sugar kit and DF-1-Y starch content kit, respectively.

2.7. Equivalent umami concentration

The equivalent umami concentration (EUC) is commonly used to characterize the umami intensity of food. It refers to the total amount of umami substances in 100 g of dry-weight food, expressed in terms of monosodium glutamate (MSG) content. The calculation formula is as follows:

$$Y = \sum aibi + 1218\left(\sum aibi\right)\left(\sum ajbj\right)$$

Y represents the EUC value (g MSG/100 g), *ai* is the mass fraction (%) of umami amino acids, *aj* is the mass fraction (%) of umami nucleotides, *bi* is the umami intensity value of amino acids relative to MSG (Glu = 1, Asp = 0.077), *bj* is the umami intensity value relative to IMP (IMP = 1, AMP = 0.18), and 1218 is the synergy constant, where the concentration units are g/100 g.

2.8. Statistical analysis

All experiments were conducted independently in three groups, with each group containing at least three parallel samples. Data were statistically analyzed using IBM SPSS Statistics 27.0, employing one-way analysis of variance (ANOVA) and Tukey's multiple comparison test, with a significance level set at $p < 0.05$. The clustering heatmap was generated using R software, while histograms and radar charts were plotted using Origin 2021. GC–MS data were qualitatively and quantitatively analyzed using Agilent Mass Hunter, while HPLC data were processed for peak extraction and integration using SHIMADZU LabSolutions Essentials. All results are presented as mean ± standard error (mean ± SE).

3. Results and discussion

3.1. Odor difference among different varieties of G. lemaneiformis

An e-nose system was employed to investigate the aroma differences among various *G. lemaneiformis* varieties. Currently, e-nose has been widely applied in the identification of aquatic species, freshness evaluation, and quality assessment (Cao et al., 2021; Qin et al., 2013). The PEN-3 was equipped with 10 sensors that corresponded to different types of VOCs of *G. lemaneiformis*, including aromatic components, nitrogen oxides, alkanes, and sulfides. Principal component analysis (PCA) and linear discriminant analysis (LDA) were applied to process the raw data collected by the e-nose. Loading analysis was performed to evaluate the contribution of each sensor to sample differentiation, thereby allowing us to assess which type of odor substance plays a major role in distinguishing the samples.

The PCA analysis for the e-nose system showed that the combined contribution of the principal components1 (PC1) and PC2 exceeded 90 %, with the PC1 accounting for 53.32 % and PC2 for 42.10 % (Fig. 1A). The PCA (calculated internally by the e-nose software, where values closer to 1 indicate greater sample differentiation) indicates notable distinctions in aroma profiles of different varieties of *G. limoniform*. The aroma of NB-18 significantly differed from those of the other two varieties, while 981 and LuLong No. 1 overlap in the graph, suggesting their similarity and difficulty in differentiation. LDA, a supervised learning algorithm, was also applied and clearly distinguished the three *G. lemaneiformis* varieties, indicating notable differences between the 981 and LuLong No.1 (Fig. 1B). In the analysis of sensor contribution rates, LDA demonstrates that, W1W, W2W, and W1S as the most significant contributors to odor differentiation (Fig. 1C). These sensors exhibited specific sensitivity to sulfides, aromatic components and short-chain alkanes, respectively. Differences in the concentrations of these compounds likely contributed to the distinctive aroma profile of NB-18.

3.2. Taste differences among different varieties of G. lemaneiformis

The e-tongue, designed to mimic the gustatory system of mammals, has been demonstrated as an effective tool for objectively evaluating the taste intensity and characteristics of seaweed extracts (Jensen et al., 2022). In this study, e-tongue was used to quantify the taste characteristics of three varieties of *G. lemaneiformis*, with the response results shown in Fig. 1D. None of the three varieties exhibited seaweed sourness (negative value), but significant differences were observed in saltiness, bitterness, astringency, and intensity. However, no significant differences were detected in the aftertaste bitterness (aftertaste-B).

3.3. Taste-related compounds in G. lemaneiformis

The quality of seaweeds is influenced by various factors, with the taste was served as a crucial indicator. To evaluate the umami potential of seaweeds as a food source, this study analyzed the contents of key umami compounds, specifically free amino acids and 5′-nucleotides. In fact, most studies on the composition of free amino acids in seaweeds after hydrolyzing by acid (Astorga-España et al., 2016; Limiñana et al., 2023), however, it is the water-soluble flavor amino acids that play a crucial role in defining the true flavor profile. Moreover, limited

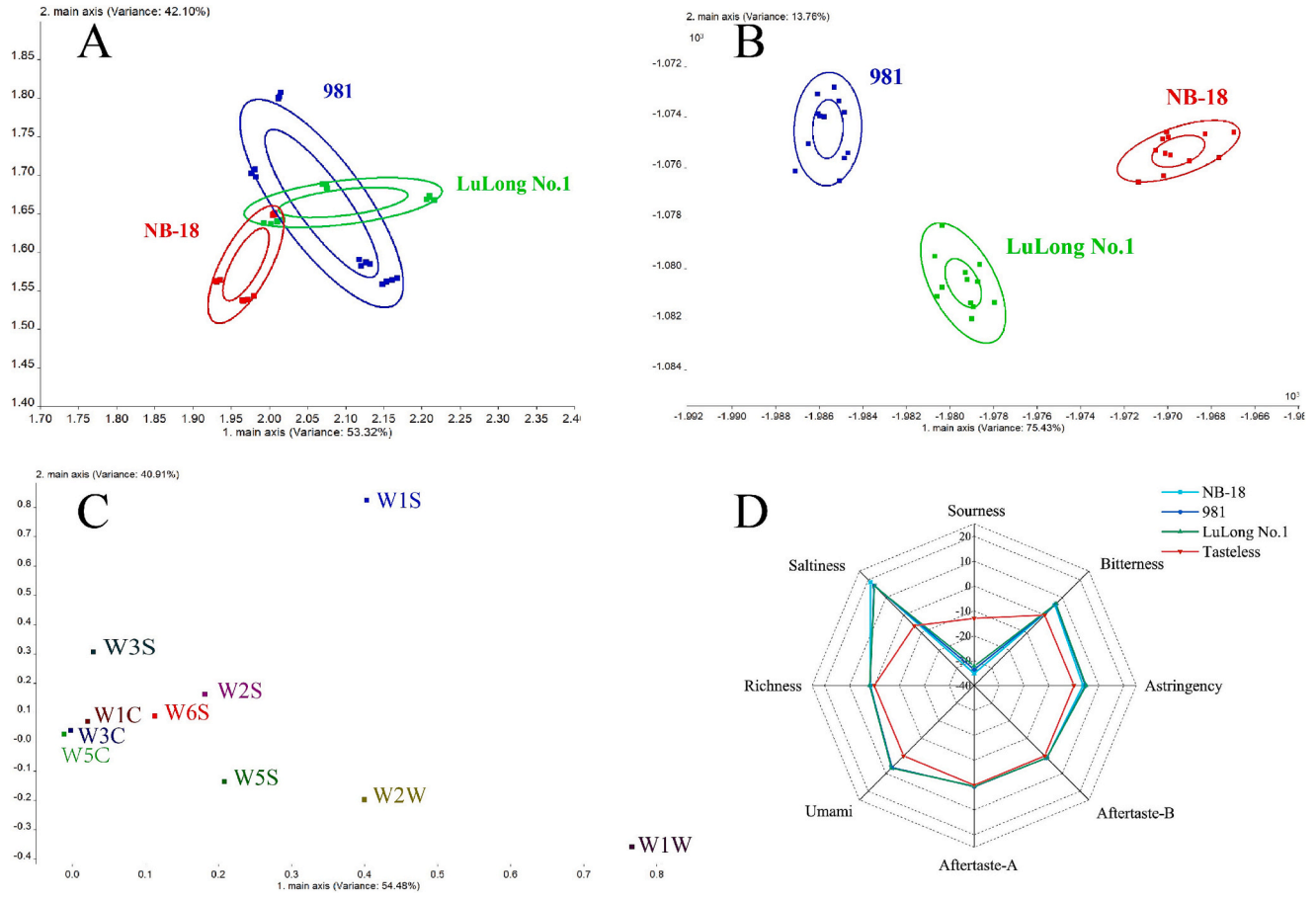

Fig. 1. Sensory evaluation of *G. lemaneiformis* using e-nose and e-tongue. (A) Principal components analysis (PCA) from the e-nose; (B) Linear discriminants analysis (LDA) from the e-nose; (C) Sensor loading analysis from the e-nose; (D) Taste radar chart from the e-tongue.

Table 1
Free amino acid content in different varieties of *G. lemaneiformis*.

Amino acids	Taste attribute	Threshold (mg/g)	Content (mg/g DW)			TAV value		
			NB-18	981	LuLong No.1	NB-18	981	LuLong No.1
L-Leucine	bitter(−)	1.9	nd	0.0215 ± 0.0010^{a}	0.0040 ± 0.0002^{b}	0.0000	0.0113	0.0021
L-Isoleucine	bitter(−)	0.9	0.1679 ± 0.0061^{c}	0.6120 ± 0.0409^{a}	0.2730 ± 0.0161^{b}	0.1866	0.6800	0.3033
L-Histidine	bitter(−)	0.2	0.0658 ± 0.0050^{c}	0.4314 ± 0.0081^{a}	0.0980 ± 0.0091^{b}	0.3288	2.1571	0.4898
L-Alanine$^{\#}$	sweet(+)	0.6	0.0999 ± 0.0054^{a}	0.0920 ± 0.0023^{b}	0.0921 ± 0.0011^{b}	0.1665	0.1533	0.1536
Glycine$^{\#}$	sweet(+)	1.3	0.0890 ± 0.0011^{b}	0.1159 ± 0.0009^{a}	0.1178 ± 0.0129^{a}	0.0685	0.0891	0.0906
L-Asparagine$^{\#}$	umami(+)		0.1489 ± 0.0085^{b}	0.1882 ± 0.0054^{a}	0.1868 ± 0.0172^{a}			
L-Glutamic acid$^{\#}$	umami(+)	0.3	10.9519 ± 0.2052^{a}	10.8020 ± 0.5596^{a}	10.1194 ± 0.5725^{a}	36.5062	36.0068	33.7314
L-Glutamine			1.2666 ± 0.0730^{b}	1.1789 ± 0.0209^{b}	1.8233 ± 0.2231^{a}			
L-Aspartate	umami(+)	1	1.0432 ± 0.0782^{b}	1.0488 ± 0.0970^{b}	1.3519 ± 0.0235^{a}	1.0432	1.0488	1.3519
L-Arginine	bitter/sweet(+)	0.5	0.0487 ± 0.0040^{b}	0.0482 ± 0.0022^{b}	0.0994 ± 0.0077^{a}	0.0975	0.0964	0.1988
L-Methionine	bitter/sweet(−)	0.3	0.0083 ± 0.0006^{b}	0.0639 ± 0.0054^{a}	0.0090 ± 0.0006^{b}	0.0278	0.2130	0.0300
L-Valine	sweet/bitter(−)	0.4	0.2079 ± 0.0066^{c}	0.7416 ± 0.0282^{a}	0.3161 ± 0.0288^{b}	0.5198	1.8541	0.7903
L-Tyrosine$^{\#}$	bitter(−)		0.0248 ± 0.0004^{c}	0.3221 ± 0.0046^{a}	0.0372 ± 0.0015^{b}	0.0096	0.1239	0.0143
L-Tryptophan			0.0009 ± 0.0003^{b}	0.0075 ± 0.0028^{a}	0.0014 ± 0.0004^{b}			
L-Threonine	sweet(+)	2.6	0.2758 ± 0.0185^{b}	0.8608 ± 0.0404^{a}	0.2575 ± 0.0236^{b}	0.1061	0.3311	0.0990
L-Lysine	sweet/bitter(−)	0.5	0.0833 ± 0.0045^{c}	0.8003 ± 0.0445^{a}	0.1538 ± 0.0116^{b}	0.1667	1.6007	0.3076
L-Proline	sweet(+)	3	0.0191 ± 0.0011^{a}	0.0137 ± 0.0006^{c}	0.0159 ± 0.0010^{b}	0.0064	0.0046	0.0053
L-Serine$^{\#}$	sweet(+)	1.5	0.2441 ± 0.0133^{b}	0.2276 ± 0.0058^{b}	0.3836 ± 0.0082^{a}	0.1627	0.1517	0.2557
L-Phenylalanine	bitter(−)	0.9	0.0008 ± 0.0001^{b}	0.0037 ± 0.0002^{a}	0.0010 ± 0.0001^{b}	0.0009	0.0041	0.0011
∑UAA			12.4529 ± 0.2837^{a}	12.6083 ± 0.6256^{a}	12.1020 ± 0.5866^{a}			
∑FAA			14.7470 ± 0.3443^{b}	17.5802 ± 0.7421^{a}	15.3412 ± 0.8353^{b}			
∑UAA/∑FAA			0.8445 ± 0.0049^{a}	0.7170 ± 0.0053^{c}	0.7891 ± 0.0132^{b}			
AMP	Umami(+)	0.5	1.3039 ± 0.2430 ^{a}	1.4118 ± 0.0423 ^{a}	1.3384 ± 0.2176 ^{a}	2.6078	2.8236	2.6768
IMP	Umami(+)	0.25	0.0010 ± 0.0001^{a}	0.0002 ± 0.0000^{c}	0.0007 ± 0.0001^{b}			
EUC			20.85	20.27	19.11			

UAA$^{\#}$: umami amino acids; FAA: free amino acids; nd: not detected.

research has combined analysis with sensory research. The contents of 2 detected 5′-nucleotides and 19 free amino acids are presented in Table 1.

3.3.1. Free amino acids between varieties

Among the three varieties, L-Glu exhibited the highest content of all free amino acids, followed by L-Asp. The content of L-Glu was significantly higher than that of other free amino acids in most seaweeds (Figueroa et al., 2023; Yuan et al., 2024), playing a crucial role in the umami taste of these algae. It is well known that L-Glu commonly exists in nature as its sodium salt (MSG), which is widely used as a food additive due to its ability to enhance the umami flavor. This enhancement also helps reduce the amount of Na^+ (NaCl) in food, aligning with health goals for sodium intake control and contributing to nutritional well-being (Milinovic et al., 2021). In this study, L-Glu accounts for over 60 % of the total free amino acids, reaching up to 74.27 % with a total content of 10.9519 ± 0.2052 mg/g in NB-18 (Table 1). However, no significant differences in L-Glu content were observed among the three varieties. L-Asp, another umami amino acid, showed the highest content in the LuLong No. 1, with 1.3519 ± 0.0235 mg/g. Notably, NB-18 exhibited the highest ratio of umami amino acid to free amino acid at 84.45 %, indicating a superior free amino acid profile. Bitter amino acids also influenced the flavor profiles. The level of L-His and L-Tyr exceeded their taste threshold (TAV > 1) in 981, suggesting that these compounds significantly contribute to its flavor. In contrast, NB-18 exhibited the lowest levels of all bitter amino acids, aligning with e-tongue results that indicated NB-18 had minimal bitterness and astringency (Fig. 1D).

The content of free amino acids in seaweed is influenced by various factors, including the species' inherent characteristics, sampling location, cultivation environment, and harvest time (Yuan et al., 2024). To minimize these effects, all three varieties in this study were harvested in the second quarter and then acclimated for one week in a laboratory recirculating aquaculture system. In this study, the highest total free amino acid content was observed in 981, with a dry weight of 17.58 mg/g, while no significant differences were found between NB-18 and LuLong No.1. It is noteworthy that some literature reports higher levels of free amino acids in seaweeds than those found in this study (Chen et al., 2017), and this discrepancy may be attributed to differences in sample extraction methods. In these studies, proteins were hydrolyzed before detecting free amino acids, resulting in the measurement of the total amino acid content after hydrolysis. In contrast, this study employed a method of direct extraction and detection of free amino acids, focusing on water-soluble flavor amino acids that contribute to taste. Similarly, Moerdijk-Poortvliet et al. (2022) utilized water or methanol-water extraction for analyzing free amino acids in seaweeds, which is akin to our study. This method enables a more accurate assessment of intrinsic free amino acids composition, offering new insights into the flavor characteristics of seaweeds. In summary, although LuLong No. 1 exhibited the highest free amino acid, it also had elevated levels of bitter amino acids. NB-18 and LuLong No.1, despite having lower free amino acid content, demonstrated a favorable balance of taste-related amino acids and the lowest bitterness, making it the variety with superior flavor profiles.

3.3.2. 5′-nucleotides between varieties

Umami can also be imparted through 5′-nucleotides. Five types of 5′-nucleotides are found in seaweeds: AMP, guanosine monophosphate (GMP), IMP, cytidine monophosphate (CMP), and uridine monophosphate (UMP). Among these, the first three play significant roles in umami flavor and are described as umami enhancers. Their synergistic effects can elicit umami flavors that are even stronger than those of MSG. In this study, umami-related 5′-nucleotides were quantitatively detected in *G. lemaneiformis* using HPLC, and the levels of AMP and IMP in the three varieties were quantified (Table 1). Notably, IMP content was the highest, ranging from 130.39 to 141.18 mg/100 g dry weight, consistent with levels reported in other seaweeds (Yuan et al., 2024), although no significant differences were observed among the three varieties. There were significant differences in AMP levels. Some studies did not detect taste nucleotides, while research on the taste amino acids and nucleotides from *Sargassum* was successfully conducted (Milinovic et al., 2020).

By comparing the concentrations of taste compounds with their taste threshold values, their potential impact on the flavor of seaweeds was assessed. Generally, a significant impact on the overall flavor of food occurs when the concentration of taste compounds exceeds their taste threshold values (i.e., TAV > 1). As shown in Table 1, the TAVs for L-Glu, L-Asp, L-His, L-Val, and L-Lys are above 1, suggesting that these amino acids significantly contributed to the flavor characteristics of seaweeds. In both NB-18 and LuLong No. 1, only the TAVs of L-Glu and L-Asp are above 1, indicating their key roles in enhancing the umami flavor of these varieties. However, in 981, in addition to these two umami amino acids, the TAVs of two bitter amino acids are also above 1, which may negatively impact the overall flavor by contributing to increased bitterness. The EUC for *G. lemaneiformis* was calculated, with the results showed that NB-18 > 981 > LuLong No. 1 (Table 1).

3.4. Volatile components of G. lemaneiformis

The aroma of seaweed is largely influenced by VOCs, which play a critical role in determining the flavor and quality of seaweeds as food products (Jensen et al., 2022). Moreover, specific VOCs can be analyzed to distinguish between different seaweed species (López-Pérez et al., 2017). To investigate the underlying reasons for differences in flavor characteristics among varieties of *G. lemaneiformis*, volatile compounds were analyzed using SPME/GC–MS. A total of 48 volatile compounds were identified, primarily including aldehydes, alcohols, ketones, and alkanes (Figs. 2, 3).

The formation of seaweed flavor is closely related to volatile compounds with low odor thresholds, with aldehydes primarily produced from lipid oxidation, which have low thresholds. Unsaturated aldehydes, such as 2-octenal and 2,4-decadienal, detected in this study, are the primary volatile flavor compounds in *G. lemaneiformis*, contributing mainly to oceanic, fishy, and fatty flavors. A total of 12 aldehydes were detected in *G. lemaneiformis*, with NB-18 exhibiting the lowest aldehyde content (Fig. 3, Table S2). The compound 2,4-decadienal, a significant fishy odor contributor, is also produced at low temperature in algae such as *Cryptomonas ovate*, *Dinobryon* sp., and *Synura uvella* samples (Guo et al., 2023), and NB-18 exhibited the lowest content in this study, with a fresh weight of 0.35 ± 0.10 μg/g (Table S2). Hexanal and heptanal are off-flavor compounds generated during the self-oxidation of lipids in the processing stage. Previous studies have indicated a high proportion of benzaldehyde, which can be derived from amino acids or formed through the oxidation of *trans*-cinnamic acid and is associated with fatty flavors (Sun et al., 2012; Yang et al., 2023). However, benzaldehyde was not found in this study, possibly due to differences in seaweed type or

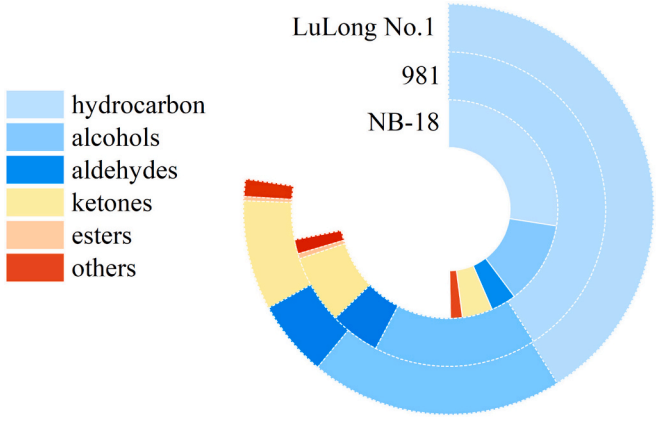

Fig. 2. Circular chart of volatile compound classification in *G. lemaneiformis*.

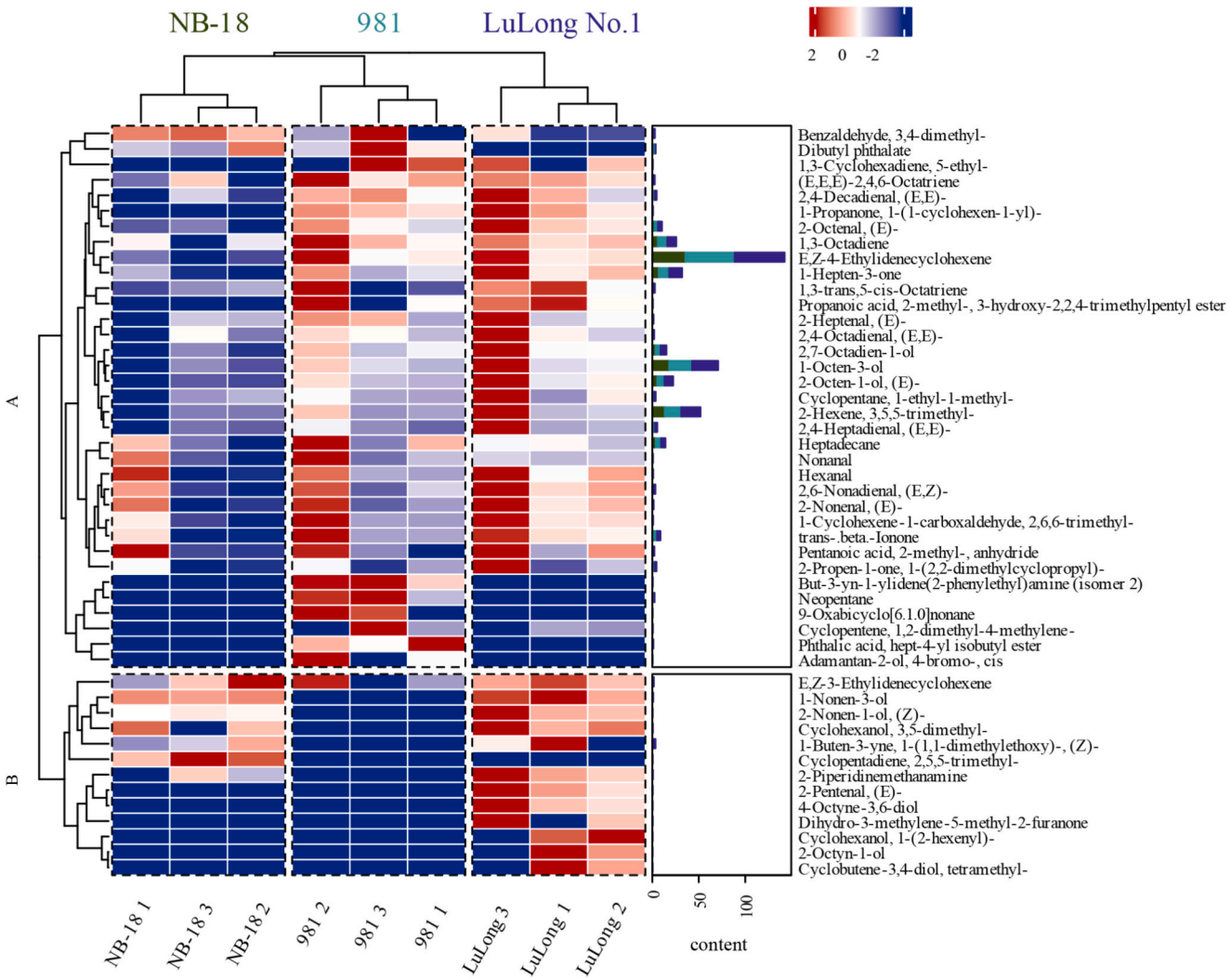

Fig. 3. Heat map and the relative content of volatile compound content in *G. lemaneiformis*.

harvest timing. Notably, it has been reported that benzaldehyde is the most abundant compound in kelp after boiling (24 %) (Yang et al., 2023). Additionally, in a study examining the harvest cycle of *Enteromorpha*, benzaldehyde levels ranged from 1379 to 1837 ppb in Autumn but dropped significantly to 36–39 ppb in spring (Mirzayeva et al., 2021).

Compared to aldehydes, alcohols are generally produced through the oxidation of linoleic acid degradation and possess higher odor thresholds. Among linear alcohols, 1-octen-3-ol, 2-octen-1-ol, and 2,7-octadien-1-ol have been identified as the dominant compounds, with the lowest level detected in NB-18, with a fresh weight of 6.05 ± 0.81, 1.79 ± 0.16, and 1.16 ± 0.21 μg/g, respectively, although they did not show significant significance with 981 (Fig. 3, Table S2). 1-octen-3-ol is commonly found in seaweed with a high concentration and plays a major role in its odor profile. This compound is a primary contributor to seaweed aroma, exhibiting high intensity. It is also a characteristic odorant in microalgae paste and mud, where it is often regarded as an off-flavor compound in food (Garicano Vilar et al., 2020; Yang et al., 2023).

Hydrocarbons have been identified as the most abundant volatile substances in *G. lemaneiformis*, primarily generated by the scission of fatty acid alkoxy radicals (Fig. 2). However, due to their high flavor threshold, they contribute little to the direct flavor of seaweed but help enhance the overall flavor profile of the product. Additionally, certain terpenes, like limonene, have been reported to help reduce off-flavors. In previous studies on red algae, hydrocarbons could constitute a significant proportion of total volatile substances, and the levels exceeding 40 % in *Spirulina* oil. In *G. lemaneiformis*, E, Z-4-ethylidenecyclohexene, 1,3-octadiene, and heptadecane were the primary hydrocarbons (Fig. 3). Among these, 1,3-octadiene is commonly present in algae and was detected in previous analyses of volatile compounds in *G. lemaneiformis*, where it was present at high levels. Heptadecane is a major volatile compound in *P. palmata* and *H. elongate* (Ecker et al., 2012). However, there are still some shortcomings in this study, such as the non-targeted volatile component detection used by GC–MS, which is insufficient in terms of the accuracy of substance identification due to the lack of reference materials. Differences in volatile compound content were observed among the varieties of *G. lemaneiformis*. Notably, NB-18 exhibited relatively lower volatile compound content levels than 981 and LuLong No.1. This lower content may contribute to the slightly superior aroma sensory attributes of NB-18, as suggested by the result of the e-nose analysis (Fig. 1A, B).

3.5. Free fatty acids of G. lemaneiformis

Fatty acids play many important roles in organisms, such as energy storage and components of cell membranes. In this study, the free fatty acids in *G. lemaneiformis* were qualitative and quantitative analyzed using GC–MS (Table S1). 14 kinds of key fatty acids were identified in three varieties of *G. lemaneiformis*, encompassing 5 saturated fatty acids

Table 2
Free fatty acid content in different varieties of *G. lemaneiformis*.

Free fatty acids	Content (mg/100 g DW)		
	NB-18	981	LuLong No.1
C14:0	41.43 ± 3.32[a]	38.85 ± 2.59[a]	21.23 ± 6.67[b]
C15:0	7.55 ± 0.20[b]	14.94 ± 0.53[a]	14.68 ± 0.65[a]
C16:0	1998.48 ± 63.73[a]	2039.56 ± 80.88[a]	1954.02 ± 71.14[a]
C18:0	764.48 ± 22.38[a]	773.82 ± 42.28[a]	759.57 ± 34.27[a]
C24:0	0.67 ± 0.09[a]	0.90 ± 0.24[a]	0.73 ± 0.24[a]
SFA	2812.62 ± 81.71[a]	2868.05 ± 121.69[a]	2750.23 ± 102.98[a]
C16:1n9t	48.86 ± 8.78[a]	56.97 ± 10.34[a]	54.82 ± 6.38[a]
C16:19c	13.11 ± 1.95[a]	10.61 ± 2.70[a]	13.42 ± 1.30[a]
C18:1n9c	88.61 ± 5.36[b]	137.32 ± 3.76[a]	133.54 ± 11.96[a]
C18:1n9t	38.29 ± 1.59[b]	43.58 ± 5.40[ab]	52.06 ± 8.07[a]
MUFA	188.86 ± 15.07[b]	248.48 ± 15.48[a]	253.84 ± 21.72[a]
C16:2	5.08 ± 0.37[b]	5.34 ± 0.56[ab]	6.28 ± 0.57[a]
C18:2n6c	9.63 ± 1.48[b]	13.39 ± 2.30[b]	20.03 ± 3.99[a]
C20:3n6	36.52 ± 3.91[a]	21.81 ± 1.75[b]	34.66 ± 2.38[a]
C20:4n6	339.64 ± 67.56[a]	128.07 ± 8.24[b]	164.04 ± 7.61[b]
C20:5n3	216.11 ± 75.88[b]	211.18 ± 14.69[b]	387.26 ± 29.69[a]
PUFA	607.00 ± 148.19[a]	379.77 ± 25.41[b]	612.28 ± 28.64[a]
ω3	216.11 ± 75.88[b]	211.18 ± 14.69[b]	387.26 ± 29.69[a]
ω6	385.80 ± 72.03[a]	163.26 ± 10.21[b]	218.73 ± 10.76[b]
ω6/ω3	1.85 ± 0.27[a]	0.77 ± 0.01[b]	0.57 ± 0.06[c]
TFA	3608.48 ± 163.08[a]	3496.31 ± 119.65[a]	3616.35 ± 97.76[a]
% of SFA	0.78 ± 0.03[b]	0.82 ± 0.01[a]	0.76 ± 0.01[b]
% of MUFA	0.05 ± 0.00[b]	0.07 ± 0.01[a]	0.07 ± 0.01[a]
% of PUFA	0.17 ± 0.03[a]	0.11 ± 0.01[b]	0.17 ± 0.01[a]

ω6/ω3: ratio of ω6 and ω3 fatty acids; TFA: total fatty acids.

(SFAs), 4 monounsaturated fatty acids (MUFAs), and 5 PUFAs, as shown in Table 2. Although the total amount of fatty acids was higher in LuLong No. 1 and NB-18, the difference was not statistically significant. Literature showed that the lipid content in algae typically does not exceed 4 % (Gressler et al., 2010). In this study, the fatty acid concentrations detected were consistent with earlier studies, further confirming the low fatty acid characteristics of *G. lemaneiformis*. Among these varieties, palmitic acid (C16:0) was the predominant SFA, accounting for approximately 2.00 % of the dry weight and more than 70 % of the total SFA. It is followed by stearic acid (C18:0) and myristic acid (C14:0). Long-chain SFAs have received attention for their potential roles in promoting platelet aggregation and thrombosis. From a nutritional and health perspective, a higher content of C18:0 compared to C14:0 is more desirable (Marques et al., 2021). In this study, the levels of C18:0 exceeded that of C14:0 in all three strains. Furthermore, the arachidonic acid (AA) and eicosapentaenoic acid (EPA), both PUFAs, also exhibited high levels in *G. lemaneiformis*. These fatty acids are notable for their unique biological activities and extensive applications in the biological, pharmaceutical, and food industries (Liu et al., 2023). These findings are consistent with previous on *Gracilaria* and the *Gelidium* (Gressler et al., 2010; Limiñana et al., 2023; Rocha et al., 2021).

For each sample, the total content of SFAs, MUFAs, and PUFAs was calculated (Table 2), revealing significant differences in fatty acid composition among the various. The fatty acid ratios of NB-18 and LuLong No. 1 closely resemble those of other red algae, such as *G. domingensis* (SFA:MUFA:PUFA = 77.7:7.5:14.8) (Gressler et al., 2010). Algae are known for their higher levels of unsaturated fatty acids compared to terrestrial plants, particularly ω-6 and ω-3 series PUFAs. These essential fatty acids cannot be synthesized by the human body and must be acquired through dietary sources (Illijas et al., 2023). Notably, higher levels of PUFA were detected in LuLong No. 1 and NB-18, with concentrations of 612 and 607 mg/100 g, respectively. The ω-6/ω-3 ratio is a critical parameter for evaluating fatty acid nutritional quality, with the World Health Organization (WHO) recommending that this ratio should be below 10 (Badmus et al., 2022). In our study, all three varieties of *G. lemaneiformis* exhibited ω-6/ω-3 ratios within the recommended range. In addition to the commonly observed *cis* fatty acids, two *trans* fatty acids containing one or more conjugated *trans* double bonds— *trans* palmitoleic acid and *trans* oleic acid—were identified. These *trans* fatty acids were present in the lowest concentrations in NB-18. And 981 had an SFA proportion of 82 %, the highest among all tested samples. In conclusion, based on fatty acid composition and nutritional quality, NB-18 demonstrated superior performance among the three varieties of *G. lemaneiformis*, while 981 exhibited a less desirable fatty acid profile, rendering it relatively less suitable for consumption.

3.6. Nutritional value analysis of *G. lemaneiformis*

Assessment of macronutrients is crucial for evaluating food quality. In this study, the basic nutritional components of NB-18, 981, and LuLong No.1 were analyzed. The evaluation of total protein in algae is typically aimed at identifying new sources of protein supplements, with protein content in different algae described in the literature as follows: red algae > green algae > brown algae. Previous studies on species of *G. lemaneiformis* reported a protein content range of 5.6 %–30 % (Francavilla et al., 2013). This study observed significant differences among the three varieties, with protein content ranging from 12 % to 16 % dry weight. The highest content was found in NB-18 (16.79 %), while the lowest was recorded in 981 (12.81 %), though all three varieties can be considered good sources of protein (Fig. 4A). Protein content not only depends on seaweed species but also closely correlated with the nitrogen content in seawater, which explains why there can be significant variations in protein content in the literature, even for the same species of seaweed (Bruhn et al., 2011). Conversely, the highest starch content was found in 981. Previous studies have reported an opposite relationship between starch and total protein under non-biotic stress (Hasan et al., 2023). During the growth of algae, both starch and protein serve as storage forms of energy and nutrients, and their synthesis and accumulation are influenced by environmental factors such as light, temperature, and nutrient availability. Under stress conditions, algae tend to prioritize starch synthesis for store energy, however, as conditions improve, the process of converting starch to protein also increases, leading to a decline in starch content and a rise in protein content (Thiviya et al., 2022). The starch concentration detected in *G. lemaneiformis* ranged from 39.29 % to 44.30 % (Fig. 4B), however, there were no significant differences among the three varieties.

Seaweed is a rich source of phenolic compounds, with red algae and brown algae generally containing higher than that in green algae (Park et al., 2023). Various phenolic compounds, such as bromophenols, phenolic acids, flavonoids, phenyl terpenes, and mycosporine-like amino acids, play a crucial role in cellular defense mechanisms of algae, enabling algae to withstand both abiotic and biotic stresses. In *Gracilaria verrucosa*, the TPC has been reported as 275.5 ± 7.5 μg GAE/g dry weight. This study shows that the TPC of *G. lemaneiformis* ranges from 1.76 to 2.73 mg GAE/g dry weight, with LuLong No. 1 exhibiting the highest TPC and 981 showing the lowest (Fig. 4C). In addition to their antioxidant properties, phenolic compounds contribute to bitterness, a characteristic noted in sensory evaluations of food (Jensen et al., 2022). Flavonoids possess antibacterial, antifungal, and anti-allergic properties. In this study, the content of flavonoids showed a similar content of 4.98–5.81 mg/g, with no statistical significance (Fig. 4D). However, this study still has a limitation in the detection of certain substances, such as flavonoids and phenolic, which could benefit from employing HPLC or LC-MS, which would provide more detailed results in future studies.

4. Conclusions

In summary, this study indicates that different varieties of *G. lemaneiformis* exhibit distinct nutritional profiles and flavor characteristics. Notably, NB-18 is rich in flavor-enhancing amino acids, with the lowest levels of bitter amino acids and volatile compounds, making it a superior variety in flavor quality. Furthermore, the detection of free fatty acids, with a particular emphasis on ω-6 and ω-3 PUFAs, indicates that *G. lemaneiformis* can confer significant health advantages. The high

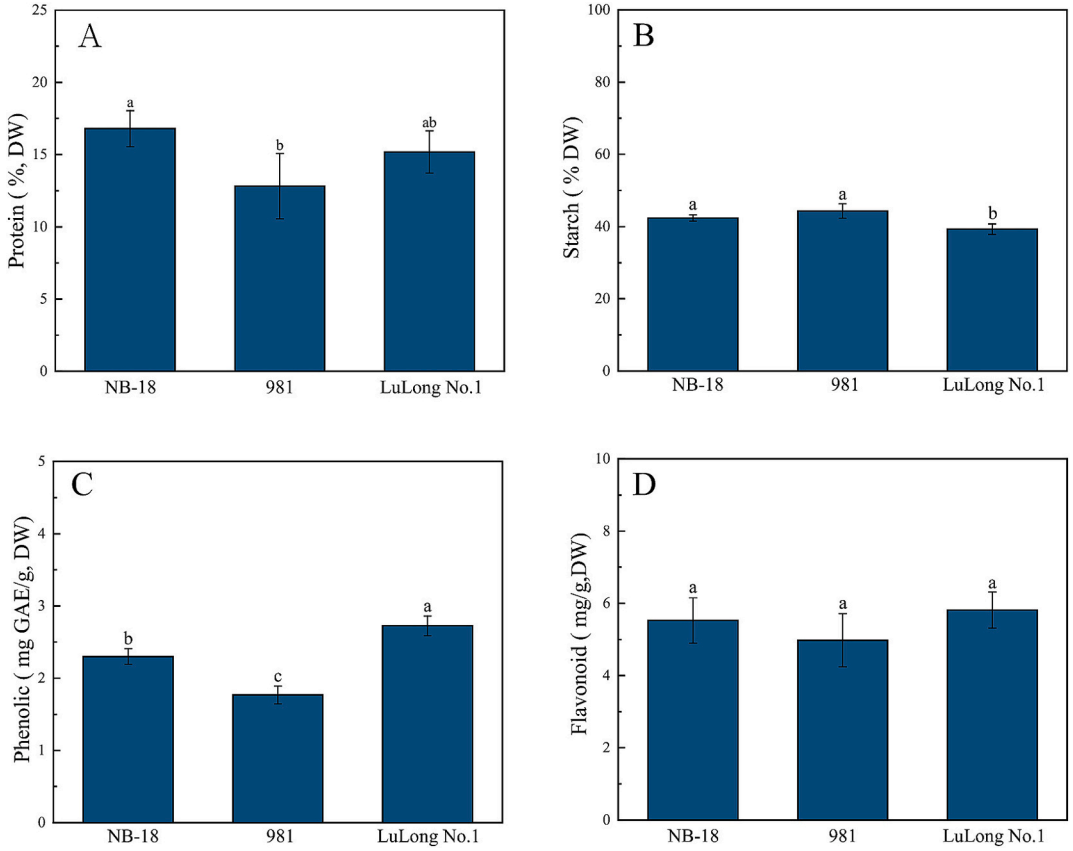

Fig. 4. Nutrient content in *G. lemaneiformis*. (A) Protein content; (B) Starch content; (C) Total phenol content; (D) Flavonoid content.

content of phenolic compounds and flavonoids further emphasizes their antioxidant properties, contributing to the sensory quality of food. Overall, these findings provide valuable insights into the potential applications of *G. lemaneiformis* in food science and highlight its value as a functional food ingredient. Future research should incorporate more nutritional parameters, which will be crucial in demonstrating the market potential of *G. lemaneiformis*.

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CRediT authorship contribution statement

Na Zhou: Writing – original draft, Visualization, Investigation, Formal analysis, Conceptualization. **Mengyao Zhao:** Investigation, Formal analysis. **Xue Sun:** Writing – review & editing, Resources, Funding acquisition. **Chaoyang Hu:** Methodology, Investigation, Formal analysis. **Nianjun Xu:** Writing – review & editing, Funding acquisition, Conceptualization.

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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fochx.2025.102332.

Data availability

Data will be made available on request.

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