



Changes in volatiles and sensory profiles during storage of dried *Ulva fenestrata*: Effects of pre-rinsing and drying temperatures in a large-scale

Downloaded from: <https://research.chalmers.se>, 2026-10-15 07:45 UTC

Citation for the original published paper (version of record):

Vall-Llosera Juanola, M., Wendin, K., Mendez, R. et al (2026). Changes in volatiles and sensory profiles during storage of dried *Ulva fenestrata*: Effects of pre-rinsing and drying temperatures in a large-scale setting. *Journal of Food Composition and Analysis*, 159. <http://dx.doi.org/10.1016/j.jfca.2026.109540>

N.B. When citing this work, cite the original published paper.



Changes in volatiles and sensory profiles during storage of dried *Ulva fenestrata*: Effects of pre-rinsing and drying temperatures in a large-scale setting

Mar Vall-Ilosera^{a,*}, Karin Wendin^{b,c}, Rufa Mendez^a, Göran Nylund^d, Henrik Pavia^e, Ingrid Undeland^{a,*}

^a Chalmers University of Technology, Department of Life Sciences– Food and Nutrition Science, Gothenburg, SE-412 96, Sweden

^b Faculty of Natural Sciences, Kristianstad University, Kristianstad, SE-291 88, Sweden

^c Department of Food Science, University of Copenhagen, Rolighedsvej 26, Frederiksberg C, DK-1958, Denmark

^d Nordic SeaFarm, Prästängsvägen 8, Strömstad, SE-452 33, Sweden

^e Department of Marine Sciences, Tjärnö Marine Laboratory, University of Gothenburg, Strömstad, SE-452 96, Sweden

ARTICLE INFO

Keywords:

Macroalgae

Aroma

Headspace solid-phase microextraction (SPME)

Sensory attributes

Antioxidant

Colour

ABSTRACT

Large-scale oven drying was investigated as a stabilising method for *Ulva fenestrata*, focusing on odour, taste, volatile organic compounds (VOC), and colour during 550 days of storage. Sea-farmed biomass was either rinsed with tap water or antioxidant solution (AO) prior to drying at 40 °C or 60 °C. During storage, all samples showed an increase in a*-values and perceived loss of greenness, consistent with chlorophyll loss. However, AO-rinsing with 60 °C-drying best preserved colour, with only a 10 % loss of chlorophyll and 15 % reduction in greenness as assessed by the sensory panel. The flavour profile changed over time, especially in non-AO-treated samples, with a decline in seaweed odour, and appearance of “hay-like” and “rosehip soup” notes. In contrast, umami taste remained unchanged regardless of treatment, which was also true for amino acid content. Key VOCs were pentanal, hexanal and heptanal, however, each following a different kinetic pattern during storage. Drying at 40 °C led to greater VOC-formation and green colour loss than 60 °C + /-AO. As an example, hexanal, concentrations were almost 90 % higher after drying at 40 °C versus 60 °C, in both non-rinsed and water-rinsed samples. Altogether, drying at 60 °C is recommended, preferably combined with AO-rinsing if seaweed smell is desired.

1. Introduction

Seaweeds are versatile food ingredients with a distinct flavour profile, such as salty, grassy and umami taste (Jönsson et al., 2023). Among green seaweeds, *U. fenestrata* is one of the emerging aquacultured species, known for its resistance to changes in abiotic conditions such as salinity (Vall-Ilosera et al., 2024). However, just like other seaweed species, *U. fenestrata* deteriorates quickly after harvest, limiting its use in the food industry. Stabilisation is therefore necessary to maintain safety and the sensory properties of *U. fenestrata* for its use in the food industry.

Oven drying is a widely used stabilization technology due to its scalability (Wirenfeldt et al., 2024), faster processing compared to freeze-drying or sun-drying, and its independence of weather conditions (Vega-Gálvez et al., 2022). However, selecting the correct drying

temperature is critical, and often becomes a compromise between seaweed properties (Regal et al., 2020) and dehydration speed, the latter crucial at industry scale. Drying at 60 °C was previously found to increase chlorophyllase activity (Hutchings, 1994), and to promote the oxidation of fatty acids generating volatile aldehydes (Michel et al., 1997). Triggers of lipid oxidation in seaweed can be e.g., lipoxygenase (LOX) (Kim and Min, 2008; Kuo et al., 1997) or trace elements (Domínguez et al., 2019), and along with its progression, particularly radical generation, pigments such as chlorophylls can also co-oxidize, whereby the conjugated diene systems providing colour are lost (Kim and Min, 2008). Several studies on seaweed have reported how drying at ≥ 60 °C resulted in larger pigment loss, especially chlorophyll, compared to drying at lower temperatures (Michel et al., 1997; Moreira et al., 2016; Uribe et al., 2019, 2018). For *Ulva* spp., this is highly critical

* Corresponding authors.

E-mail addresses: marv@chalmers.se (M. Vall-Ilosera), undeland@chalmers.se (I. Undeland).

<https://doi.org/10.1016/j.jfca.2026.109540>

Received 23 January 2026; Received in revised form 28 August 2026; Accepted 20 September 2026

Available online 21 September 2026

0889-1575/© 2026 The Author(s). Published by Elsevier Inc. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

since the characteristic green colour is a quality indicator (Uribe et al., 2019).

Thus, removal or inactivation of pro-oxidants such as metals and/or LOX is along with radical scavenging desirable to prevent both bleaching and compositional changes; the latter comprising not only aldehyde developments but also potential losses of sensitive amino acids and endogenous antioxidants. In a previous work on LOX from *Ulva lactuca*, it was found that inactivation took place at temperatures of $> 50^{\circ}\text{C}$ (Kuo et al., 1997), while rinsing procedures resulted in leaching of metals and salts (Poeloengasih et al., 2019). Very limited work is however, done on direct routes to stabilise dried seaweed against oxidation. Only one study reported the use of a whey coating to protect *U. fenestrata* and *Porphyra umbilicalis* during and after drying at 40°C (Harrysson et al., 2021). Although the whey solution decreased aldehyde development, it did not prevent the loss of polyunsaturated fatty acids and vitamin C over 370 days (Harrysson et al., 2021). A successful related technology, which has previously been applied to herring side streams, involves soaking or dipping the raw materials in antioxidant solutions prior to further processing (Wu et al., 2021). In repeated studies on this topic, the oxidation lag phase of the raw material was extended from 1 to 12 days on ice. Compared to adding antioxidants post stabilisation, e.g., during refinement into a product, a pre-dipping entails protection also during the actual stabilisation process, which can then follow into the end product. Further, in relation to for example pulsed electric field (PEF), pressure- or heat-based methods to specifically inhibit enzymes, antioxidant-dipping is also significantly less energy-consuming and tackles both enzymatic and non-enzymatic oxidation. As a secondary effect, pre-rinsing can also dilute ash, thus, beneficial for example, for partial removal of heavy metals (van Tuinen et al., 2023).

Overall, while there is existing data on the relation between volatiles and sensory descriptors for dried or semi-dried brown and red seaweed (López-Pérez et al., 2017; Stévant et al., 2020; Vilar et al., 2021), to the best of our knowledge, only two studies have been done on *Ulva* spp. (López-Pérez et al., 2017; Michel et al., 1997). Of these, the French study by Michel et al. (1997) is the only one following storage-induced developments in *U. lactuca*. However, none of the studies rely on large-scale drying, which limits their extrapolation to industrial settings (Stévant and Rebours, 2021).

Based on the above, we hypothesised that large-scale drying at 60°C would improve the dehydration efficiency compared to a lower drying temperature (here 40°C), but at the same time, that it would jeopardize quality due e.g., to lipid and pigment oxidation. As a route to reduce metal-induced oxidation at the higher temperatures, (Crobotova et al., 2019; Cui et al., 2023; Maestre et al., 2011) and thereby slow down sensory deterioration, we hypothesised that dipping or rinsing the seaweed biomass in an antioxidant solution containing both metal chelators and radical scavengers prior to drying at 60°C would be an effective strategy. Such a treatment could also leach out some of the low molecular weight (LMW) metals. To test these hypotheses, we here subjected differently pre-treated and dried *U. fenestrata* to long-term storage while following instrumental colour changes, volatile

compounds, sensory attributes, amino acid composition, pigments and LOX-activity. Elements were also analyzed at start of the storage. Five different process combinations were used, comprising rinsing in water with or without an antioxidant, as well as large-scale oven drying at 40 or 60°C .

2. Material and methods

2.1. Seaweed material

Sea-farmed *U. fenestrata* was harvested from the Nordic Seafarm cultivation site (Tjärnö, Sweden) in May 2023. Two separate batches were collected: Batch 1 on May 2nd and 3rd and Batch 2 on May 9th and 10th (Fig. 1). After landing, the biomass was manually cleaned to remove epiphytes and other non-seaweed materials.

The biomass was then subdivided into 70 kg lots per treatment. On May 2 and 9, each 70 kg material was subjected to one of the three pre-treatments (Fig. 1). One lot was left untreated (NR60), one was rinsed in chilled water at 8°C for 30 s (R60), and the remaining lot was rinsed with an antioxidant solution (AO) of 2 % AO (w/w), Duralox MANC-213 (Kalsec, UK) in water at 8°C , for 30 s (RI60). Rinsed seaweed biomass were drained by gravity with a sieve to remove excess AO solution or rinse water. All 3 treated sub-lots were then loaded into an industrial dryer (AB Alvan Blanch, England) and dried at 60°C . The dryer was initially run at an inflow temperature of 69.6°C and continued until the outflow temperature reached 60°C . Then, both the inflow and outflow temperatures were maintained at 60°C until all three sub-lots had a water activity (a_w) of 0.25. During the drying period, a pitchfork was used every hour to mix and loosen the biomass to ensure comparable heat distribution.

For drying at 40°C , two sub-lots of 70 kg each were harvested on May 3rd and 10th. One lot was rinsed in chilled tap water, as explained above (R40). While the remaining lot was left untreated (NR40). Drying was done at an initial inflow of 50°C , reduced to 40°C once the outlet reached equilibrium. As with the 60°C drying, the endpoint was defined at a_w 0.25. Based on the hypothesis that 60°C drying would be most critical from the perspective of metal-induced oxidation (Cui et al., 2023), drying at 40°C was not combined with AO-treatment, something which also allowed for more frequent sampling points during storage, while still keeping down the total sample number.

For readability, all samples will be referred to by the following abbreviations: NR60, R60, RI60, NR40, and R40. The biomass varied significantly between the two batches. Batch 2, was harvested at a later time point, exhibiting signs of lower quality by being paler and with higher yellowness. Consequently, Batch 1 is presented as it more accurately reflects the biomass composition under optimal harvest conditions. Nevertheless, statistical analysis was performed for both batches 1 and 2, and both showed similar trends over the storage period across the different treatments. Key volatiles and yellowness for batch 2 are found in the supplementary (Fig.S7 and S8)

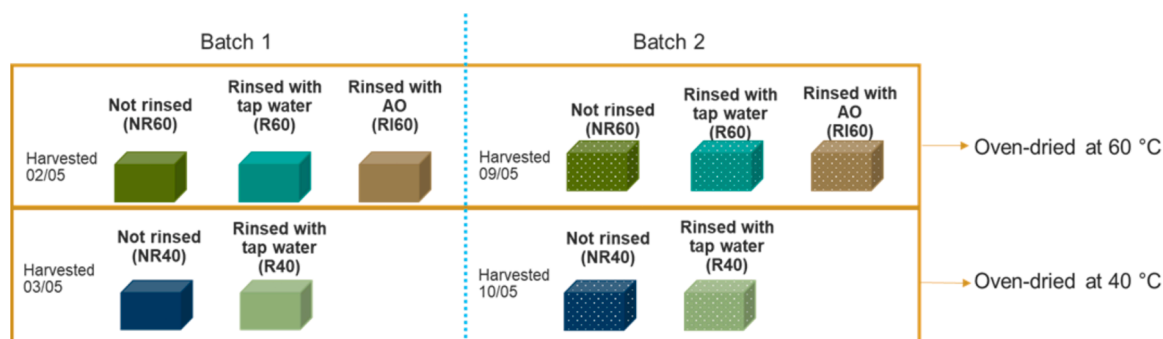


Fig. 1. Experimental design followed in this study.

2.1.1. Drying curves

Drying curves were constructed by sampling three random samples taken from different parts of the dryer (the bottom, middle and surface of the biomass layer) every hour for every treatment from the start of the drying process until the samples reached the set a_w of 0.25. The measurements were performed in triplicate using a Novasina LabMaster-aw (Novasina AG, Switzerland). The a_w of the dried biomass was assessed again at the end of the storage.

2.1.2. Storage conditions

After drying was completed, 100 g of whole dried *U. fenestrata* were packed in polyethene bags, a type which is already used by industry, and thermally sealed. Multiple bags were packed for each treatment. The bags were then placed in a cardboard box (560 × 330 × 406 mm) and stored in the dark at room temperature of 21 ± 4 °C and a relative humidity of 27 % at the start of the trial in early spring. Sampling was done at 0, 60, 180, 415 and 550 days based on previous research outcomes (Harrysson et al., 2021). At each time point, a random bag was removed and placed at - 80 °C until further analysis. Prior to analysis, the seaweed material was ground using a coffee grinder until > 90 % of the powdered dried *U. fenestrata* had a particle size of < 0.25 mm.

2.2. Moisture and ash content

The moisture content was measured gravimetrically using the AOAC method 925.10. Subsequently, the ash content was determined by dry incineration, following the AOAC method 938.08. Moisture and ash were measured on days 0 and 550 ($n = 3$) and are reported on a dry weight basis.

2.3. Colourimetric analysis

Colour measurements were done on powdered *U. fenestrata*. Approximately 1 g of each sample was spread into a 40 mm diameter TPPM Petri dish (TPP, Switzerland), covering the entire bottom. Colour coordinates (L^* , a^* , b^*) were obtained in triplicate using Chroma Meter CR-400 (Konica Minolta, USA) with a D65 illuminant and 10° standard observer angle. Multiple reads were obtained from three different locations of the plate at all storage time points ($n = 3$).

2.4. Chlorophyll and carotenoids analysis

Chlorophyll a and b, as well as, carotenoids were determined on all 5 sample types based on the description by Steinhagen et al. (2021), for timepoints 0, 180 and 550 days.

2.5. Amino acid composition

Amino acid analysis followed the same procedure as described by Harrysson et al. (2018), with some modifications. One hundred milligrams of dry *U. fenestrata* were dissolved in 4 mL of 6 M HCl, and hydrolysis was conducted at 110 °C for 24 h. After filtering with a 0.25 µm PET filter, 1 µl of the filtrate was dissolved in 190 µl of 0.2 M acetic acid, and flushed with nitrogen.

Two microliters of hydrolyzed sample was injected into the LC-MS system, an Agilent 1260 HPLC (Agilent Technologies, Germany) with a column from Phenomenex (C18 (2) 250 µm X 4.6 µm, X 3 µm). The system is coupled with Agilent 6120 quadrupole in positive mode (Agilent Technologies, Germany).

Amino acid quantification was performed using a standard mix, Pierce Amino Acid Standard H (Ref. 20088, Thermo Fisher Scientific Inc., USA), containing 24 amino acids. The standard curve had a concentration range of 0.25–0.0078 µmol/mL for each amino acid dissolved in 0.2 M acetic acid. Only time points 0, 180, and 550 days were selected for amino acid analysis, which was performed in triplicate ($n = 3$).

2.6. Lipoxigenase (LOX) activity

Macroalgal LOX activity was determined using the methods described by Kuo et al. (1997) and Tsai et al. (2008) for *Ulva* spp. with some modifications. Briefly, 1 g seaweed powder was suspended in 19 mL extraction buffer of 50 mM Phosphate buffer (pH 7.5) with 0.2 mM CaCl_2 , 0.05% Triton-165 and 1 mM reduced glutathione. Followed by a 30 min chilled incubation with homogenisation at 16000 rpm for 2 min using IKA-ultraturrax. The suspension was then clarified by centrifugation at 20000 x g for 30 min at 4 °C, and stored until analysis.

Fresh assay buffer (2.7 mL) of same concentration as the extraction buffer containing 100 µM linoleic acid and 0.01 % Tween-20 was dispensed in 5 mL tubes prewarmed at 25 °C. Then 300 µl of the seaweed extract was loaded, mixed and incubated for 15 min at 25 °C during which absorbance was monitored at 234 nm. The reaction was terminated with 15 µl of 12 N HCl until pH was 3, and LOX activity was calculated following the formula reported by Vick (1991) and reported as units (U) per gram (dw).

2.7. Volatile compound analysis

Volatile compounds were analysed by headspace solid-phase microextraction (HS-SPME) coupled with gas chromatography-mass spectrometry (GC-MS). One gram of dried milled seaweed was placed in a 20 mL amber vial (Skandinaviska Genetec AB, Sweden), capped with an 18 mm screw cap and 1.3 mm silicone/PTFE septum. Samples were pre-incubated at 37 °C for 15 min in the autosampler AOC 5500 (Shimadzu, Japan), before exposing a 75 µm CAR/PDMS SPME fibre (Supelco, Merck, USA) to the headspace for 15 min. In order to simulate the conditions during sensory analysis, no water was added to the dried seaweed and the samples were incubated at 37 °C, as this temperature reflects that of the mouth.

The SPME fiber was then inserted into the injection port of the GC (splitless mode, TQ-8050 (Shimadzu, Japan), equipped with a ZB-1701 column (Phenomenex, USA) operating with a temperature program of: 35 °C (3 min hold), ramp to 70 °C at 3 °C min⁻¹ (2 min hold), then to 200 °C at 10 °C min⁻¹, followed by 260 °C at 20 °C min⁻¹ (5 min hold). Each sample was extracted and analysed in triplicate.

Quantification was based on external calibration using a six-point standard curve ranging from 3 to 100 ng g⁻¹ dry *Ulva*, (or up to 150 ng g⁻¹ for high-abundance analytes, split injection 1:2). Standards were spiked into a pooled matrix of all dried samples. Quantified analytes included hexanal, heptanal, octanal, nonanal, 2,4-heptadienal, pentanal, 1-amybutanol, benzaldehyde, and 2-pentylfuran, all purchased from Merck (Merck inc., USA). The standard curves are provided in the Supplementary Table S7.

2.8. Sensory properties

Sensory analysis was conducted at Kristianstad University in compliance with ISO 13299:2016. The analytical panel was formed by seven panellists selected and trained in accordance with ISO 8586:2012. The panel evaluated the sensory attributes based on a consensus vocabulary developed prior to the main analysis (Supplementary Table S2). For each powdered seaweed sample, 4 g were placed into a plastic container 3.25 oz (Height: 36 mm; Diameter top: 73 mm; Diameter bottom: 52.8 mm), closed, and equilibrated at room temperature (21 °C) for 2 h prior to analysis. Samples were randomised per assessor and analysed in triplicate using EyeQuestions software (version 6, The Netherlands).

The sensory assessments were performed on separate occasions, and to ensure comparability across sessions, the sensory ratings were z-score normalised using the mean of the second session.

2.9. Elemental composition

Dried *U. fenestrata* samples were subjected to acid digestion and analysed by ICP-SFMS, by a certified laboratory using a combination of internal standard and external calibration (Engström et al., 2004; Österlund et al., 2009; Rodushkin et al., 2008).

2.10. Statistical analysis

All statistical analyses were performed in RStudio (version 4.4.2) using the following packages: "dplyr", "agricolae", "FSA", "MASS", "Hmisc", "ggcorplot", "pls" and "emmeans". The data was tested for normality and homogeneity of variance using the Shapiro–Wilk and Levene's tests, respectively. Where assumptions were met, a two-way ANOVA was carried out followed by a post-hoc Tukey's HSD test to identify significant differences ($p < 0.05$). When assumptions failed, even after logarithmic transformation, the Kruskal–Wallis test was done, followed by a Dunn's test post-hoc analysis with the Benjamini–Hochberg correction.

Pearson correlation analysis was performed in SPSS (version 29, IBM, USA) to explore the associations between colour, volatiles, and sensory attributes. Partial least-squares regression (PLSR) was executed using mean-centred values ($n = 3$ for all measurements), following the validation and method as explained by Stévant et al. (2026).

3. Results and Discussion

3.1. Drying curves, moisture and ash content

Drying at 40 °C required more time to reach the set a_w compared to drying at 60 °C (Supplementary Fig.S1). After 3 h, the NR60 and R60 samples presented significantly lower a_w values than those dried at 40 °C and RI60 samples (Supplementary Table S1). The low drying rate for RI60 could be due to the formation of a “glazing” layer on the blades during rinsing with AO, which might have delayed the drying. For samples dried at 40 °C, pre-rinsing had no significant effect on the a_w kinetics during drying.

The moisture content of rinsed and non-rinsed samples was not significantly different before drying, suggesting that rinsing did not induce neither significant water loss, nor uptake in *U. fenestrata* (Table 1). After drying, the moisture content was similar for all samples, ranging from 5.25 % to 7.74 %. Rinsing prior to drying significantly lowered the ash content to 20–25 % in dried *U. fenestrata*, compared to

Table 1

Moisture and ash content (%) as well as water activity (a_w) for all treated samples, before and after drying, and after 550 days of storage. Data are shown as mean values $\pm$ standard deviation (SD), $n = 3$. Different superscripts lower-case letters indicate significant differences within the same treatment ($p < 0.05$), whereas, different upper case letters indicate significant differences between treatments ($p < 0.05$).

Sample	Day	Moisture%	Ash%	A_w
NR60	Before drying	83.1 $\pm$ 0.20 ^A	-	0.97 $\pm$ 0.009 ^A
	After drying	5.25 $\pm$ 0.08 ^A	29.61 $\pm$ 0.20 ^{AB}	0.16 $\pm$ 0.003 ^A
	550	12.78 $\pm$ 0.09 ^A	28.99 $\pm$ 0.52 ^{AB}	0.38 $\pm$ 0.001 ^A
NR40	Before drying	83.38 $\pm$ 0.30 ^A	-	0.94 $\pm$ 0.013 ^A
	After drying	7.76 $\pm$ 0.16 ^A	30.21 $\pm$ 0.0 ^{AA}	0.17 $\pm$ 0.001 ^A
	550	13.73 $\pm$ 0.02 ^A	30.00 $\pm$ 0.35 ^{AA}	0.43 $\pm$ 0.001 ^A
R60	Before drying	84.30 $\pm$ 0.20 ^A	-	0.97 $\pm$ 0.009 ^A
	After drying	5.90 $\pm$ 0.03 ^A	24.08 $\pm$ 0.10 ^{BA}	0.12 $\pm$ 0.002 ^A
	550	12.90 $\pm$ 0.05 ^A	27.03 $\pm$ 1.55 ^{BA}	0.39 $\pm$ 0.001 ^A
R40	Before drying	84.89 $\pm$ 0.15 ^A	-	0.94 $\pm$ 0.013 ^A
	After drying	7.74 $\pm$ 0.14 ^A	25.07 $\pm$ 0.14 ^{BA}	0.12 $\pm$ 0.001 ^A
	550	13.19 $\pm$ 0.09 ^A	26.42 $\pm$ 1.38 ^{BB}	0.39 $\pm$ 0.005 ^A
RI60	Before drying	85.59 $\pm$ 0.30 ^A	-	0.97 $\pm$ 0.009 ^A
	After drying	5.46 $\pm$ 0.08 ^A	22.64 $\pm$ 0.33 ^{CA}	0.24 $\pm$ 0.001 ^A
	550	13.02 $\pm$ 0.13 ^A	23.05 $\pm$ 1.51 ^{CA}	0.40 $\pm$ 0.003 ^A

28–30 % ash content found in non-rinsed *U. fenestrata* on day 0. These results are in line with previously reported ash content for oven-dried *U. fenestrata* after pre-washing in fresh water and unwashed *U. fenestrata*; 24.9 % and 38.1 %, respectively (Harrysson et al., 2021).

After 550 days, the moisture content of all samples doubled as also reflected with the a_w across treatment (Table 1). This suggests that *U. fenestrata* was hygroscopic, capturing the humidity of the remaining air in the bag when packed until reaching an equilibrium during storage. Absorption of moisture was also seen by Regal et al. (2020) when *A. taxiformis* was oven-dried at 60 °C and subsequently stored at room temperature for 3 months. Similar to the present study, these authors also did not see any changes in ash content parallel to the moisture change during storage.

The a_w of all samples after 550 days were above the minimum identified for oxidation reactions such as lipid oxidation to occur (0.3 a_w) (McClements and Decker, 2007). This can be a contributing reason to the increases in hexanal, pentanal, and colour loss as further outlined below.

3.2. Colour stability over storage

As hypothesised, dried *U. fenestrata* showed significant colour changes during the long-term storage, which was previously reported by Harrysson et al. (2021), and was likely due to the chlorophyll co-oxidizing with lipids (Kim and Min, 2008). As shown in Fig. 2A, overall colour changes were minimal ($\Delta E < 2$) during the first 180 days except for *U. fenestrata* pre-rinsed i.e., R40 and RI60, and the not pre-rinse NR40 sample. After that period, all treatments, regardless of rinsing or drying temperatures, exhibited a ΔE of > 3 , which is considered the threshold for the human eye to detect colour differences (Silva et al., 2019). Pictures of the powder analysis for each time point can be seen in Supplementary Fig S5.

The green hue, reflecting chlorophyll, is a characteristic feature of *Ulva* spp. represented in the CIELAB coordinates as a^* -value. The lower or more negative the a^* -value, the greener the sample. Initially, the samples dried at 40 °C resulted in a significantly higher greenness compared to those dried at 60 °C (Fig. 2B), which could be a result of previously described thermal instability of chlorophyll above 50 °C (Andrés-Bello et al., 2013). From samples dried at 60 °C, the RI60 was found to have the least green hue directly after drying, possibly due to the acidic nature of the antioxidant solution. The Duralox-treated samples had a pH of 4.25 vs pH 7 of rinsed and no rinse samples. Acidic environment in combination with higher drying temperature could stimulate Mg^{2+} -loss from the porphyrin ring, leading to a more olive-green colour (Andrés-Bello et al., 2013).

Over time, the a^* -value increased for all samples, indicating a loss of greenness, which was significant after 415 days. At the end of storage *U. fenestrata* dried at 40 °C showed the most considerable changes, with R40 and NR40 revealing Δa^* -value of 3.6 and 4.2 from day 0 – 550 days, respectively. Compared to Δa^* -value of 2.5 in NR60 from day 0 – 550 days (Fig. 2B), RI60 and R60 had a Δa^* -value of 3.5 and 2.8, respectively.

Directly after drying, the samples presented positive b^* -values, indicating a predominance of yellow hue with no significant difference among treatments. Over time, in contrast to greenness, yellowness (b^* -value) remained unchanged for 3 out of the 5 treatments (NR60, R40 and R60). However, RI60 had a statistically significant increase of 25 % after 415 days compared to the initial b^* -value (Fig. 2C), while NR40 showed a significant reduction of 21 % between day 0 and 415 of storage.

Regarding lightness (L^* -value), initially, all samples presented no significant difference directly after drying. However, over time, the L^* -value increased and significant changes were seen after 415 days. After 550 days, water-rinsed samples had a significantly higher L^* -value than untreated samples (Fig. 2D). Specifically, R40 exhibited the highest L^* -value, followed by R60 $>$ NR40 $>$ NR60 $>$ NR40 $>$ RI60.

In agreement with our data, previous studies reported an increase in

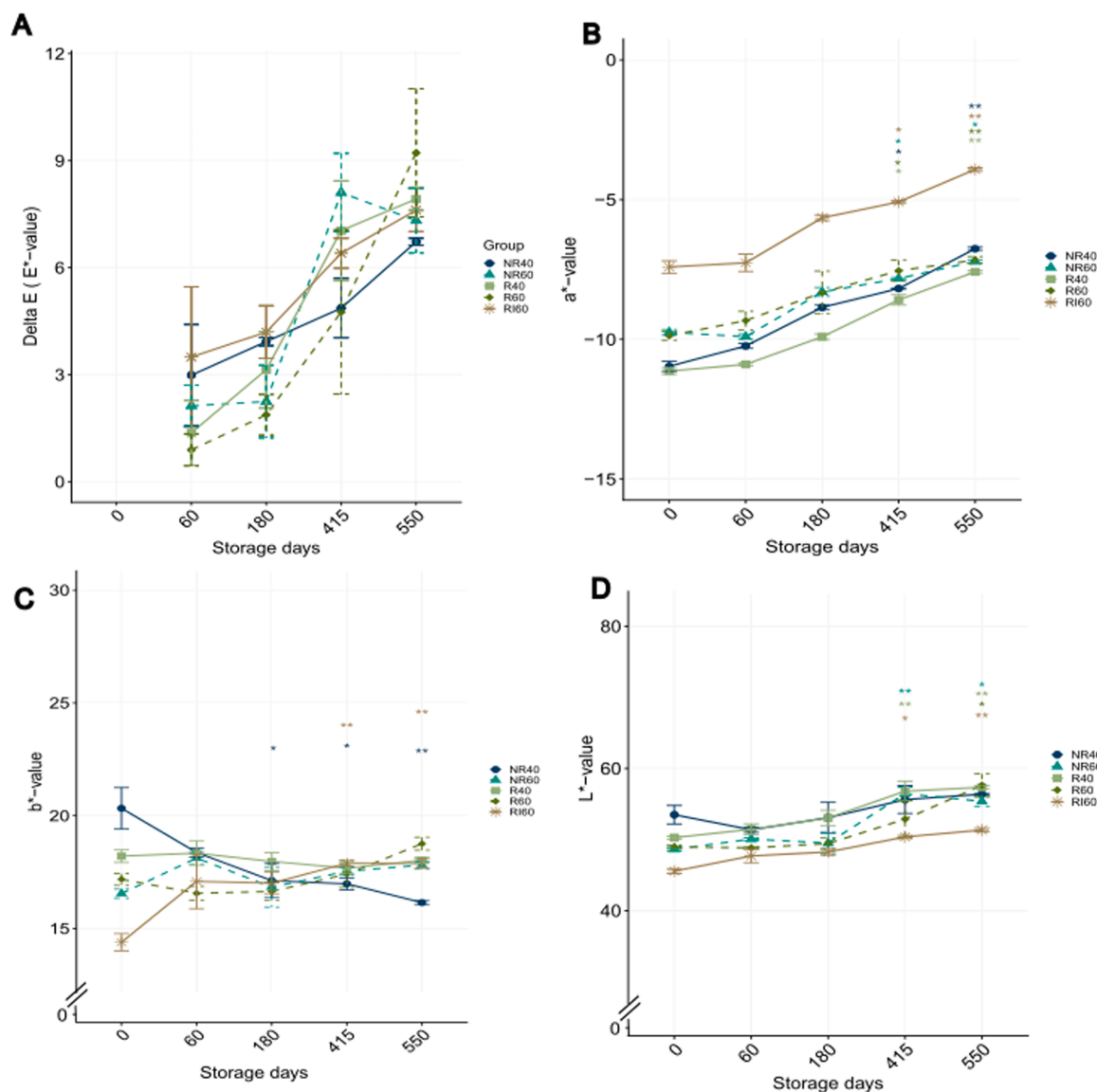


Fig. 2. Colour changes in *U. fenestrata* during storage are shown as: (A) total colour difference (ΔE , range 0–12), (B) a^* -value or redness (a , range 0 to –13), (C) L^* -value or lightness (L , range 0–100), and (D) b^* -value or yellowness (b , range 0–30). Treatments include samples rinsed in water and dried at 40 °C (NR40, $\bullet$) or 60 °C (NR60, $\blacktriangle$), untreated samples dried at 40 °C (R40, $\blacksquare$) or 60 °C (R60, $\blacklozenge$), and samples rinsed in antioxidant solution (AO) and dried at 60 °C (RI60, $\blacklozenge$). Statistical significance compared with day 0 is indicated by asterisks: $p < 0.1$ (*), $p < 0.05$ (**), and $p < 0.01$ (***).

a^* -value in oven-dried (40 °C) *U. fenestrata* after 150 days of storage (Harrysson et al., 2021). A likely reason for the loss of greenness is co-oxidation with lipids during storage resulting in loss of chlorophyll; triggered e.g., by LOX and trace elements in the biomass (Kim and Min, 2008). LOX activity of *U. fenestrata* dried at 40 °C remained stable throughout the 550 days of storage (Supplementary Fig S4). After drying, the total element content decreased when *U. fenestrata* was rinsed, although still present in substantial amounts (Supplementary Table S4). The lower a^* -value observed for RI60 at time 0 was initially thought to result from chlorophyll loss. However, high chlorophyll a and b content was found in this sample on day 0 (Supplementary Fig S2). A possible explanation is that absorbance-based chlorophyll measurements used in this study could not distinguish between chlorophyll a and chlorophyllide a or pheophytin a (McClements and Decker, 2007; Osório et al., 2020). The latter formed under the acidic conditions, which were the case in this sample (pH 4.7 compared to pH 7 in the rest of samples). Pheophytin a is known to contribute to a green-olive colour, while chlorophyllide a has more of a blue-green colour (Heaton and Marangoni, 1996).

The initial a^* -values were also reduced for *U. fenestrata* rinsed in water, indicating that rinsing *per se* resulted in leakage of minerals or enzymes that led to pigment loss during the drying, e.g., via co-oxidation pathways. This was supported by lower chlorophyll content for those samples rinsed in water and dried at 40 °C (Supplementary Fig S2). Samples dried at 60 °C yielded less greenness losses during storage compared to 40 °C, which could be linked to the significant decrease in LOX-activity (Supplementary Fig S4). Previous work by Kuo et al. (1997) on seaweed LOX reported 35 °C as the optimal temperature for the enzymes, while it abruptly decreased around 50 °C. Further, LOX from mackerel was previously found to be inhibited ≥ 60 °C (Liu et al., 2023). Thus, a possible explanation for the partial activity loss over time when *U. fenestrata* was dried at 60 °C could be due to an inactivation threshold of 50 °C in this case. For future studies, higher temperatures than 60 °C, should be explored for inactivating LOX in seaweed during drying.

However, drying at lower temperature (40 °C) resulted in a larger decrease in yellowness (b^* -value) over time compared to drying at 60 °C (Fig. 2C), which corresponded to a more pronounced loss of carotenoids

at the end of the storage (Supplementary Fig S3). As for chlorophyll, these changes could reflect pigment-co-oxidation with lipids (McCauley et al., 2018), given that carotenoids are strong radical scavengers (Mortensen and Skibsted, 1997). On the contrary, RI60 increased in yellowness (b*-value) over time, despite a loss of carotenoids. This phenomenon is however likely not oxidation-based, but rather stem

from yellow pigments from the antioxidant solution, becoming more visible as greenness decreased. Overall, significant colour changes were thus observed in all treatments already after 415 days of storage, with NR60 showing the least alterations across L*a*b*-coordinates.

Table 2

Volatile compounds in the differently pre-treated and dried *U. fenestrata* over the storage time for all samples, expressed as mean ±SD (ng/ g dried *U.fenestrata*), and the corresponding odour threshold (ODT) as determined for semi-dried golden pompano, egg yolk and water.

Volatiles		Aldehydes (n-alkanals)				
		Hexanal	Pentanal	Heptanal	Octanal	Nonanal
Samples	ODT Days	4.5 ^x	12–42 ^{yz}	3 ^x	0.7 ^x	1 ^x
NR40	0	98.11 ± 6.73 ^{abA}	54.91 ± 8.36 ^{abA}	65.24 ± 33.43 ^{aA}	n.d	1.17 ± 0.65 ^{aA}
	60	51.34 ± 10.14 ^{abA}	30.39 ± 7.82 ^{aA}	25.86 ± 32.14 ^{aA}	n.d	3.96 ± 1.24 ^{aAB}
	180	26.66 ± 3.20 ^{aAB}	32.82 ± 8.94 ^{aA}	11.20 ± 2.74 ^{aA}	n.d	2.54 ± 1.81 ^{aAB}
	415	69.23 ± 22.17 ^{abA}	51.66 ± 15.75 ^{abAB}	8.59 ± 7.41 ^{aA}	n.d	1.44 ± 0.72 ^{aA}
	550	94.88 ± 11.22 ^{abAB}	96.46 ± 17.79 ^{abA}	9.67 ± 6.68 ^{aA}	n.d	0.90 ± 0.25 ^{aA}
NR60	0	52.03 ± 11.34 ^{abAB}	19.44 ± 5.76 ^{aAB}	31.53 ± 8.42 ^{aA}	n.d	1.09 ± 0.68 ^{aA}
	60	32.91 ± 15.40 ^{abA}	27.81 ± 1.68 ^{aA}	8.89 ± 3.33 ^{aA}	n.d	0.93 ± 0.47 ^{aAB}
	180	23.28 ± 14.30 ^{abAB}	54.39 ± 21.94 ^{aA}	3.21 ± 1.28 ^{aA}	n.d	0.85 ± 0.22 ^{aAB}
	415	44.66 ± 0.88 ^{abAB}	30.75 ± 5.27 ^{aAB}	5.25 ± 7.34 ^{aA}	n.d	1.08 ± 0.39 ^{aA}
	550	61.00 ± 3.60 ^{aAB}	53.62 ± 21.47 ^{aAB}	8.12 ± 4.30 ^{aA}	n.d	2.92 ± 3.83 ^{aA}
R40	0	80.18 ± 4.93 ^{abAB}	28.39 ± 10.10 ^{aAB}	50.14 ± 4.73 ^{aA}	n.d	2.06 ± 1.41 ^{aA}
	60	49.74 ± 2.64 ^{abA}	18.98 ± 2.98 ^{aA}	32.49 ± 26.35 ^{abA}	n.d	1.53 ± 0.29 ^{aAB}
	180	43.27 ± 7.40 ^{aA}	47.82 ± 2.61 ^{abA}	22.06 ± 16.70 ^{abA}	n.d	0.83 ± 0.33 ^{aAB}
	415	79.56 ± 4.28 ^{abA}	64.21 ± 5.30 ^{abA}	14.62 ± 7.97 ^{abA}	n.d	0.83 ± 0.16 ^{aA}
	550	109.04 ± 1.74 ^{bA}	83.60 ± 4.59 ^{bAB}	3.69 ± 2.91 ^{bA}	n.d	0.88 ± 0.17 ^{aA}
R60	0	42.22 ± 5.12 ^{abB}	12.54 ± 3.18 ^{abB}	33.16 ± 27.99 ^{aA}	n.d	1.00 ± 0.41 ^{aA}
	60	27.99 ± 11.81 ^{abA}	21.55 ± 10.07 ^{abA}	17.69 ± 18.70 ^{aA}	n.d	0.81 ± 0.19 ^{aA}
	180	12.12 ± 0.59 ^{aAB}	33.62 ± 0.92 ^{abAB}	4.82 ± 0.30 ^{aA}	n.d	0.60 ± 0.01 ^{aA}
	415	45.38 ± 21.51 ^{abAB}	30.68 ± 20.76 ^{abAB}	15.51 ± 24.87 ^{aA}	n.d	0.94 ± 0.20 ^{aA}
	550	124.56 ± 35.61 ^{bAB}	101.96 ± 19.25 ^{bAB}	9.54 ± 5.94 ^{aA}	n.d	0.76 ± 0.12 ^{aA}
RI60	0	94.88 ± 6.23 ^{aA}	28.92 ± 8.01 ^{aAB}	17.04 ± 14.05 ^{aA}	30.04 ± 1.91 ^a	64.41 ± 8.39 ^{aA}
	60	20.17 ± 9.20 ^{abA}	29.69 ± 8.53 ^{aA}	10.51 ± 10.79 ^{aA}	2.15 ± 1.15 ^{ab}	8.91 ± 5.97 ^{abB}
	180	7.50 ± 5.20 ^{bb}	20.34 ± 13.06 ^{aA}	5.52 ± 4.53 ^{aA}	0.68 ± 0.51 ^b	3.86 ± 2.38 ^{abB}
	415	18.97 ± 7.10 ^{abB}	15.40 ± 10.42 ^{ab}	1.40 ± 0.83 ^{aA}	1.34 ± 0.73 ^{ab}	1.69 ± 0.60 ^{abA}
	550	55.51 ± 9.72 ^{abB}	34.31 ± 11.62 ^{ab}	5.95 ± 4.69 ^{aA}	1.01 ± 0.86 ^{ab}	2.87 ± 1.93 ^{bA}
		Aldehydes cnt. Aromatic Unsaturated		Alcohols		Furans
		Benzaldehyde	2,4-Heptadienal	3-methyl butanol	2-pentyl furan	
Samples	ODT Days	350 ^x	3600 ^y	12 ^y	6 ^y	
NR40	0	0.24 ± 0.64 ^{aA}	1.49 ± 0.91 ^{aA}	0.27 ± 0.22 ^{aA}	0.00 ± 0.00 ^{aA}	
	60	1.04 ± 0.17 ^{abA}	3.70 ± 0.63 ^{abA}	0.28 ± 0.11 ^{aA}	0.02 ± 0.03 ^{abA}	
	180	2.43 ± 1.07 ^{abA}	3.53 ± 1.65 ^{abA}	0.01 ± 0.25 ^{aA}	0.01 ± 0.01 ^{abA}	
	415	11.88 ± 3.04 ^{abA}	8.67 ± 2.27 ^{ba}	0.31 ± 0.23 ^{aAB}	0.31 ± 0.03 ^{abA}	
	550	16.86 ± 3.08 ^{bA}	7.44 ± 2.70 ^{ba}	0.30 ± 0.23 ^{aA}	0.54 ± 0.20 ^{bA}	
NR60	0	0.01 ± 0.45 ^{aA}	1.30 ± 0.99 ^{aA}	0.15 ± 0.01 ^{aA}	0.00 ± 0.00 ^{aA}	
	60	3.07 ± 4.94 ^{aA}	3.18 ± 2.85 ^{abA}	0.16 ± 0.02 ^{aA}	0.06 ± 0.10 ^{aA}	
	180	1.11 ± 0.88 ^{aA}	2.22 ± 0.81 ^{abA}	0.29 ± 0.12 ^{aA}	0.00 ± 0.00 ^{aA}	
	415	8.25 ± 0.80 ^{aA}	8.95 ± 2.42 ^{ba}	0.42 ± 0.24 ^{aAB}	0.18 ± 0.04 ^{aA}	
	550	6.25 ± 4.50 ^{aAB}	5.45 ± 1.65 ^{abA}	0.11 ± 0.34 ^{aA}	0.10 ± 0.13 ^{aA}	
R40	0	0.84 ± 0.99 ^{aA}	2.05 ± 1.46 ^{aA}	0.16 ± 0.00 ^{aA}	0.00 ± 0.00 ^{aA}	
	60	1.48 ± 0.18 ^{abA}	5.21 ± 1.62 ^{abA}	0.21 ± 0.05 ^{abA}	0.00 ± 0.00 ^{abA}	
	180	2.61 ± 1.02 ^{abA}	4.83 ± 2.22 ^{abA}	0.17 ± 0.00 ^{abA}	0.02 ± 0.04 ^{abA}	
	415	11.64 ± 1.06 ^{abA}	9.73 ± 0.98 ^{ba}	0.01 ± 0.34 ^{abA}	0.63 ± 0.10 ^{bA}	
	550	11.25 ± 1.74 ^{bAB}	5.11 ± 0.63 ^{abA}	0.68 ± 0.72 ^{ba}	0.47 ± 0.12 ^{abA}	
R60	0	0.16 ± 0.16 ^{aA}	1.01 ± 0.51 ^{aA}	0.17 ± 0.03 ^{aA}	0.00 ± 0.00 ^{aA}	
	60	0.30 ± 0.46 ^{abA}	1.89 ± 1.99 ^{aA}	0.18 ± 0.02 ^{aA}	0.00 ± 0.00 ^{aA}	
	180	0.62 ± 0.10 ^{abA}	2.05 ± 0.41 ^{aA}	0.11 ± 0.09 ^{aA}	0.00 ± 0.00 ^{aA}	
	415	5.35 ± 4.61 ^{abA}	5.22 ± 2.17 ^{aA}	0.25 ± 0.07 ^{aAB}	0.20 ± 0.29 ^{aA}	
	550	8.79 ± 1.42 ^{bb}	6.85 ± 3.71 ^{aA}	0.18 ± 0.00 ^{aA}	0.28 ± 0.22 ^{aA}	
RI60	0	0.17 ± 0.13 ^{aA}	0.23 ± 0.02 ^{aA}	0.18 ± 0.02 ^{aA}	0.00 ± 0.00 ^{aA}	
	60	0.01 ± 0.57 ^{aA}	2.65 ± 1.69 ^{abA}	0.33 ± 0.30 ^{aA}	0.00 ± 0.00 ^{aA}	
	180	1.10 ± 0.53 ^{abA}	1.89 ± 1.03 ^{abA}	0.18 ± 0.02 ^{aA}	0.00 ± 0.00 ^{aA}	
	415	7.99 ± 1.33 ^{abA}	5.72 ± 2.06 ^{ba}	3.54 ± 4.74 ^{ab}	0.18 ± 0.14 ^{aA}	
	550	12.21 ± 1.72 ^{bAB}	5.06 ± 0.95 ^{ba}	5.27 ± 9.10 ^{aA}	0.27 ± 0.19 ^{aA}	

^aLower-case subscripts indicate significance within the same group over storage time.

^bUpper-case subscripts indicate the significance of the same time point between groups.

^x Odor threshold, values given for dry material of semi-dried golden pompano (ng/ g DW) (Qiu et al., 2023).

^y Odor threshold given in water (ppb) (Vilar et al., 2021).

^z Odor threshold given in egg yolk (ng / g) (Xiang et al., 2024).

3.3. Total amino acids and amino acid profile

The total amino acid (TAA) content directly after drying did not differ significantly across all treatments, with samples having approximately 60 mg TAA per g dried *Ulva* (Supplementary Table S3). Thus, even though certain amino acids such as histidine are very prone to oxidation (Uribe et al., 2019), temperatures up to 60 °C had no significant effect to the seaweed material in the present study. Similarly, there was no selective leaching of amino acids during the rinsing, impacting the TAA content.

Likewise, long-term storage of 550 days did not affect the TAA content across treatments. These findings are consistent with previous studies on brown seaweeds, including *F. vesiculosus*, *F. distichus*, and *A. nodosum*, which reported no changes in the TAA content after drying at 20 °C and subsequent storage for 365 days (Obluchinskaya and Daurtseva, 2020).

The most abundant amino acids in the *U. fenestrata* biomass used in the present study were glutamic and aspartic acid, leucine and alanine. This is consistent with previous reports revealing a dominance of glutamic acid followed by aspartic acid in *Ulva* spp. dried at 25 °C (Yaich et al., 2011) and 38 °C (Jönsson et al., 2023). Three of the dominating amino acids are known to contribute to the taste profile of seaweed, with glutamic and aspartic acid being associated with bitter and umami tastes, while for leucine, only bitterness has been described (Jönsson et al., 2023; Milinovic et al., 2020).

In this study, the glutamic acid content of the dried biomass varied between 7.41 and 11.69 mg/ g dried *Ulva*, while aspartic acid ranged between 6.13 and 9.51 mg/ g dried *Ulva* (Supplementary Table S3). These values are in line with previously reported content in *Ulva* spp. dried at 38 °C, with glutamic and aspartic acid being present at 8.1 mg/ g dried *Ulva* and 7.5 mg/ g dried *Ulva*, respectively (Jönsson et al., 2023). In *U. lactuca* dried at 25 °C, values of 9.8 mg/ g dried *Ulva* and 9.76 mg / g dried *Ulva* were reported for glutamic and aspartic acid, respectively (Yaich et al., 2011).

3.4. Volatile organic compounds (VOCs)

Across all samples, 18 volatile organic compounds (VOCs) were detected, of which 9 were successfully quantified and identified (Supplementary Table S5). An additional 7 VOCs from the 18 detected ones were identified using standards (Supplementary Table S5). The remaining 2 compounds were matched against the spectral database NIST11 that met identification criteria of score $\geq 90\%$ and thus were tentatively identified. Their peak areas are reported in the supplementary information (Supplementary Table S6).

The VOC profile of *U. fenestrata* was complex, and understanding its differences over time as a function of the rinsing and drying treatments is challenging. In this section, only the 9 quantified volatiles are discussed and are grouped based on their relative abundance.

3.4.1. Most abundant VOCs

The most abundant VOCs in the dried *U. fenestrata* were the short-/medium-chained hexanal, heptanal, and pentanal (Table 2), with hexanal being the predominant VOC over time. The former (hexanal) is a linear aldehyde formed e.g., via lipoxygenase (LOX)- and/or fatty acid hydroperoxide lyase-mediated oxidation of polyunsaturated fatty acids (PUFA), especially linoleic acid (Balbas et al., 2015; Sánchez-García et al., 2019). As well as, formed by the oxidation catalysed by trace elements as iron and copper (McClements and Decker, 2007). Previous work has also identified hexanal as the major VOC in fresh *U. rigida* (Sánchez-García et al., 2019), and in brown cooked *L. digitata* (Garrido-Bañuelos et al., 2022). This specific aldehyde is responsible for green, grassy, and oily odours in seaweed (Balbas et al., 2015; Figueroa et al., 2023; Sánchez-García et al., 2019), and is correlated to hay-like odour after storage of *P. palmata* (Stévant et al., 2020).

On day 0, the highest concentration of hexanal was observed for

NR40 and RI60, with 98 and 94.88 ng hexanal/ g dried *Ulva*, respectively, whereas NR60 had the lowest hexanal concentration (49 ng/ g dried *Ulva*), (Table 2). The formation of hexanal during drying has been reported for paprika powder (Cremer and Eichner, 2000) and carrots (Duan and Barringer, 2012), particularly when the moisture level fell to around 4 %. In the present study, the moisture content was found to be similar among all samples after drying, and its kinetics was not monitored. However, when looking into the changes in a_w during drying, both RI60 and NR40 had the least steep slope (Supplementary Fig S1), indicating longer time at higher water activity. This could lead to the acceleration of lipid oxidation e.g., by 11-hydroperoxigenase (Tsai et al., 2008), thus resulting in larger formations of hexanal.

During storage, the concentration of hexanal then declined significantly during the first 180 days; for NR40 and RI60 samples, by 74 % and 92 %, respectively. This could be linked to the presence of endogenous antioxidants as tocopherols, carotenoids and phenolic compounds (McClements and Decker, 2007) in the biomass, which may have paused drying-induced lipid oxidation during early storage. Also our previous work on lipid oxidation compounds of stored *U. fenestrata* reported a stable content of HHE, HNE and MDA during the first 150 days of storage (Harrysson et al., 2021). Another pathway might have been the further transformation of hexanal into its alcohol formed, 1-hexanol (Ughetti et al., 2024), however, we were not able to quantify this alcohol in the present study to confirm this hypothesis.

Beyond 180 days, hexanal concentration increased again in all samples, except for in RI60 (Table 2). All values exceeded the initial values (Day 0), while for RI60, hexanal levels at both 415 and 550 days remained below the initial value of 94.88 ng/ g dried *Ulva* on day 0. The rise of hexanal after prolonged storage could reflect both enzymatic or non-enzymatic oxidation of PUFAs in the seaweed biomass (Stévant et al., 2020). The former could be due to the discussed acidity of the AO-rinsing solution, which could aid in the solubilisation of iron, which in turn could stimulate both the Fenton reaction (Jung et al., 2009) and cleavage of pre-formed lipid hydroperoxides (Kim and Min, 2008). Among enzymes, LOX was proven to still be active after drying at 60 °C, although its activity decreased during storage. The partial prevention of hexanal formation by Duralox reflects its multi-action, containing radical scavengers, reducing agents and chelating agents (Wu et al., 2021). Furthermore, an inhibitory effect on LOX-activity was seen by the Duralox (Supplementary Fig S4), which may explain the lower hexanal formation observed in the later stages of the storage of RI60. It has earlier been described how the polyphenol esculetin (6,7-dihydroxycoumarin) inhibits LOX (Lee and Lillard, 1997), making it likely that also rosemary-derived polyphenols could have an effect (Kuo et al., 1997; Wu et al., 2023). Also, LOX has maximum activity around neutrality (Kuo et al., 1997), while the decreased pH of RI60 negatively affected the enzyme.

Another major volatile previously reported in *U. rigida* (Sánchez-García et al., 2019), *Laminaria digitata* (Garrido-Bañuelos et al., 2022) and in the microalgae *Streptomyces platensis* (Ughetti et al., 2024), was heptanal, which has been previously linked to seaweed, fish and lake water odours in *Ulva* spp. using GC-MS-O (Vilar et al., 2021). It is formed via oxidation of unsaturated fatty acids i.e. oleic and linoleic acids (Domínguez et al., 2019; Xiang et al., 2024). In the present study, heptanal was highest immediately after drying, without significant differences between samples (Table 2). During storage, the concentration of heptanal declined across all treatments, with the largest loss (90 %) seen in the R40 after 550 days. Heptanal was thus mainly formed during drying, which is aligned with the fact that this aldehyde can develop during thermally induced oxidation of lipids (Ashok et al., 2025). During storage, heptanal decrease could be due to its transformation to other VOCs such as ketones or alcohols (Ughetti et al., 2024).

Pentanal was the third most abundant VOC, and unlike hexanal and heptanal, it remained at low concentrations during the first 60 days of storage (Table 2), after which it gradually increased for all treatments,

especially for samples rinsed in water. Pentanal has been linked to spicy, fruity and nutty aromas in seaweed and fish (Vilar et al., 2021; Zhang et al., 2025). After 550 days, R40 and R60 had increased by a factor 2.5 and 8, respectively, and was significantly different from levels on day 0. RI60, presented the lowest pentanal content after 550 days, having 34.31 ng pentanal/ g dried *Ulva*, which was significantly lower than both samples rinsed in water, R40 and R60. Pentanal is mainly formed via oxidation of linoleic acid (Domínguez et al., 2019; Zhang et al., 2023), and the results indicate that leaching of pro-oxidants as transition elements when rinsing (Supplementary Table S4) and LOX (Supplementary Fig S4) into rinsing solutions was of importance for its formation.

3.4.2. Less abundant VOCs

Among the less abundant VOCs, nonanal and octanal, representing medium- and long-chain aldehydes, respectively (López-Pérez et al., 2017). Both aldehydes are reported as autooxidation products of oleic acid (He et al., 2021), and have previously been reported in both fresh and cooked *Ulva* spp (Sánchez-García et al., 2019). They are associated with fatty, citrus, or green aromas. Interestingly, octanal was only found in the samples rinsed in AO solution, and its concentration was highest at time 0, after which it decreased over storage, a change that was significant already after 60 days (Table 2). Such volatile could have come from the AO solution, although additional tests, not presented using the same methods, octanal was not found in the AO-solution. Differently, nonanal was found in all samples, although the concentration was again significantly higher when rinsed in AO solution compared to the rest of the treatments. Similarly to octanal, the highest levels were seen on day 0, after which they decreased with time. The results contrast with previous findings in shrimp, where dipping in the same AO solution resulted in lower nonanal levels during subsequent cold storage (Jensen et al., 2024). A hypothesis is that, under the drying conditions of this study, the tocopherol and rosemary-derived polyphenols (mainly carnosol and carnosic acid) of Duralox may have stimulated iron-mediated oxidation of oleic acid via formation of alkoxy radicals, resulting in the formation of both nonanal and octanal (Kim and Min, 2008). The lower pH of RI60 may also have played a role in stimulating hydroperoxide breakdown by metals or acid *per se* (Jung et al., 2009).

Another VOCs found in this study was 2,4-heptadienal (Table 2), which is a saturated aldehyde linked to grassy, vegetable and cucumber odour of green and brown seaweed (Sánchez-García et al., 2019; Vilar et al., 2021). It is formed from 12-hydroperoxide emerging in the oxidation of linolenic acid. In the present study, it steadily increased over time, which was significant after 415 days in all samples except R60, which had significantly lower levels on the rest and previous timepoints (Table 2).

The benzaldehyde concentration in the dried samples started off low immediately after drying, but it then increased slightly between 180 and 550 days of storage (Table 2). The highest concentration was found for NR40 after 550 days of storage (16.86 ng/g dry *Ulva*) which was significantly higher than R60 after 550 days (8.26 ng/ g dry *Ulva*) (Table 2). This aromatic compound is derived from Strecker degradation (Coleman et al., 2023; Ughetti et al., 2024), i.e., the reaction between an amino acid with a di-carbonyl from lipid oxidation or the Maillard reaction (Coleman et al., 2023; Cremer and Eichner, 2000) and it contributes to almond-like and cherry-aromas as well as bitterness (Sánchez-García et al., 2019).

Three-Methyl butanol, another Strecker product (Ughetti et al., 2024) which is described as fruity i.e. malty (Xiang et al., 2024), was present at lower concentrations than the other five VOCs above, and no variations were seen over storage time within the same treatment (Table 2). However, RI60 had higher levels than R40 after 415 days of storage.

Two-pentyl furan was the only furan that could be quantified. It was present in all samples, although in very low concentrations. Over time, there were however slight increases, which were significant in samples

dried at 40 °C, (Table 2). This VOC can be derived e.g., from autoxidation of linoleic acid via cyclisation (Ho and Chen, 1994), due to singlet oxygen energy (Kim and Min, 2008). Although, the drying and storage were done in darkness, repeated sampling to monitor water activity might have introduced light during drying.

The decrease of heptanal, octanal and nonanal over time could be a result of their transformation to other VOCs. It is known that aldehydes can be lysed or oxidised to alkanes, alcohols, esters or organic acids (Ughetti et al., 2024), not measured in the present study. An example is hexanal, which can be the precursor for 1-hexanol.

Future studies should evaluate e.g., purge-and-trap for VOC extraction, as it is not dependent on fiber affinity or selectivity of compounds, nor limited by fiber saturation. Further, the use of olfactory gas chromatography (GC-O), could aid in identifying which volatiles are responsible for the specific detected sensory attributes after drying and storage. Additionally, the use of AO-rinsing coupled with low drying temperatures (40 °C) should be explored since, based on the present results, lower temperature drying conditions showed the highest LOX activity (Supplement Fig S4) and higher levels of volatile compounds derived from lipid oxidation Section 3.4.

3.4.3. Odour thresholds

Odour threshold values (ODT) for the VOCs quantified in this study (Table 2) are based on previous studies conducted both in water and on a dry basis analysis. From the main aldehydes evaluated, heptanal and hexanal were found to exceed the ODT at all time points, suggesting that they may contribute significantly to the odours of the *U. fenestrata* with green and herbaceous notes (Sánchez-García et al., 2019). Regarding pentanal, R40, R60 and NR60 surpassed the ODT of 42 ng/ g DW set for egg after 180 days, while untreated and low-temperature dried samples had pentanal content above the ODT already on day 0. However, when *U. fenestrata* was rinsed in AO solution, it remained below the ODT throughout the storage. While the longer-chained aldehydes, octanal and nonanal, surpassed the ODT just after drying, both fell below their ODT for all samples during storage, except RI60 whose nonanal concentration remained above the ODT after 550 days (Table 2), possibly giving citrus green aromas.

The remaining volatiles: 2-pentylfuran, 2,4-heptadienal, and 3-methyl butanol, did not surpass their ODT regardless of treatment or storage (Table 2).

3.5. Sensory attributes of *U. fenestrata*

The sensory profiles of the *U. fenestrata* samples were assessed by 7 trained assessors for all treatments. After drying, all samples, regardless of pre-treatment or drying temperature, were found to have similar seaweed odour intensity (~ 35 %) as seen in Fig. 3. On the other hand, mineral odour was rated at lower intensity when *U. fenestrata* was dried at a lower temperature (40 °C) compared to when dried at 60 °C. This was more pronounced when comparing R40 and RI60 treatments on day 0.

As expected, storage time had a significant effect on the odour intensity perceived by the assessors. Seaweed odour, initially found to be one of the most intense attributes, decreased over time and was substantially lowered after 415 days (Supplementary Fig. S6). After 550 days, a loss of approximately 60 % was seen for all samples except for RI60, which retained the most intense seaweed smell, only losing 30 % from day 0 (Fig. 3). The loss of marine smell was in line with previous findings of (Stévant et al., 2020) using semi-dried (20 % moisture) and dried (6 % moisture) *P. palmata*. After 126 days of storage, both these samples had lost marine and fish-odour; more so at higher moisture content (Stévant et al., 2020). Using GC-O, seaweed smell of different brown (*Halomonas elongata*, *Undaria pinnatifida*, *Alaria esculenta* and *Laminaria japonica*) and red seaweed species (*P. umbilicalis* and *P. palmata*) has previously been attributed to heptanal (Vilar et al., 2021). Even though this correlation was not found in the present data

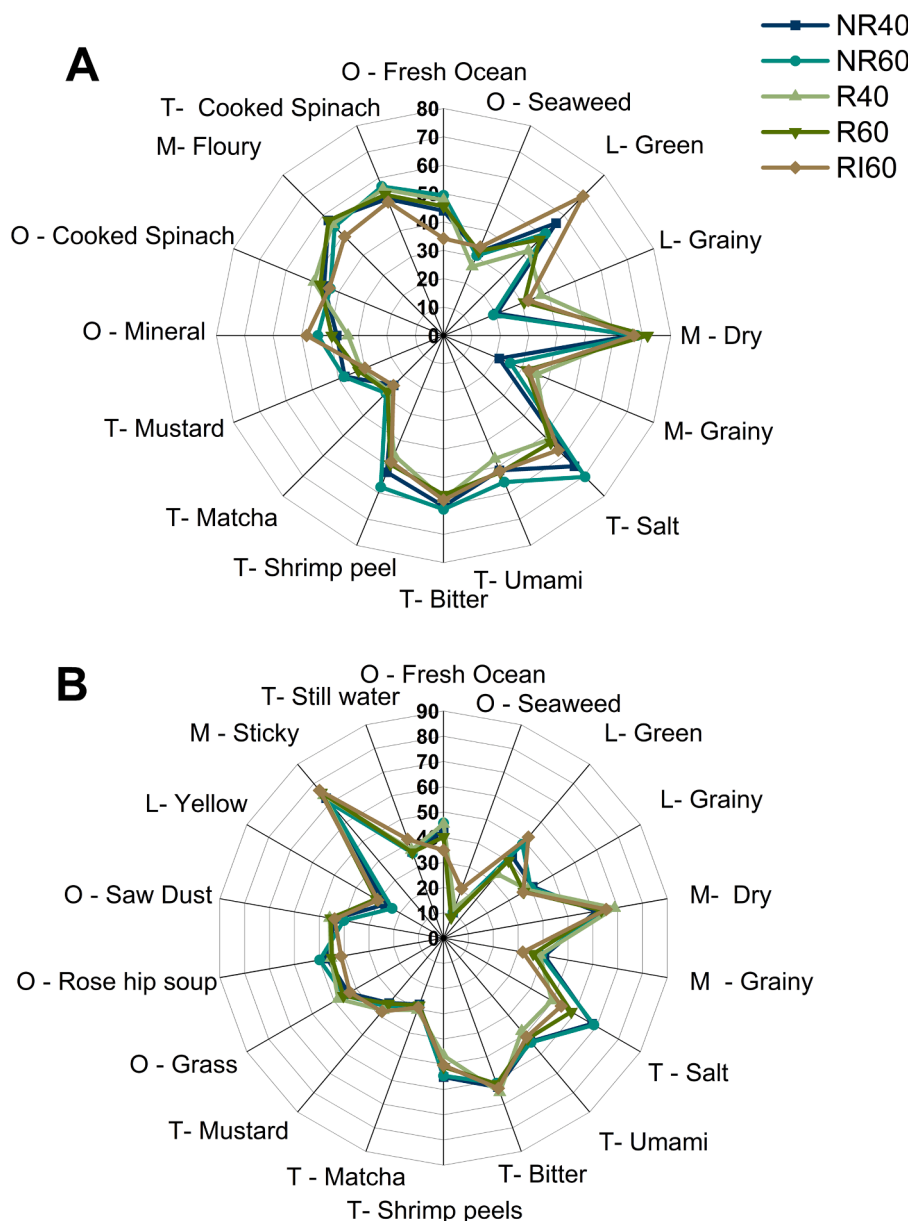


Fig. 3. Spider chart of sensory attributes of *U. fenestrata* based on odour (O-), appearance (L-), mouthfeel (M-), and taste (T-). Samples were either rinsed in water and dried at 40 °C (R40) or 60 °C (R60), left untreated and dried at 40 °C (NR40) or 60 °C (NR60), or rinsed in a stabilizing solution (AO) and dried at 60 °C (RI60). Top chart (A) shows results after 0 days (no storage), and bottom chart (B) after 550 days of storage.

set derived from the first batch of *U. fenestrata* biomass, it is worth mentioning that in the replicate experiment (batch 2), and also when the mean of both batches was used, a significant positive correlation between seaweed smell and heptanal content was found ($r = 0.631$, $p = 0.001$). As the perceived seaweed odour decreased, sawdust (hay-like) odour, as well as grass and rose-hip soup odours developed and were assessed after 180 days of storage. Hay-like odour has previously been reported in dried *U. lactuca* (López-Pérez et al., 2017), and in semi-dried *P. palmata* after 126 days of storage, which is related to the maturation process occurring during storage, in presence of moisture (Stévant et al., 2020). In the present study, a similar maturation was observed, which could result from both enzymatic and non-enzymatic reactions due to the increased moisture (from ~6–12%) and a_w (~0.2–0.35) from day 0–550 days, respectively. While 1-octen-3-ol (Vilar et al., 2021), 2,4-heptadienal and nonanal (Stévant et al., 2020) have previously been linked to hay odour and were present in this study, only 2,4-heptadienal and nonanal VOCs were quantifiable, but neither of

them was above its ODT in the later time points. This means other VOCs, or the unique VOC combination, was responsible for the hay/saw dust odour.

Green colour, as emphasised in Section 3.2, is a key characteristic for *Ulva* spp. On day 0, RI60 was rated as having the most intense green colour (70 % intensity). However, during storage, the intensity of the green colour decreased for all treatments except NR60, which had stable greenness intensity of 50 % on day 550 (Fig. 2B). These results are supported by the analytical colour measurements for all samples except NR60, which showed a decrease in green hue (i.e. raised a^* -values) for all treatments over time.

Despite the decline in intensity of green colour in RI60, it had maintained the greenest colour among all treated *U. fenestrata* biomasses after 550 days, with 55 % intensity. This agreed with the results that chlorophyll a and b were found at higher concentrations on day 0 and throughout storage when *U. fenestrata* was rinsed in AO-solution (Supplementary Fig S2). Interestingly, drying at 40 °C resulted in less

perceived greenness than drying at 60 °C after 180 days, particularly for R40 after 415 and 550 days (Supplementary Fig S6). The lower temperature resulted in longer drying times (Section 3.1), which possibly stimulated co-oxidation of lipids and pigments, via degradation of chlorophyll with enzymes as seen previously in oven dried *U. fenestrata* at 40 °C (Harrysson et al., 2021). The sensory results are also supported by the content of chlorophyll a and b (Supplementary Fig S2) and the instrumental colourimetric measurements which revealed larger losses of a*-value for samples dried at 40 °C, especially R40.

Yellow colour was not assessed until after 180 days and onwards, and results were aligned with the colourimetric measurements, which indicated that b^* -values were stable up to day 415. After this, RI60 had the highest yellowness rated by the panel, which was confirmed by b^* -values but not carotenoid data; the latter showing an opposite trend, as already discussed in [Section 3.2](#).

The texture perceived across all treatments differed on day 0 and after storage. Immediately after drying, rinsed samples, regardless of the drying temperature, were perceived as less grainy in the mouth compared to non-rinsed ones. The lack of temperature effect in our study contradict previous results reporting that the instrumentally monitored firmness of dehydrated *G. chilensis* was higher after drying at higher temperatures (70 °C vs 25 °C) (Tello-Ireland et al., 2011). A reason could be that in the present study, the whole *U. fenestrata* blades were milled, likely evening out texture differences, compared to previous work with whole blades (Tello-Ireland et al., 2011).

When it comes to taste attributes, umami, bitterness, wasabi, shrimp peel taste and saltiness were among the most prominent ones perceived and remained at similar intensity over the storage. The main difference found in the sample set was that saltiness was significantly reduced when *U. fenestrata* was rinsed, which was in line with their lower ash content (Section 3.1).

3.6. Correlation analysis

In order to further explore the possible relationship between sensory attributes, VOC composition and colourimetric measurements, Pearson

correlation and partial least square regression (PLSR) analyses were performed.

The PLSR results (Fig. 4) suggested that samples dried at lower temperatures (NR40 and R40) were positively associated with volatiles developed in later stages of the storage (Section 3.4), such as benzaldehyde, 2-pentylfuran, 2,4-heptadienal and pentanal. The clustering in the left lower quadrant of samples dried at 40 °C at later time points (T4 and T5), while earlier time points (T1, T2 and T3) in the opposite quadrants (right-upper quadrant), suggests the possibility of both enzymatic and non-enzymatic oxidation occurring after 180 days.

In contrast, all time points for samples treated with the AO solution (RI60) are clustered together and were positively associated with perceived greenness and the volatiles nonanal and octanal. These associations, indicating that rinsing with AO solution helped maintaining the green colour based on sensory analysis, and that it steered the VOC profile towards higher nonanal and octanal content, the latter which needs further evaluations to explain.

Significant correlations found between sensory attributes and volatile compounds included a positive correlation between heptanal and the odour of rose hip soup ($r = 0.663$, $p = 0.037$), as well as fresh ocean odours ($r = 0.501$, $p = 0.011$). The correlation is hypothesised to be based on the decrease in heptanal over time. Heptanal has been attributed to fresh, citrus and herbal aromas (Vilar et al., 2021). Additionally, benzaldehyde and 2,4-heptadienal were positively correlated to matcha taste ($r = 0.431$, $p = 0.031$; $r = 0.516$, $p = 0.008$, accordingly), which agrees with the fact that both benzaldehyde and 2,4-heptadienal previously have been associated with seaweed-like smell in matcha (Zhang et al., 2025).

In contrast, negative correlations were found between on the one hand hexanal, pentanal and 2-pentyl-furan and on the other, seaweed smell ($r = -0.585$, $p = 0.002$; $r = -0.553$, $p = 0.004$; $r = -0.729$, $p = 0.000$, respectively) and perceived green colour ($r = -0.433$, $p = 0.031$; $r = 0.523$, $p = 0.007$ and $r = -0.412$, $p = 0.04$, accordingly). This is likely a result of lipid oxidation and its co-oxidation of pigments occurring over time.

Overall, the correlation emphasises a close relation between some of

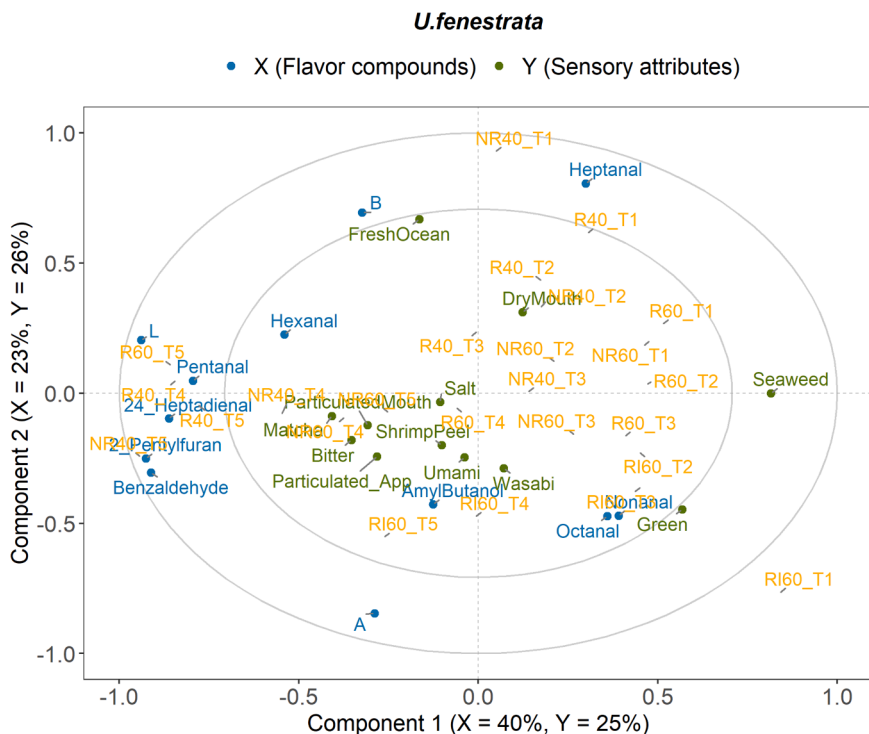


Fig. 4. PLSR of dried and milled *U.fenestrata* with sensory attributes in orange (X - coordinates), while volatile analysis and CIEL L* a* b* coordinates are present in dark blue (Y - coordinates). The samples are coloured in green. Timepoints are presented as day 0 (T1), 60 (T2), 180 (T3), 415 (T4), and 550 (T5).

the VOCs detected and sensory attributes, while the PLSR plot (Fig. 4) revealed that drying temperatures and rinsing affected their evolution over time.

4. Conclusions

This study contributes to a better understanding of the changes occurring during long-term storage of differently pre-treated and oven dried sea lettuce (*U. fenestrata*). From a nutritional point of view, amino acid content and composition remained unchanged, regardless of the treatment and storage time. With respect to colour stability, drying at 60 °C maintained the green colour of *U. fenestrata* to a higher extent than drying at 40 °C, as evidenced by both the instrumental data and sensory assessment. Furthermore, samples pre-rinsed in AO were perceived as having the highest green colour after 550 days (30 % intensity vs 8–10 %). These results were also supported by the chlorophyll a content (0.82 µg/g sample vs 0.41–0.47 µg/g sample), which was better retained during storage when pre-rinsing with AO-solution was employed.

Although non-rinsed *U. fenestrata* dried at 60 °C could be stored for 415 days in darkness without significant changes in green colour, there were changes in the sensory profile towards hay and rosehip odours. This was likely related to the increases in hexanal and benzaldehyde, with ascribed hay and floral/fruity aromas. If seaweed smell is desired, *U. fenestrata* could be rinsed in AO solution prior to drying; a treatment which preserved this odour attribute up to 550 days. In general, rinsing with AO solution resulted in fewer oxidation-derived aldehydes formed towards the end of the storage. If the aim is to protect against both lipid and pigment oxidation, AO-rinsing likely would be better combined with low temperature drying. Sensory analyses further highlighted a robustness of the biomass in the sense that it retained many taste attributes regardless of both pre-treatment and drying temperature.

The volatile compound kinetics observed in this study revealed a compound specific evolution during storage, indicating a possible classification: those starting off high immediately after drying, followed by a decline over storage (heptanal, octanal and nonanal), and those starting off low, increasing over storage (pentanal, 2,4-heptadienal and benzaldehyde). Some also showed a U-shaped pattern (hexanal), which could be an interesting area for future research on VOC transformation and recurrence in seaweed.

Overall, the insight into volatile compounds and sensory attributes found in this study can be valuable both for future sensory studies, and for tailoring food applications of *Ulva* sp. biomass. Results revealed that differently processed and stored biomass can be optimal for different end-uses of the biomass -e.g., as a flavour enhancers, colourants or nutrient carriers. However, to obtain higher resolution in such tailored use, further understanding of the volatiles that were not quantified nor identified in the present study would be valuable.

CRedit authorship contribution statement

Mar Vall-Ilosera: Writing – review & editing, Writing – original draft, Visualization, Investigation, Data curation, Conceptualization. **Karin Wendin:** Writing – review & editing, Resources, Investigation, Data curation. **Rufa Mendez:** Writing – review & editing, Investigation, Data curation. **Göran Nylund:** Writing – review & editing, Resources, Conceptualization. **Henrik Pavia:** Writing – review & editing, Conceptualization. **Ingrid Undeland:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

Ethics declaration

Written informed consent to take part in the study and to publish the article has been obtained from all participants or their legal representatives. The privacy rights of participants have been observed.

This study was performed in compliance with relevant laws, regulatory frameworks and guidelines where the research took place. Ethics

committee approval was not required under relevant laws and institutional guidelines. The authors declare that the present study on the sensory analysis of *Ulva fenestrata* did not undergo formal documentation from a human ethics committee. The research falls under the Swedish Ethic Review Act of research conducted in Sweden that includes sensitive personal data. Nevertheless, all assessors voluntarily joined the study and provided informed consent after receiving comprehensive information about the test, including potential allergens and associated risks. The sensory assessments were done anonymously; therefore, no information from the test can be traced to or used to identify participants, in accordance with the General Data Protection Regulation (GDPR). Furthermore, no sensitive personal data, as defined by the Swedish Data Protection Act (2018:218) and Ordinance (2018:219), was used or collected. Further, the consent form given to the participants can be found in the Supplementary Information S9.

Ethical statement

The authors declare that the present study on the sensory analysis of *Ulva fenestrata* did not undergo formal documentation from a human ethics committee. The research falls under the Swedish Ethic Review Act of research conducted in Sweden that includes sensitive personal data. Nevertheless, all assessors voluntarily joined the study and provided informed consent after receiving comprehensive information about the test, including potential allergens and associated risks. The sensory assessments were done anonymously; therefore, no information from the test can be traced to or used to identify participants, in accordance with the General Data Protection Regulation (GDPR). Furthermore, no sensitive personal data, as defined by the Swedish Data Protection Act (2018:218) and Ordinance (2018:219), was used or collected. Further, the consent form given to the participants can be found in the Supplementary Information S9.

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.

Acknowledgements

The authors would like to thank Marcus Johansson from Kristianstad University for performing the sensory analysis. This study was funded by Formas - the Swedish Research Council for Sustainable Development based on the BlueGreen project (Grant No. 2021–02340), and the Blue Food – Centre for Future Seafood phase I and II (Grants No. 2020–02834 and 2024–01023). Also, funded was obtained from Region Västra Götaland (grant number RUN 2020–00352 and MRU 2025–00008).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.jfca.2026.109540](https://doi.org/10.1016/j.jfca.2026.109540).

Data availability

Data will be made available on request.

References

- Andrés-Bello, A., Barreto-Palacios, V., García-Segovia, P., Mir-Bel, J., Martínez-Monzó, J., 2013. Effect of pH on Color and Texture of Food Products. *Food Eng. Rev.* <https://doi.org/10.1007/s12393-013-9067-2>.
- Ashok, A., Policegoudra, R., Chauhan, O.P., Kumar, R., 2025. Impact Differ. Therm. Non-Therm. Process. Methods Heavy Met. volatile Compd. Bioact. Compd. Edible Green. Seaweed (*Ulva* Reticul.) Potential. *Food Appl.* <https://doi.org/10.2139/ssrn.5282216>.

- Balbas, J., Hamid, N., Liu, T., Kantono, K., Robertson, J., White, W.L., Ma, Q., Lu, J., 2015. Comparison of physicochemical characteristics, sensory properties and volatile composition between commercial and New Zealand made wakame from *Undaria pinnatifida*. *Food Chem.* 186, 168–175. <https://doi.org/10.1016/j.foodchem.2015.03.079>.
- Coleman, B., Van Poucke, C., De Witte, B., Casciaro, V., Moerdijk-Poortvliet, T., Muylaert, K., Robbins, J., 2023. The effect of drying, cell disruption and storage on the sensory properties of *Nannochloropsis* sp. *Algal Res.* 71. <https://doi.org/10.1016/j.algal.2023.103092>.
- Cremer, D.R., Eichner, K., 2000. Formation of volatile compounds during heating of spice paprika (*Capsicum annuum*) powder. *J. Agric. Food Chem.* 48, 2454–2460. <https://doi.org/10.1021/jf991375a>.
- Cropotova, Janna, Mozuraityte, Revilija, Standal, Inger Beate, Rustad, Turid, 2019. Assessment of lipid oxidation in Atlantic mackerel (*Scomber scombrus*) subjected to different antioxidant and sous-vide cooking treatments by conventional and fluorescence microscopy methods. *Food Control* 104, 1–8. <https://doi.org/10.1016/j.foodcont.2019.04.016>. <https://linkinghub.elsevier.com/retrieve/pii/S095671315930163X>.
- Cui, K., Liu, N., Sun, Y., Sun, G., Wang, S., Yang, M., Wang, X., Zhou, D., Ge, Y., Wang, D., Wang, M., 2023. Effect of drying processes on the occurrence of lipid oxidation-derived 4-hydroxy-2-hexenal and 4-hydroxy-2-nonenal in Spanish mackerel (*Scomberomorus niphonius*). *Food Sci. Nutr.* 11, 1013–1023. <https://doi.org/10.1002/fsn3.3138>.
- Domínguez, R., Pateiro, M., Gagaoua, M., Barba, F.J., Zhang, W., Lorenzo, J.M., 2019. A comprehensive review on lipid oxidation in meat and meat products. *Antioxidants* 8, 429. <https://doi.org/10.3390/antiox8100429>.
- Duan, H., Barringer, S.A., 2012. Changes in furan and other volatile compounds in sliced carrot during air-drying. *J. Food Process. Preserv.* 36, 46–54. <https://doi.org/10.1111/j.1745-4549.2011.00550.x>.
- Engström, E., Stenberg, A., Seniukh, S., Edelbro, R., Baxter, D.C., Rodushkin, I., 2004. Multi-elemental characterization of soft biological tissues by inductively coupled plasma-sector field mass spectrometry. *Anal. Chim. Acta* 521, 123–135. <https://doi.org/10.1016/j.aca.2004.06.030>.
- Figueroa, V., Holdt, S.L., Jacobsen, C., Aguilera, J.M., 2023. Effects of cooking on the composition of volatiles, total phenolic compounds, and antioxidant capacity of three Chilean seaweeds. *J. Appl. Phycol.* 35, 3057–3068. <https://doi.org/10.1007/s10811-023-03099-5>.
- Garrido-Bañuelos, G., Miljkovic, A., Morange, C., Mihnea, M., Lopez-Sanchez, P., 2022. Assessing the volatile composition of seaweed (*Laminaria digitata*) suspensions as function of thermal and mechanical treatments. *LWT* 162. <https://doi.org/10.1016/j.lwt.2022.113483>.
- Harrysson, H., Hayes, M., Eimer, F., Carlsson, N.G., Toth, G.B., Undeland, I., 2018. Production of protein extracts from Swedish red, green, and brown seaweeds, *Porphyra umbilicalis* Kützinger, *Ulva lactuca* Linnaeus, and *Saccharina latissima* (Linnaeus) J. V. Lamouroux using three different methods. *J. Appl. Phycol.* 30, 3565–3580. <https://doi.org/10.1007/s10811-018-1481-7>.
- Harrysson, H., Krook, J.L., Larsson, K., Tullberg, C., Oerbekke, A., Toth, G., Pavia, H., Undeland, I., 2021. Effect of storage conditions on lipid oxidation, nutrient loss and colour of dried seaweeds, *Porphyra umbilicalis* and *Ulva fenestrata*, subjected to different pretreatments. *Algal Res.* 56. <https://doi.org/10.1016/j.algal.2021.102295>.
- He, J., Wu, X., Zhou, Y., Chen, J., 2021. Effects of different preheat treatments on volatile compounds of camellia (*Camellia oleifera* Abel.) seed oil and formation mechanism of key aroma compounds. *J. Food Biochem.* 45. <https://doi.org/10.1111/jfbc.13649>.
- Heaton, J.W., Marangoni, A.G., 1996. Chlorophyll degradation in processed foods and senescent plant tissues. *Trends Food Sci. Technol.* 7, 8–15. [https://doi.org/10.1016/0924-2244\(96\)81352-5](https://doi.org/10.1016/0924-2244(96)81352-5).
- Ho, C.-T., Chen, Q., 1994. Lipids in food flavors 2–14. <https://doi.org/10.1021/bk-1994-0558.ch001>.
- Hutchings, J., 1994. Chemistry of food colour. in: *Food Colour and Appearance*. Chapman & Hall, pp. 367–469.
- Jensen, Hanne Aarslev, Sørensen, Ann-Dorit Moltke, Mejhlholm, Ole, Bøknæs, Niels, Jacobsen, Charlotte, 2024. Effect of different antioxidants and application methods on the shelf-life of whole, cooked, frozen Northern shrimp (*Pandalus borealis*). *Food Chemistry Advances* 5, 100764. <https://doi.org/10.1016/j.focha.2024.100764>.
- Jönsson, M., Merkel, A., Fredriksson, C., Karlsson, E.N., Wendin, K., 2023. Nutritional, physicochemical, and sensory characterization of four common Northern European seaweed species intended for food. *Algal Res.* 75, 103258. <https://doi.org/10.1016/j.algal.2023.103258>.
- Jung, Y.S., Lim, W.T., Park, J.Y., Kim, Y.H., 2009. Effect of pH on Fenton and Fenton-like oxidation. *Environ. Technol.* 30, 183–190. <https://doi.org/10.1080/09593330802468848>.
- Kim, J.H., Min, D., 2008. Chemistry of Lipid Oxidation. In: Akoh, C.C., Min, D.B. (Eds.), *Chemistry, Nutrition, and Biotechnology, Food Lipids*. CRC Press, pp. 299–318. <https://doi.org/10.1201/9781420046649.pt3>.
- Kuo, J.-M., Hwang, A., Yeh, D.-B., 1997. Purification, substrate specificity, and products of a Ca²⁺-stimulating lipoygenase from sea algae (*Ulva lactuca*).
- Lee, K.I.T., Lillard, D.A., 1997. Effects of esculetin as a lipoygenase inhibitor in soybean extracts. *J. Food Lipids* 4, 119–127. <https://doi.org/10.1111/J.1745-4522.1997.TB00086.X>.
- Liu, Q., Lei, M., Zhao, W., Li, X., Zeng, X., Bai, W., 2023. Formation of Lipid-Derived Flavors in Dry-Cured Mackerel (*Scomberomorus niphonius*) via Simulation of Autooxidation and Lipoygenase-Induced Fatty Acid Oxidation. *Foods* 12. <https://doi.org/10.3390/foods12132504>.
- López-Pérez, O., Picon, A., Nuñez, M., 2017. Volatile compounds and odour characteristics of seven species of dehydrated edible seaweeds. *Food Res. Int.* 99, 1002–1010. <https://doi.org/10.1016/j.foodres.2016.12.013>.
- Maestre, Rodrigo, Pazos, Manuel, Medina, Isabel, 2011. Role of the Raw Composition of Pelagic Fish Muscle on the Development of Lipid Oxidation and Rancidity during Storage. *Journal of Agricultural and Food Chemistry* 59 (11), 6284–6291. <https://doi.org/10.1021/jf200686z>. <https://pubs.acs.org/doi/10.1021/jf200686z>. (Accessed 11 May 2011).
- McCauley, J.L., Winberg, P.C., Meyer, B.J., Skropeta, D., 2018. Effects of nutrients and processing on the nutritionally important metabolites of *Ulva* sp. (*Chlorophyta*). *Algal Res.* 35, 586–594. <https://doi.org/10.1016/j.algal.2018.09.016>.
- McClements, D.J., Decker, E.A., 2007. Lipids, in: *Fennema's Food Chemistry*. Taylor and Francis group, pp. 155–216.
- Michel, F., Priol, J., Galaup, P., Demaimay, M., Bigot, C., 1997. Effect of two drying technics on the volatile compounds of two alimetary algae, *Ulva* sp. and *Palmaria palmata* [Effet de deux techniques de séchage sur les composés volatils de deux algues alimentaires *Ulva* sp. et *Palmaria palmata*]. *Sci. Aliments* 17, 601–617.
- Milinic, J., Campos, B., Mata, P., Diniz, M., Noronha, J.P., 2020. Umami free amino acids in edible green, red, and brown seaweeds from the Portuguese seashore. *J. Appl. Phycol.* 32, 3331–3339. <https://doi.org/10.1007/s10811-020-02169-2>.
- Moreira, R., Chenlo, F., Sineiro, J., Arufe, S., Sexto, S., 2016. Drying temperature effect on powder physical properties and aqueous extract characteristics of *Fucus vesiculosus*. *J. Appl. Phycol.* 28, 2485–2494. <https://doi.org/10.1007/s10811-015-0744-9>.
- Mortensen, A., Skibsted, L.H., 1997. Importance of Carotenoid Structure in Radical-Scavenging Reactions. *J. Agric. Food Chem.* 45, 2970–2977. <https://doi.org/10.1021/jf970010s>.
- Obluchinskaya, E., Daurtseva, A., 2020. Effects of air drying and freezing and long-term storage on phytochemical composition of brown seaweeds. *J. Appl. Phycol.* 32, 4235–4249. <https://doi.org/10.1007/s10811-020-02225-x>.
- Osório, C., Machado, S., Peixoto, J., Bessada, S., Pimentel, F.B., Alves, R.C., Oliveira, M. B.P.P., 2020. Pigments content (Chlorophylls, Fucoxanthin and Phycobiliproteins) of different commercial dried algae. *Page 337 Separations* 2020 7, 33. <https://doi.org/10.3390/SEPARATIONS7020033>.
- Österlund, H., Rodushkin, I., Ylinenjärvi, K., Baxter, D.C., 2009. Determination of total chlorine and bromine in solid wastes by sintering and inductively coupled plasma-sector field mass spectrometry. *Waste Manag.* 29, 1258–1264. <https://doi.org/10.1016/j.wasman.2008.07.017>.
- Poelogaasih, C.D., Srianih, M., Jatmiko, T.H., Prasetyo, D.J., 2019. Postharvest handling of the edible green seaweed *Ulva lactuca*: Mineral content, microstructure, and appearance associated with rinsing water and drying methods. in: *IOP Conference Series: Earth and Environmental Science*. Institute of Physics Publishing. <https://doi.org/10.1088/1755-1315/253/1/012006>.
- Qiu, D., Duan, R., Wang, Y., He, Y., Li, C., Shen, X., Li, Y., 2023. Effects of different drying temperatures on the profile and sources of flavor in semi-dried golden pompano (*Trachinotus ovatus*). *Food Chem.* 401. <https://doi.org/10.1016/j.foodchem.2022.134112>.
- Regal, A.L., Alves, V., Matos, J., Bandarra, N.M., Afonso, C., Cardoso, C., 2020. Drying process, storage conditions, and time alter the biochemical composition and bioactivity of the anti-greenhouse seaweed *Asparagopsis taxiformis*. *Eur. Food Res. Technol.* 246, 781–793. <https://doi.org/10.1007/s00217-020-03445-8>.
- Rodushkin, I., Engström, E., Sörlin, D., Baxter, D., 2008. Levels of inorganic constituents in raw nuts and seeds on the Swedish market. *Sci. Total. Environ.* 392, 290–304. <https://doi.org/10.1016/j.scitotenv.2007.11.024>.
- Sánchez-García, F., Mirzayeva, A., Roldán, A., Castro, R., Palacios, V., García-Barroso, C., Durán-Guerrero, E., 2019. Evolution of volatile compounds and sensory characteristics of edible green seaweed (*Ulva rigida*) during storage at different temperatures. *J. Sci. Food Agric.* 99, 5475–5482. <https://doi.org/10.1002/jsfa.9808>.
- Silva, A.F.R., Abreu, H., Silva, A.M.S., Cardoso, S.M., 2019. Effect of oven-drying on the recovery of valuable compounds from *Ulva rigida*, *Gracilaria* sp. and *Fucus vesiculosus*. *Mar. Drugs* 17. <https://doi.org/10.3390/md17020090>.
- Steinhagen, S., Enge, S., Larsson, K., Olsson, J., Nylund, G.M., Albers, E., Pavia, H., Undeland, I., Toth, G.B., 2021. Sustainable large-scale aquaculture of the northern hemisphere sea lettuce, *Ulva fenestrata*, in an off-shore seafarm. *J. Mar. Sci. Eng.* 9, 1–19. <https://doi.org/10.3390/jmse9060615>.
- Stévant, P., Ólafsdóttir, A., Déléris, P., Dumay, J., Fleurence, J., Ingadóttir, B., Jónsdóttir, R., Ragueneau, É., Rebours, C., Rustad, T., 2020. Semi-dry storage as a maturation process for improving the sensory characteristics of the edible red seaweed dulse (*Palmaria palmata*). *Algal Res.* 51, 102048. <https://doi.org/10.1016/j.algal.2020.102048>.
- Stévant, P., Rebours, C., 2021. Landing facilities for processing of cultivated seaweed biomass: a Norwegian perspective with strategic considerations for the European seaweed industry. *J. Appl. Phycol.* 33, 3199–3214. <https://doi.org/10.1007/s10811-021-02525-w>.
- Stévant, P., Skipnes, D., Jensen, S., Ólafsdóttir, A., Jónsdóttir, R., Sund, R., Clayton-Cuch, D., Aarslev Jensen, H., Figueroa Hurtado, V., Emblem Larssen, W., 2026. Food processing and fermentation of the kelps *Alaria esculenta* and *Saccharina latissima* – effects on sensory properties and flavour-active compounds. *Mendeley Data* 1. <https://doi.org/10.17632/8yb7dnrzc.1>.
- Tello-Ireland, C., Lemus-Mondaca, R., Vega-Gálvez, A., López, J., Di Scala, K., 2011. Influence of hot-air temperature on drying kinetics, functional properties, colour, phycobiliproteins, antioxidant capacity, texture and agar yield of alga *Gracilaria chilensis*. *LWT* 44, 2112–2118. <https://doi.org/10.1016/j.lwt.2011.06.008>.
- Tsai, C.J., Li, W.F., Pan, B.S., 2008. Characterization and immobilization of marine algal 11-lipoxygenase from *Ulva fasciata*. *JAOCs J. Am. Oil Chem. Soc.* 85, 731–737. <https://doi.org/10.1007/s11746-008-1262-6>.

- Ughetti, A., D'Eusanio, V., Strani, L., Russo, A.L., Roncaglia, F., 2024. Influence of Drying and Storage Conditions on the Volatile Organic Compounds Profile of *Spirulina Platensis*. *Separations* 11. <https://doi.org/10.3390/separations11060180>.
- Uribe, E., Vega-Gálvez, A., García, V., Pastén, A., López, J., Goñi, G., 2019. Effect of different drying methods on phytochemical content and amino acid and fatty acid profiles of the green seaweed, *Ulva* spp. *J. Appl. Phycol.* 31, 1967–1979. <https://doi.org/10.1007/s10811-018-1686-9>.
- Uribe, E., Vega-Gálvez, A., Vargas, N., Pastén, A., Rodríguez, K., Ah-Hen, K.S., 2018. Phytochemical components and amino acid profile of brown seaweed *Durvillaea antarctica* as affected by air drying temperature. *J. Food Sci. Technol.* 55, 4792–4801. <https://doi.org/10.1007/s13197-018-3412-7>.
- Vall-Ilosera, M., Steinhagen, S., Pavia, H., Undeland, I., 2024. Brining as an effective method to stabilise sea lettuce (*Ulva fenestrata*) -impact on colour, texture, chemical characteristics and microbial dynamics. *Algal Res.* 83, 103700. <https://doi.org/10.1016/j.algal.2024.103700>.
- van Tuinen, S., Faassen, E., Gsell, A., 2023. Processing-mediated reduction of elemental contaminants in seaweed food and feed. *Prod. Process. -Mediat. Reduct. Contam. Lev. Seaweed Prod. Wagening*. <https://doi.org/10.18174/629186>.
- Vega-Gálvez, A., Uribe, E., Gómez-Pérez, L.S., García, V., Mejías, N., Pastén, A., 2022. Drying kinetic modeling and assessment of mineral content, antimicrobial activity, and potential α -Glucosidase activity inhibition of a green seaweed (*Ulva* spp.) Subjected to different drying methods. *ACS Omega* 7, 34230–34238. <https://doi.org/10.1021/acsomega.2c03617>.
- Vick, B.A., 1991. A spectrophotometric assay for hydroperoxide lyase. *Lipids* 26, 315–320. <https://doi.org/10.1007/BF02537143>.
- Vilar, E.G., O'Sullivan, M.G., Kerry, J.P., Kilcawley, K.N., 2021. A chemometric approach to characterize the aroma of selected brown and red edible seaweeds / extracts. *J. Sci. Food Agric.* 101, 1228–1238. <https://doi.org/10.1002/jsfa.10735>.
- Wirenfeldt, C.B., Hermund, D.B., Feyissa, A.H., Hyldig, G., Holdt, S.L., 2024. Nutritional value, bioactive composition, physico-chemical and sensory properties of *Ulva* sp. and *Fucus vesiculosus* depending on post-harvest processing: a drying comparison study. *J. Appl. Phycol.* <https://doi.org/10.1007/s10811-024-03210-4>.
- Wu, H., Sajib, M., Undeland, I., 2021. Controlling hemoglobin-mediated lipid oxidation in herring (*Clupea harengus*) co-products via incubation or dipping in a recyclable antioxidant solution. *Food Control.* 125, 107963. <https://doi.org/10.1016/j.foodcont.2021.107963>.
- Wu, H., Axelsson, J., Kuhlén, M., Fristedt, R., Undeland, I., 2023. Pilot-scale antioxidant dipping of herring (*Clupea harengus*) co-products to allow their upgrading to a high-quality mince for food production. <https://doi.org/10.1021/acssuschemeng.2c07164>.
- Xiang, X., Chen, L., Dong, S., Li, Z., Liu, Y., Wu, Y., Li, S., Ye, L., 2024. Targeted metabolomics reveals the contribution of degradation and oxidation of lipids and proteins mediated by pH to the formation of characteristic volatiles in preserved egg yolk during pickling. *Food Res. Int.* 195. <https://doi.org/10.1016/j.foodres.2024.114945>.
- Yaich, H., Garna, H., Besbes, S., Paquot, M., Blecker, C., Attia, H., 2011. Chemical composition and functional properties of *Ulva lactuca* seaweed collected in Tunisia. *Food Chem.* 128, 895–901. <https://doi.org/10.1016/j.foodchem.2011.03.114>.
- Zhang, W., Yang, X., Zhang, J., Lan, Y., Dang, B., 2023. Study on the changes in volatile flavor compounds in whole highland barley flour during accelerated storage after different processing methods. *Foods* 12. <https://doi.org/10.3390/foods12112137>.
- Zhang, Y., Wu, X., Shi, Y., Qu, F., Qi, D., Qian, W., Zhang, X., Hu, J., 2025. Identification of key odorants responsible for the seaweed-like aroma quality of Shandong matcha. *Food Res. Int.* 204. <https://doi.org/10.1016/j.foodres.2025.115945>.