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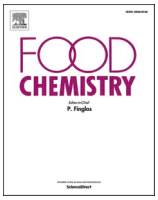

Evolution of microbial community and the volatilome of fresh-cut chili pepper during storage under different temperature conditions: Correlation of microbiota and volatile organic compounds

Zudi Li [a,b], Wenting Zhao [b,**], Pan Wang [b], Shuang Zhao [b], Dan Wang [b], Xiaoyan Zhao [a,b,*]

[a] College of Food Science, Shenyang Agricultural University, Shenyang, Liaoning 110866, China
[b] Institute of Agri-food Processing and Nutrition, Beijing Academy of Agriculture and Forestry Sciences, Beijing Key Laboratory of Agricultural Products of Fruits and Vegetables Preservation and Processing, Key Laboratory of Vegetable Postharvest Processing, Ministry of Agriculture and Rural Affairs, Beijing 100097, China

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ABSTRACT

The effect of temperature conditions on the evolution of microbial communities and volatile organic compounds (VOCs) in fresh-cut chili peppers during storage was investigated. Results showed that *Proteobacteria* and *Actinobacteriota* were the dominant phyla in fresh-cut chili peppers. During storage, bacterial communities changed more dramatically than fungi. Different temperature conditions significantly affected the shift of bacteria at the genus level. At the beginning of storage, *Rhodococcus*, *Pantoea*, and *Pseudomonas* dominated the bacteria. However, on day 8, *Pantoea* and *Enterobacter* became the predominant genera at 5 °C and high temperatures (10, 15 °C, dynamic temperature), respectively. No significant variability in bacterial species was observed between different batches. Additionally, 140 VOCs were determined in fresh-cut chili peppers. Twenty-two VOCs were screened and could be recommended as potential spoilage markers. Based on Spearman's correlation analysis results, *Enterobacter* and *Enterococcus* were the most positive microorganisms correlated with spoilage markers.

1. Introduction

Fresh-cut market has grown sharply in recent years due to increasing demand of consumers for healthy, convenient, and nutritional foods. Chili peppers (*Capsicum annuum* L.) are one of the most popular vegetables all around the world and are commonly found in the fresh-cut market because of their pungency, flavor, and health benefits. Fresh-cut processing used in fruit and vegetables usually accelerates physiological and biochemical changes that result in quality deterioration during storage, especially invasion and proliferation of microorganisms, which limits the shelf-life of fresh-cut products and leads to considerable economic loss for the fresh-cut industry.

There are high populations of naturally occurring microbial communities in fruits and vegetables (Manthou, Coeuret, Chaillou, & Nychas, 2022). The groups are high in species diversity and homogeneous in structure on whole samples. However, in the case of fresh-cut form, the microflora changes, and the balance is disrupted. Moreover, during the storage, the microbial composition was influenced by temperature, storage time, and washing operations (Manthou et al., 2022; Manthou, Coeuret, Chaillou, & Nychas, 2021; Rosberg, Darlison, Mogren, & Alsanius, 2021). Among these microflora, spoilage organisms, only a small part, grow during storage and result in quality deterioration of the product according to the storage conditions (Ioannidis et al., 2018). Therefore, the study of the microbial community changes in fresh-cut products will contribute to improving processing and storage methods in the future.

Microbial growth can cause deterioration in quality attributes of fresh-cut fruit and vegetables, such as texture and flavor. Electronic nose (e-nose) and GC–MS are commonly used for flavor analysis and qualitative and quantitative analysis of volatile organic compounds (VOCs). VOCs are important indexes for evaluating the flavor of food during storage. Also, it can provide reliable measurable markers for spoilage or specific microbial growth (Amaro et al., 2018). For example, propene, (E)-1,3-pentadiene, C_5H_8, methyl isopropyl sulfide, and styrene were recorded as the potential markers for pathogenic infection in onion bulbs caused by *Fusarium oxysporum* (Wang et al., 2019). 2-Nonanone

* Corresponding author at: College of Food Science, Shenyang Agricultural University, Shenyang, Liaoning 110866, China.
** Corresponding author.
E-mail addresses: zhaowenting@iapn.org.cn (W. Zhao), wangpan@iapn.org.cn (P. Wang), zhaoshuang@iapn.org.cn (S. Zhao), wangdan@iapn.org.cn (D. Wang), zhaoxiaoyan@iapn.org.cn (X. Zhao).

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was found to accumulate in *Vagococcus* inoculated brown shrimp (Calliauw, Horemans, Broekaert, Michiels, & Heyndrickx, 2016). *Rahnella aquatilis* were positively correlated with the formation of 3-methyl-1-butanol, which was often seen as a potential marker of spoilage (Ioannidis et al., 2018). Therefore, it renders the possibility of spoilage assessment for fresh-cut fruits and vegetables through VOC determination.

Temperature control is the most essential and common practice to limit microbial spoilage and maintain the freshness of fresh-cut products during storage. Storage temperature is recommended to be 5 °C or less in food service facilities and retail food stores (FDA, 2012). However, temperature abuse often occurs during distribution, retail display, and household storage (Huang, Luo, Zhou, Zheng, & Nou, 2019). So far, it is remarkable that little research has been done on how storage temperatures affect the composition of microbiota and changes in qualities, especially in VOCs. Therefore, the objective of this study is: (1) to assess the evolution of microbial community of fresh-cut chili peppers stored at different temperatures by high-throughput sequencing; (2) to determine the effects of storage temperatures on the changes in qualities, firmness, weight loss, and VOCs, and screen the potential volatile spoilage markers; (3) to analyze the relationships between microbial genera and quality attributes, especially VOCs, to explain the microorganisms leading to spoilage.

2. Material and methods

2.1. Sample preparation

Green chili pepper (*Capsicum annuum* L., Hangjiao No. 2) was harvested in Shouguang, Shandong, China (36°86′ N, 118°80′ E). At the laboratory, peppers with uniform size, no pests and wounds were washed in tap water and disinfected with sodium hypochlorite solution (200 mg/L) for 2 min. The peppers were cut into 8 mm thick rings and washed with deionized water. Then, the fresh-cut peppers (200 g in each bag) were packed using ethylene vinyl alcohol copolymer (EVOH) bags with an O_2 permeability of 8.9 $cm^3\ m^{-2}\ d^{-1}\ MPa^{-1}$ (Xuri Paper Plastics Packaging Co., ltd in China). Finally, samples were stored at 5, 10, 15 °C and dynamic temperatures (DT) (8 h at 5 °C, 8 h at 10 °C and 8 h at 15 °C in each day) for 8 days, respectively. During storage, the samples were collected every two days and divided into two portions, of which one portion was used for determination of microbial counts, pH, texture, and e-nose, while the other portion was immediately frozen in liquid nitrogen and then kept at −80 °C for microbial community and VOCs analysis. Three batches were processed on different dates for microbial community analysis. Three replicates were performed for each temperature condition.

2.2. DNA extraction and PCR amplification

According to the procedures recorded by Xu et al. (2021) and Peng et al. (2023), the microbial DNA was extracted, purified, and inspected. Then, the hypervariable region of the bacteria 16S rRNA gene was amplified (primer pairs: 799F (5'-AACMGGATTAGATACCCKG-3′) and 1392R (5'-ACGGGCGGTGTGTRC-3′)). The amplification condition: Initial denaturation at 95 °C for 3 min; 27 cycles of denaturation at 95 °C for 30 s, annealing at 55 °C for 30 s, and extension at 72 °C for 45 s; then, a final extension at 72 °C for 10 min. A second round was repeated for 13 cycles with primers of 799F (5'-AACMGGATTAGATACCCKG-3′) and 1193R (5'-ACGTCATCCCCACCTTCC-3′) using the same amplification condition as the first round. As for fungi, the ITS region of 18S rDNA was amplified using a primer set (the forward primer ITS1F (5′-CTTGGTCATTTAGAGGAAGTAA-3′) and the reverse primer ITS2R (5′-GCTGCGTTCTTCATCGATGC-3′)), which were equipped with unique identifier tags. The amplification conditions for fungi were the same as the amplification of bacteria, except that the number of PCR cycles was 35. Finally, the reaction products were cooled to 4 °C. Then the PCR products were extracted, purified, and quantified by Quantus™ Fluorometer (Promega, USA).

2.3. Illumina MiSeq sequencing and data processing

Pyrosequencing and bioinformatics processing were referred to in previous studies (Xu et al., 2021). Purified amplicons were pooled and paired-end sequenced according to the standard protocols by Majorbio Bio-Pharm Technology Co. Ltd. (Shanghai, China). Then the raw fastq files were demultiplexed, and quality filtered.

2.4. Microbial counts

Microbial counts were determined according to the reported method (Zhang et al., 2020) with minor modifications. Fresh-cut chili peppers (15 g) were homogenized with 135 mL 0.8% NaCl solution for 2 min in a beating homogenizer (BagMixer 400 W, Interscience Lab Inc., Hanover, MA, USA). After that, the mixed solutions were serially diluted at a ratio of 1:10. Then, the diluted suspension was mixed with plant counting agar and potato dextrose agar, then incubated at 37 ± 1 °C (48 h) and incubated at 28 ± 1 °C (5 days) to obtain total bacterial counts (TBC) and mold and yeast counts, respectively.

2.5. Texture analysis

Fresh-cut chili peppers were used for texture analysis. For firmness measurement, a flat cylindrical probe (10 cm diameter) mounted on a TA-XT plus texture analyzer (Stable Micro Systems Ltd., Godalming, UK) was used. The probe traveled down 7 mm from a height of 10 mm at a speed of 0.5 mm/s. The maximum force (N) was recorded as firmness.

2.6. Determination of weight loss and pH

Samples were homogenized and then used for pH determination using a pH meter at room temperature (Metler-Toledo Instruments Co., Ltd., Shanghai, China). Weight loss rate was expressed according to the formula below.

$$\text{Weight loss rate} = \frac{\text{weight before storage} - \text{weight after storage}}{\text{weight before storage}} \times 100\%$$

2.7. E-nose analysis

Fresh-cut peppers were homogenized then the homogenized samples (3 g) were placed in 30 mL headspace vials and then equilibrated for 30 min at 25 °C. E-nose analysis was performed through an e-nose system (PEN3, Air Sense Analytics GmbH, Germany), which included 10 sensors (W1C, W5S, W3C, W6S, W5C, W1S, W1W, W2S, W2W, W3S). Description of 10 sensors is given in Supplementary Table 1. The measurement conditions were as follows: sampling time: 150 s; airflow velocity: 300 mL/min; purging time: 100 s. Each sensor's values from 142 s to 142 s were selected for analysis.

2.8. Determination of VOCs

The VOCs of peppers were determined through GC–MS combined with headspace solid-phase microextraction (HS-SPME) (Agilent Technologies, Santa Clara, CA, USA) (Xu et al., 2021). Frozen peppers were ground into powder using liquid nitrogen grinder (IKA A11 basic; IKA Werke GmbH & Co. KG, Staufen, Germany). The frozen powders (1.0 g) were placed into 20 mL headspace vials containing 3 mL saturated sodium chloride solution. Then 20 μL 2-methyl-3-heptanone (8.16 mg/L) was added to each vial as an internal standard. After that, the vial was immediately incubated in a heating block at 70 °C for 15 min. A SPME fiber (5191–5874, Agilent Technologies, Santa Clara, CA, USA) was exposed to headspace of the vial at 70 °C for 40 min. VOCs were

desorbed from SPME fibers at the inlet at 250 °C for 5 min. The temperature of MS column (DB-5, 30 m × 0.25 mm, 0.25 μm film thickness; Agilent, Santa Clara, CA, USA) was initially set at 40 °C (3 min), increased to 150 °C at 5 °C/min, and finally increased to 250 °C at 10 °C/min (10 min). The ion source temperature of MS was 230 °C, with a mass range of *m/z* 33–500 and a 70 eV electronic ionization energy.

The identification of compounds was performed using the NIST17 mass spectrum database at a quality match score of >80% and the retention index (RI) of each volatile compound. The RI was calculated from retention time of n-alkanes (C7-C30) and compared with those recorded in the NIST Chemistry WebBook (https://webbook.nist.gov/chemistry/).

2.9. Statistical analysis

Data of microbial counts, firmness, weight loss, and pH values were analyzed by one-way analysis of variance (ANOVA) and Duncan's test ($p < 0.05$) using SPSS (version 17.0; Chicago, IL, USA). Orthogonal partial least squares discriminant analysis (OPLS-DA) and partial least-squares discriminant analysis (PLS-DA) were performed using the SIMCA-P software (version 11.5; Umetrics, Umeå, Sweden) and MetaboAnalyst 5.0 (https://www.metaboanalyst.ca/), respectively. Data plotting was conducted by Originpro 8 software (OriginLab Corporation, Northampton, MA, USA). The correlation index of bacterial genera and off-odor compounds, as well as physicochemical properties, was calculated by Spearman's correlation. A high correlation coefficient ($|r| \geq 0.4$) with $p < 0.05$ between microbiota and quality attributes was visualized via Cytoscape (3.9.1) software.

3. Results and discussion

3.1. Microbial counts of fresh-cut chili peppers during storage

TBC and mold and yeast counts of fresh-cut chili peppers were 2.95 and 1.74 log CFU/g on day 0, respectively (Fig. 1), and showed an increasing trend during storage under all temperature conditions. After 8 days of storage, TBC at 5 °C, 10 °C and 15 °C increased to 3.81, 5.25, and 8.66 log CFU/g, respectively (Fig. 1a). Mold and yeast counts increased to about 3.38, 5.17, and 8.46, respectively (Fig. 1b). As expected, the microbial growth was faster at higher temperatures. Storage at 5 °C showed a lower growth rate than other higher temperatures. The microbial count monitored under DT condition increased faster than that recorded at 10 °C during storage. The final counts of DT (6.77 log CFU/g for bacteria counts and 6.75 log CFU/g for molds and yeasts) were only secondary to that of 15 °C. A study on fresh-cut green bell peppers reported that 5.0 log CFU/g of TBC is suggested to be the tolerance limit (Chen, Zhang, Bhandari, & Guo, 2018). Samples were under this acceptable limit at 5 °C during the whole storage, while reached that at day 8, 4, and 6 when stored at 10, 15 °C, and DT, respectively.

3.2. Shifts in the bacterial community of fresh-cut chili peppers during storage

The richness and diversity of bacterial communities were expressed by the α-diversity indices (Chao and Shannon indices), respectively (Supplementary Fig. 1). As storage time prolonged, the Sobs index first increased and then decreased. At the same time, the Shannon index showed a decreasing trend (Fig. 2a, b), indicating the richness and diversity decreased during the late storage period. Lopez-Velasco, Welbaum, Boyer, Mane, and Ponder (2011) also found the same trends after packaging and storing spinach. This result could be due to atmospheric changes in packages during storage. The α-diversity of fresh-cut chili peppers was also affected by storage temperatures. As shown in Fig. 2c, d, the highest Chao and Shannon indices were observed in samples stored at DT, followed by samples at 10 °C, 15 °C, and 5 °C. It represented that DT conditions had a higher level of complexity. A similar result has been reported by Manthou et al. (2022) that the bacterial community of baby spinach stored at dynamic temperature had a higher α-diversity compared to samples stored at 8 °C and 12 °C.

Changes in bacterial community at phylum and genus levels of fresh-cut chili peppers during storage under different temperatures were shown in Supplementary Fig. 2 and Fig. 2, respectively. All samples mainly contained four bacterial phyla (*Proteobacteria*, *Actinobacteriota*, *Firmicutes*, *Bacteroidota*). *Proteobacteria* (52.82%) and *Actinobacteriota* (45.00%) were dominant on day 0, followed by *Bacteroidota* (1.27%) and *Firmicutes* (0.80%). During storage, the abundance of *Proteobacteria* at all storage temperatures decreased firstly and then increased after 6 days. The abundance reached between 55.02% and 99.26% for four temperature conditions on day 6. The trends could be due to the shift of dominant bacteria from *α-Proteobacteria* and *β-Proteobacteria* to *γ-Proteobacteria* (Vahdatzadeh, Deveau, & Splivallo, 2019). Lopez-Velasco et al. (2011) also reported that *γ-Proteobacteria* increased during the storage of spinach. This bacterium was widely reported as the dominant food spoilage bacteria in rotten fruits and correlated with the formation of spoilage volatile markers (Vahdatzadeh et al., 2019).

The abundance of bacterial community at genus level was observed from Fig. 2, it showed that *Rhodococcus*, *Pantoea*, and *Pseudomonas* had high abundance at day zero of storage. These were common endophytic bacteria in peppers and are usually found in fresh-cut produce after cutting (Xu, Huang, Meng, Chen, & Han, 2022). After 4 days of storage, the abundance of *Rhodococcus* increased at all temperature conditions,

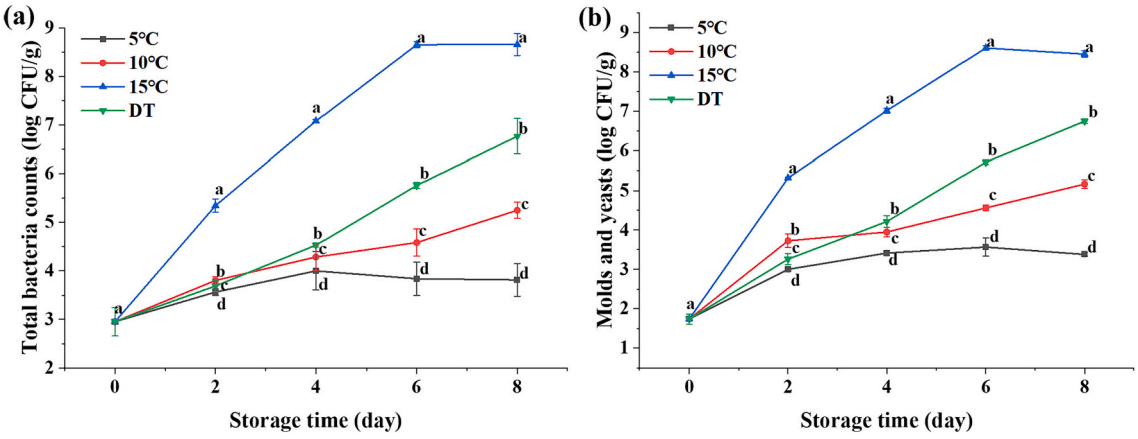

Fig. 1. Total bacteria (a) and molds and yeasts (b) counts of fresh-cut chili peppers stored at different temperatures. The different letters indicate significant differences in different storage temperatures at the same storage time ($p < 0.05$).

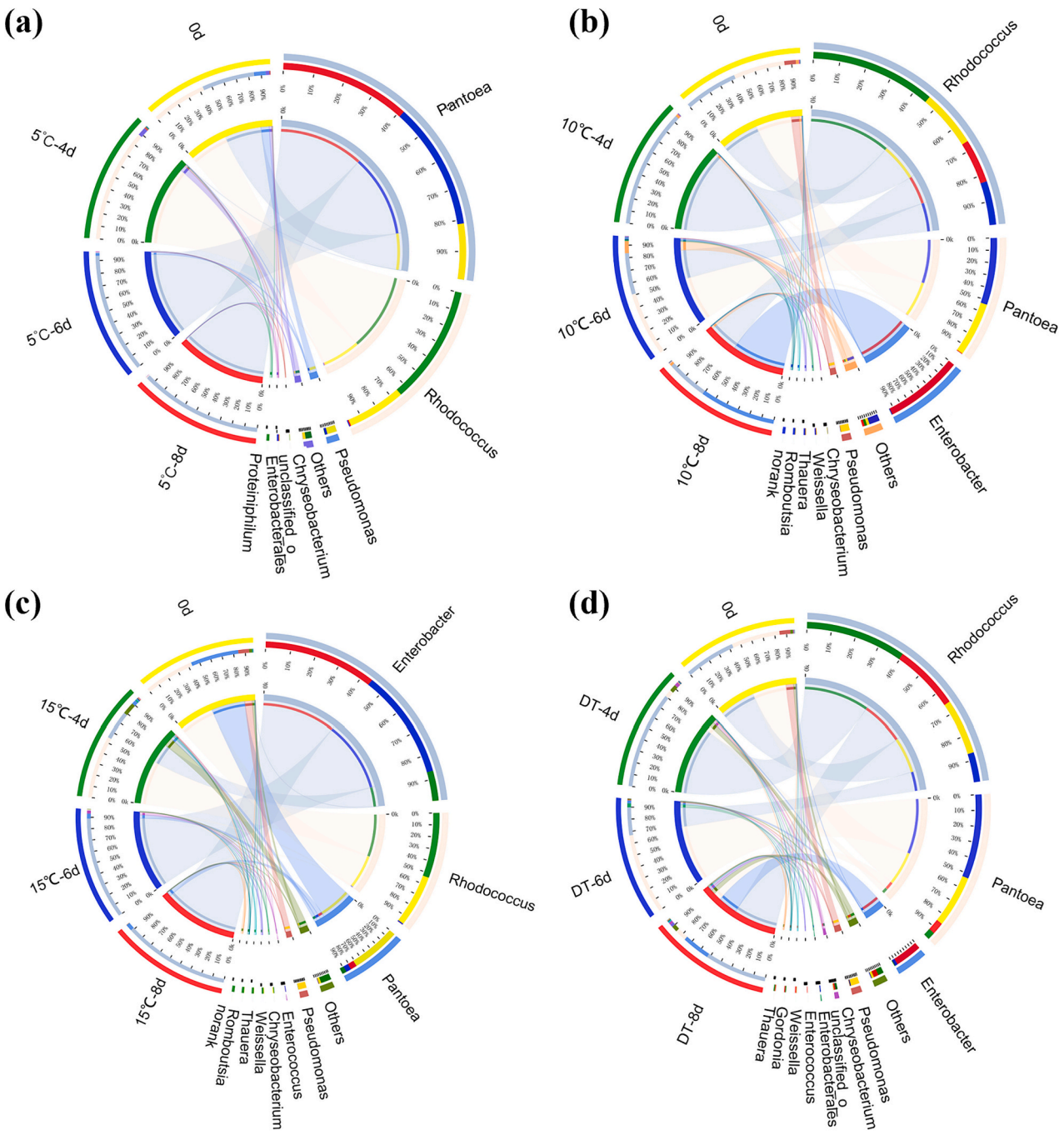

Fig. 2. The relative abundance of bacterial community at the genus level of fresh-cut chili peppers stored at different temperatures: (a) 5 °C, (b)10 °C, (c)15 °C, (d) DT.

accompanied by the decrease of *Pantoea* and *Pseudomonas*. *Pseudomonas* was aerobic bacteria, so its drop could be due to oxygen consumption in the package. *Rhodococcus* may have a higher competitive ability against facultative anaerobe *Pantoea* during the early storage. Following the next storage time, *Rhodococcus* showed decreasing trends, and it was replaced by other genera (*Pantoea*, *Enterobacter*, and so on).

Storage temperature drove a strong change in the bacterial community structure. From Fig. 2, *Pantoea*, *Rhodococcus*, and *Pseudomonas* were dominant bacterial genera of 5 °C during the storage. Under 15 °C, the dominant genera were *Enterobacter*, followed by *Rhodococcus* and *Pantoea*. The genera distribution at 10 °C and DT was similar, mainly including *Rhodococcus*, *Pantoea*, and *Enterobacter*. Specifically, *Pantoea* showed an increased abundance after 6 days and progressively dominated in samples of 5 °C on day 6 and 8 (96.51% and 98.96%). However, the abundance of *Pantoea* only increased to 4.38% and 5.64% at 15 °C. The results showed that *Pantoea* was the dominant genus at low temperature during the late storage period and decreased with the increased storage temperatures. Differently, *Enterobacter* was not detected at 5 °C, while its abundance was relatively high in 10, 15 °C, and DT groups. Especially at 15 °C, it reached 91.44% and 93.92% on day 6 and 8 and dominated at the late storage, which indicated that high temperature storage caused a faster proliferation of *Enterobacter* than low temperature. A similar result has been reported in fresh-cut watermelon that *Enterobacter* was more abundant at higher temperatures in the last days (Hu et al., 2022). Moreover, *Enterobacter* was widely reported as spoilage bacteria genera in previous studies (Hu et al., 2022;

Leneveu-Jenvrin et al., 2020; Li, Li, Yi, & Zeng, 2024). For 10 °C and DT groups, the abundance of *Pantoea* was 52.40% and 68.69% on day 6, then decreased to 0.51% and 9.93% on day 8, respectively. Correspondingly, on day 8, *Enterobacter* replaced *Pantoea* and became the dominant genus in 10 °C and DT groups. Therefore, it is speculated that *Pantoea* will eventually shift to *Enterobacter* at the end of storage regardless of the storage temperature. The abundance of *Enterobacter* at 15 °C and DT increased on day 4, which occurred earlier than 10 °C (day 6). Thus, the abundance of *Enterobacter* could be used as a potential indicator to determine whether the cold chain of fresh-cut chili pepper was complete.

Interestingly, compared to other temperatures, more kinds of bacterial genera, such as *Chryseobacterium*, *Enterococcus*, *Weissella*, *Thauera*, *Gordonia*, *Romboutsia*, *Exiguobacterium*, *Corynebacterium*, *Bacteroides*, *Bacillus*, *Prevotella, Microbacterium* and *Lactobacillus* had higher abundance in DT at the end of storage (Supplementary Table 2), which could be the reason for its higher richness and diversity. DT conditions may lead to quality deterioration by maintaining the survival of more species of bacteria. Such as *Weissella*, a typical lactic acid bacterium, survived in kimchi (Liang et al., 2020).

3.3. Shifts in the fungal community of fresh-cut chili peppers during storage

During the whole storage, the richness of the fungal community increased first and then decreased. While the diversity showed a fluctuating trend (Supplementary Fig. 3a, b). As for different storage temperatures, the groups with the higher richness and diversity were DT and 5 °C, respectively (Supplementary Fig. 3c, d).

Heatmap analysis of fungal community at the phylum level (Supplementary Fig. 4a) showed that *Basidiomycota* (47.37%) and *Ascomycota* (46.35%) were dominant fungal communities at day 0. After genera (abundances of <1%) were combined (Others), 30 major fungal genera were shown in the storage of fresh-cut chili peppers, which was higher than the numbers of bacterial genera. Among the 30 dominant fungal genera, *Apiotrichum*, *unclassified_o_Saccharomycetales*, *Cutaneotrichosporon*, *unclassified_p_Ascomycota*, *Rhodotorula*, *Cladosporium* and *Naganishia* were the most predominant (Supplementary Fig. 4b). During the storage at all temperature conditions, the structures of the fungal community changed slightly and didn't show temperature dependence. This finding was inconsistent with a previous study, which reported that the fungal community of fresh-cut pineapple had a leading role in the quality changes and changed significantly with the storage temperature and time (Leneveu-Jenvrin et al., 2020). It may be due to the difference in raw materials. The high sugar content of pineapple supported the dominant growth of yeast and mold (da Cruz Almeida et al., 2018). On the contrary, the bacterial community may play a vital role in fresh-cut vegetables with lower sugar content. Studies have confirmed that bacteria are vegetables' most abundant inhabitants, which are derived from mechanical damage or root systems (Manthou et al., 2022). Moreover, Xu et al. (2022) emphasized the importance of foodborne pathogens and spoilage bacteria in the fresh-cut vegetable processing line. Therefore, the bacterial community that changed much during storage was used for further analysis in this study.

3.4. Variation of bacterial community dynamics among different batches

To clarify the difference in bacterial community dynamics in different batches, Non-metric multidimensional scaling (NMDS) on Bray-Curtis distances analysis was performed to statistically compare the bacterial community of fresh-cut chili pepper stored in three batches (Supplementary Fig. 5). Samples from different batches clustered closely, which indicated that the initial bacterial communities and their succession during storage in different batches were similar. Paillart et al. (2017) also reported that similar patterns in bacterial population dynamics were observed in three repeated batches. Gu et al. (2018) reported no significant difference in the α-diversity of microbial communities on spinach between two repeat batches.

3.5. Changes in physicochemical properties of fresh-cut chili peppers during storage

Firmness and pH of fresh-cut chili peppers at all temperatures decreased significantly during storage except for 5 °C (Table 1). The decrease at 15 °C was earlier, quicker, and more severe than at DT and 10 °C after 8 days of storage. On day 8, the firmness and pH at DT were significantly lower than that of samples at 10 °C. Weight loss gradually increased at all temperatures during storage. Severe weight loss occurred in samples stored at 15 °C, followed by DT, 10 °C, and 5 °C. These results indicated that changes in physicochemical properties are temperature-dependent. Quality deterioration was closely associated with microbial spoilage. Franco and Perez-Diaz (2012) reported that *Enterobacter* was generally considered as a spoilage bacterium in fermented cucumber pickles and produced propionic and acetic acids. Organic acids could also accumulate significantly during storage due to anaerobic fermentation caused by lactic acid bacteria (*Enterococcus*, *Weissella*, and *Lactobacillus*), which resulted in the decline of pH value (Hu et al., 2022; Paillart et al., 2017). Moreover, *Enterobacter* was reported to show polygalacturonase activity, which could cause cell wall degradation, ultimately resulting in tissue softening (Escobar-Mucino et al., 2020).

Additionally, the quality indicators above-mentioned remained relatively stable until day 8, 6, 2, and 4 when samples were stored at

Table 1
Hardness, pH, and weight loss of fresh-cut chili peppers stored at different temperatures. The different letters indicate significant differences in different storage temperatures at the same storage time ($p < 0.05$).

	Storage temperature			
Storage time (day)	5 °C	10 °C	15 °C	DT
Firmness (N)				
0	99.34 ± 8.86a	99.34 ± 8.86a	99.34 ± 8.86a	99.34 ± 8.86a
2	94.77 ± 8.18ab	99.48 ± 8.76ab	92.84 ± 8.15b	101.04 ± 6.68a
4	96.58 ± 9.64a	92.07 ± 5.06a	82.77 ± 5.25b	91.88 ± 8.91a
6	102.29 ± 10.87a	91.82 ± 8.30b	53.22 ± 4.71d	73.72 ± 7.63c
8	93.52 ± 6.18a	69.64 ± 7.28b	41.80 ± 3.17d	61.45 ± 6.38c
pH				
0	6.62 ± 0.00a	6.62 ± 0.00a	6.62 ± 0.00a	6.62 ± 0.00a
2	6.64 ± 0.01a	6.60 ± 0.12a	6.61 ± 0.04a	6.58 ± 0.09a
4	6.66 ± 0.01a	6.58 ± 0.09a	6.35 ± 0.02b	6.58 ± 0.04a
6	6.65 ± 0.04a	6.38 ± 0.01b	6.15 ± 0.02c	6.37 ± 0.06b
8	6.63 ± 0.01a	6.24 ± 0.07b	5.40 ± 0.01d	6.09 ± 0.02c
Weight loss (%)				
0	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a
2	0.07 ± 0.07b	0.07 ± 0.03b	0.54 ± 0.05a	0.03 ± 0.02b
4	0.21 ± 0.02c	0.19 ± 0.00c	0.85 ± 0.01a	0.46 ± 0.01b
6	0.30 ± 0.02d	0.67 ± 0.03c	6.21 ± 0.02a	1.84 ± 0.12b
8	0.41 ± 0.02d	3.37 ± 0.12c	10.29 ± 0.25a	6.00 ± 0.12b

5,10,15 °C and DT. It indicated that peppers spoiled beyond this period, corresponding to the respective temperature conditions. The results were in accordance with the limit of TBC.

3.6. Changes in e-nose responses of fresh-cut chili peppers during storage

Changes in response values of e-nose sensors of samples stored at 5, 10, 15 °C and DT conditions were shown in Fig. 3. It can be observed that W1S (sensitive to alkanes), W1W (sensitive to sulfur organic compounds, terpenes), W2S (sensitive to alcohols and aldehydes), and W5S (sensitive to nitrogen oxides) showed significant increasing trends during the storage, suggesting that various compounds such as alkanes, terpenes, alcohols, aldehydes, and nitrogen oxides increased during storage (Jiang et al., 2023). The results indicated flavor quality deteriorated with extended storage time at all temperatures. The most apparent change was observed at 15 °C, followed by DT, 10 °C, and 5 °C, which indicated that the flavor quality changed more severely at higher temperatures and fluctuating temperature conditions.

The e-nose data were analyzed through OPLS-DA to determine the differences in volatile patterns of fresh-cut peppers stored at different storage conditions (Supplementary Fig. 6). The data show that the fit is good (R2X = 0.731) and predictability (Q2 = 0.656). Two groups can be obtained in Supplementary Fig. 6a. The sample (day 0) was located in the fourth quadrant. Samples stored at 5 °C, 10 °C (day 2–6), 15 °C (day 2), and DT (day 2–4) clustered the first group, while the other group contained peppers stored at 10 °C (day 8), 15 °C (day 4–8) and DT (day 6–8). Two groups represented fresh and spoiled samples, respectively, which was consistent with the results of traditional physicochemical properties. Similar discrimination has also been reported in the freshness assessment of fresh-cut green bell peppers (Chen et al., 2018). The loading plot (Supplementary Fig. 6b) of sensors showed that W1W, W1S, W2S, W5S, W2W, W6S, and W3S had higher influences on the distribution of samples, which will be used for further correlation analysis between core bacterial genus and quality attributes.

3.7. Changes in VOCs of fresh-cut chili peppers during storage

3.7.1. VOCs identification

GC–MS identified a total of 140 VOCs, which fell into 11 chemical classes: esters, aldehydes, alcohols, alkenes, alkanes, ketones, acids, phenols, alkynes, furans, and others (Supplementary Table 3). Many VOCs, 4-methylpentyl-2-methylpropanoate (v4), methyl salicylate (v11), 4-methylpentyl 2-methylbutanoate (v12), cis-3-Hexenyl-2-methylbutyrate (v14), isopentyl 8-methylnon-6-enoate (v25,), (E)-2-hexenal (v39), linalool (v73), (E)-3,7,11-trimethyl-1,6,10-dodecatrien-3-ol (v77), aromandendrene (v93), α-ionone (v115), trans-β-ionone (v117), 2-methoxy-4-vinylphenol (v130), p-xylene (v139), 2-methoxy-3-(2-methylpropyl)-pyrazine (v140) have been reported in previous studies of peppers (Xu et al., 2021). (*Z*)-Hexanoic acid, 3-hexenyl ester (v19), and 4-Oxohex-2-enal (v42) were reported for the first time in peppers. Additionally, among all VOCs, v4, v14, v19, 3-methyl-butanoic acid, phenylmethyl ester (v20), oxalic acid, allyl hexadecyl ester (v24), sulfurous acid, hexyl pentadecyl ester (v29), 1-undecanol, acetate (v32), v42 and 1-ethoxy-4,4-dimethyl-2-pentene (v85) were only detected during the early storage (day 0–4). All of these showed a decreasing trend during the whole storage at all temperatures. Therefore, these VOCs could be termed as freshness markers of fresh-cut chili peppers. In a previous study, V14 has also been reported in fresh chili peppers, contributing to intense notes (Trovato, Vento, Creti, Dugo, & Mondello, 2022). Chen, Zhang, and Guo (2019) reported that v19 had a high

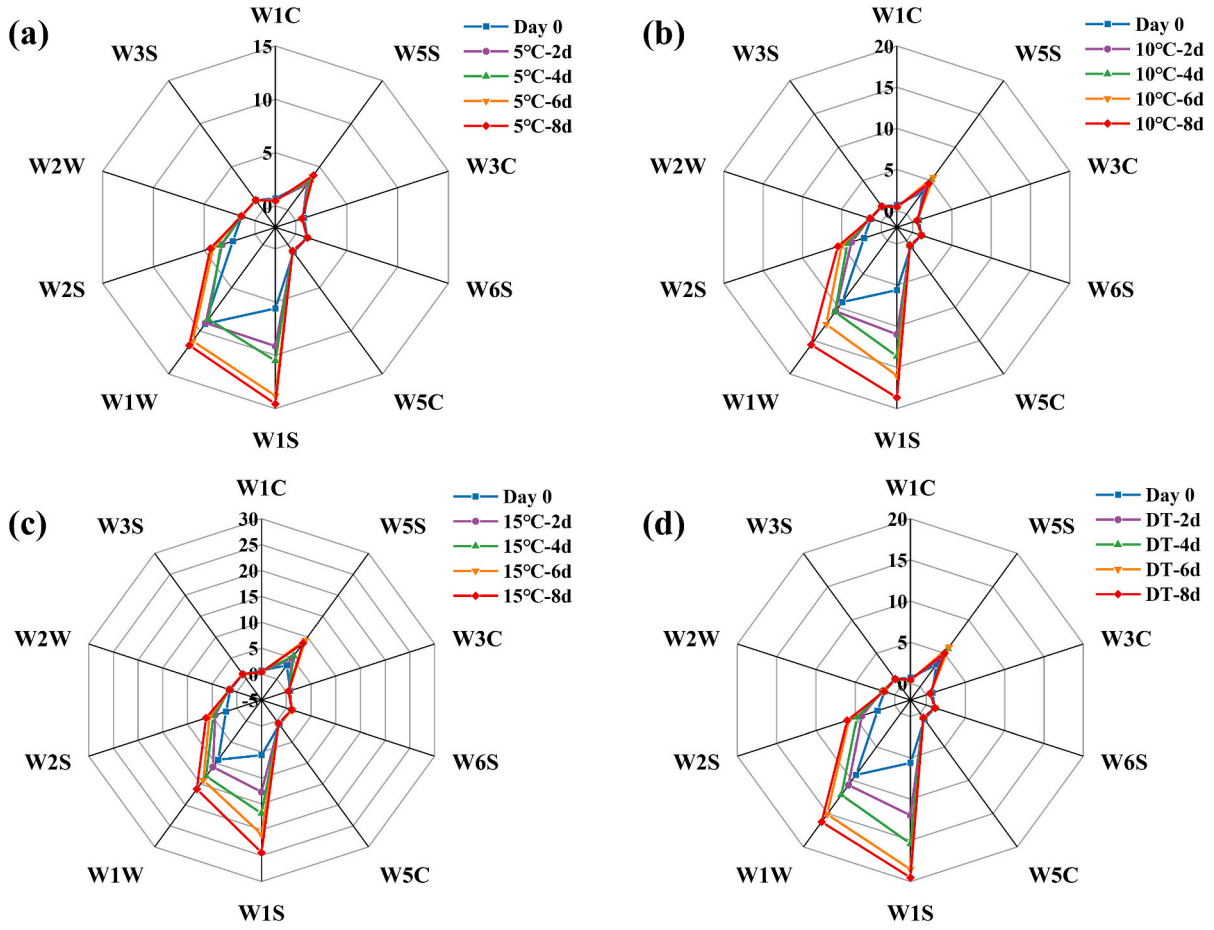

Fig. 3. Radar responses from electronic nose (E-nose) detection of fresh-cut chili peppers stored at different temperatures: (a) 5 °C, (b)10 °C, (c)15 °C, (d) DT.

content in fresh-cut broccoli and decreased when spoiled.

3.7.2. Total volatiles content

During the storage period, the total content of VOCs decreased slightly after 2 days under all temperature conditions (Fig. 4a.), which indicated the loss of green aroma (More et al., 2022). A similar result was reported in fresh-cut apples: the cumulative VOC concentrations decreased during storage compared to the samples immediately after cutting (Rux et al., 2020). During the storage period from day 4 to day 8, the content of VOCs in the peppers stored at 5 °C maintained a relatively low level and exhibited a stable trend. While the content in samples stored at 10, 15 °C and DT showed increasing trends, especially at 15 °C. A study has also observed VOCs accumulated during the late storage period in fresh-cut fruit and vegetables and deemed this phenomenon as flavor deterioration and off-odor formation (More et al., 2022). High temperature conditions promoted total volatile production more than lower temperatures. VOCs are secondary metabolites produced by the degradation of primary metabolites, such as carbohydrates, amino acids, peptides, and fatty acids. The increase of VOCs during storage could be due to metabolic acceleration as a response to microbial growth and physical injury. Thus, the flavor deterioration was temperature-dependent, and high temperature led to faster generation of off-odors during the late storage period. Notably, the total content on day 4 was higher in the samples stored at DT than in all other temperatures. It probably suggested that an earlier off-odor production occurred in fresh-cut chili peppers stored at DT compared to other storage temperatures. That could be due to the physiological metabolism and microbial growth caused by temperature fluctuation (Xin et al., 2021).

3.7.3. Volatile composition

Similar to the changing trend of VOCs, all chemical classes except for esters showed first decreasing trends but increased afterward (Fig. 4a). From day 2 to day 8, most chemical classes at 5 °C maintained constant with low levels. In contrast, those at other temperatures showed increasing trends, especially at 15 °C. Notably, most categories except for esters, phenols, and furans on day 4 accumulated much higher at DT condition than at other storage temperatures, which suggested that DT caused a large accumulation of volatile substances earlier. Microorganism plays a vital role in metabolic pathways related to flavor deterioration. The increases in the content of aldehydes, alcohols, and organic acids could be due to microbial fermentation metabolism with the development of storage time (Pothakos et al., 2014). Following, esters are generally derived from the esterification of short-chain acids with alcohols by the esterase produced by microorganisms (Ye et al., 2020). In this research, the growth rate of microorganisms increased under 15 °C and DT, which could cause a higher production of VOCs.

3.7.4. PLS-DA

A PLS-DA was performed to distinguish the differences in volatile profiles of samples at different storage times (Fig. 4b). The model fit parameters of R2 and Q2 were 0.891 and 0.825, respectively, indicating a good fit and acceptable predictability. The samples at day 0 (fresh) were clustered at the figure's left. With the extended storage time, the samples were gradually far away from fresh samples. And fresh-cut chili peppers were separated from each other at all the storage days, especially on day 0, 4, and 8. This result indicated that the flavor deteriorated with the extension of storage time (Mendoza-Enano, Stanley, & Frank, 2019). The effects of different storage times were assessed using variable importance projection (VIP) analysis, and compounds with VIP of $\geq$1.0 were considered important in the discrimination between different groups of samples. Based on this criterion, 38 differential volatiles were screened from the 140 VOCs, of which 22 VOCs increased with the extension of storage time (Fig. 4c), which could be seen as potential spoilage markers. These 22 volatiles including 2 esters (benzoic acid, 2-hydroxy-, ethyl ester (v18), 9-oxononanoic acid ethyl ester (v23)), 5 aldehydes ((E)-2-octenal (v46), phenylglyoxal (v47), (E)-2-nonenal (v50), (E, E)-2,4-nonadienal (v53), (E, E)-2,4-decadienal (v55)), 3 alcohols (3-methyl-1-butanol (v58), 4-methyl-1-pentanol (v62), 4-ethylcyclohexanol (v67)), 1 alkenes (3-ethyl-2-methyl-1,3-hexadiene (v83)), 2 alkanes (octane (v97), 1-butenylidene-cyclohexane (v100)), 4 ketones (2-sec-butylcyclohexanone (v110), 5-hydroxycyclooctane-1,2-dione (v112), 4-(2,6,6-trimethyl-2-cyclohexen-1-yl)-2-butanone (v114), 4-(2,6,6-trimethyl-1-cyclohexen-1-yl)-2-butanone (v116)), 3 acids (nonanoic acid (v121), 9-decenoic acid (v123), n-hexadecanoic acid (v127,), 1 phenol (2-methoxy-phenol (v129)) and 1 furan (2,3-dihydro-Benzofuran (v137)). All of these compounds represented differential volatile metabolites and contributed to the specificity of the samples with unpleasant flavors. Similarly, V46, v55, and v62 in samples usually represented a role of these compounds in the odors giving a perception of lack of freshness (Mendoza-Enano et al., 2019; Yahya, Lignou, Wagstaff, & Bell, 2019). Compounds, including v50 (musty), v53 (Fat, dirty, (Guneser & Yuceer, 2017)), v121 (sweaty, rancid, fat, (Xiao et al., 2010)) and v127 (waxy, creamy fatty, dairy, groundy (Ye et al., 2020)), have been detected in minimally processed carrots, tomato pomace, rotten aerobic packaged meat and fermented paojiao, respectively. Additionally, v55 was identified as the key VOC in sour meat as the main contributor to odor (Lv et al., 2019). V58, with a disgustful smell or fermentative-like off-odor, also accumulated in chill-stored blue crabs and was suggested as a potential spoilage marker (Ioannidis et al., 2018).

3.8. Correlation analysis between core bacterial genus and quality attributes

The relationship between bacterial genus with abundance in the top 20 and the quality attributes in fresh-cut chili peppers was analyzed using Spearman's correlation, as shown in Fig. 5. A total of 18 bacterial genera were significantly related to physicochemical qualities (e-nose responses, firmness, weight loss, pH, TBC) and VOC metabolites (potential spoilage markers in Section 3.7.4) (Fig. 5, Supplementary Table 4).

Enterobacter was identified as the most influential genus due to its significant correlation with 18 potential spoilage markers and physicochemical qualities. The abundance of *Enterobacter* was positively correlated with TBC. These results suggested that the growth and metabolism of *Enterobacter* could have a significant effect on the deterioration of physicochemical and flavor characteristics. It has been reported that *Enterobacter* was the primary spoilage bacterial microorganism in vegetables, which could invade the tissue of raw materials and lead to soft rot diseases (Li et al., 2024). Moreover, *Enterobacter* was reported as the main contributor to the production of volatile compounds in northeast sauerkraut during the fermentation process (Yang et al., 2020). Hence, quality deterioration at high temperatures in this study may be closely related to the growth of *Enterobacter*.

The abundance of *Enterococcus* was also positively correlated with the formation of 18 potential spoilage markers and the loss of physiochemical qualities. Therefore, *Enterococcus* was another dominant working genus in the quality deterioration process. As a typical lactic acid bacterium, *Enterococcus* could promote carbohydrate consumption and pH decline (de Castro, Montano, Casado, Sanchez, & Rejano, 2002). This genus also played a crucial role in the spoilage of fresh-cut watermelon and was positively correlated with the formation of aldehydes, alcohols, and furans (Hu et al., 2022). Additionally, the abundance of *Enterococcus*, which was positively correlated with TBC, increased during the late storage at 15 °C and DT (Fig. 2). Therefore, high temperature and DT conditions may also accelerate quality deterioration by promoting the growth of *Enterococcus*.

Unclassified_o_Enterobacterales and *Pantoea* were positively correlated with the accumulation of nonanoic acid (v121) and 4-(2,6,6-trimethyl-2-cyclohexen-1-yl)-2-butanone (v114), respectively. Additionally, *Unclassified_o_Enterobacterales also* positively correlated with weight loss

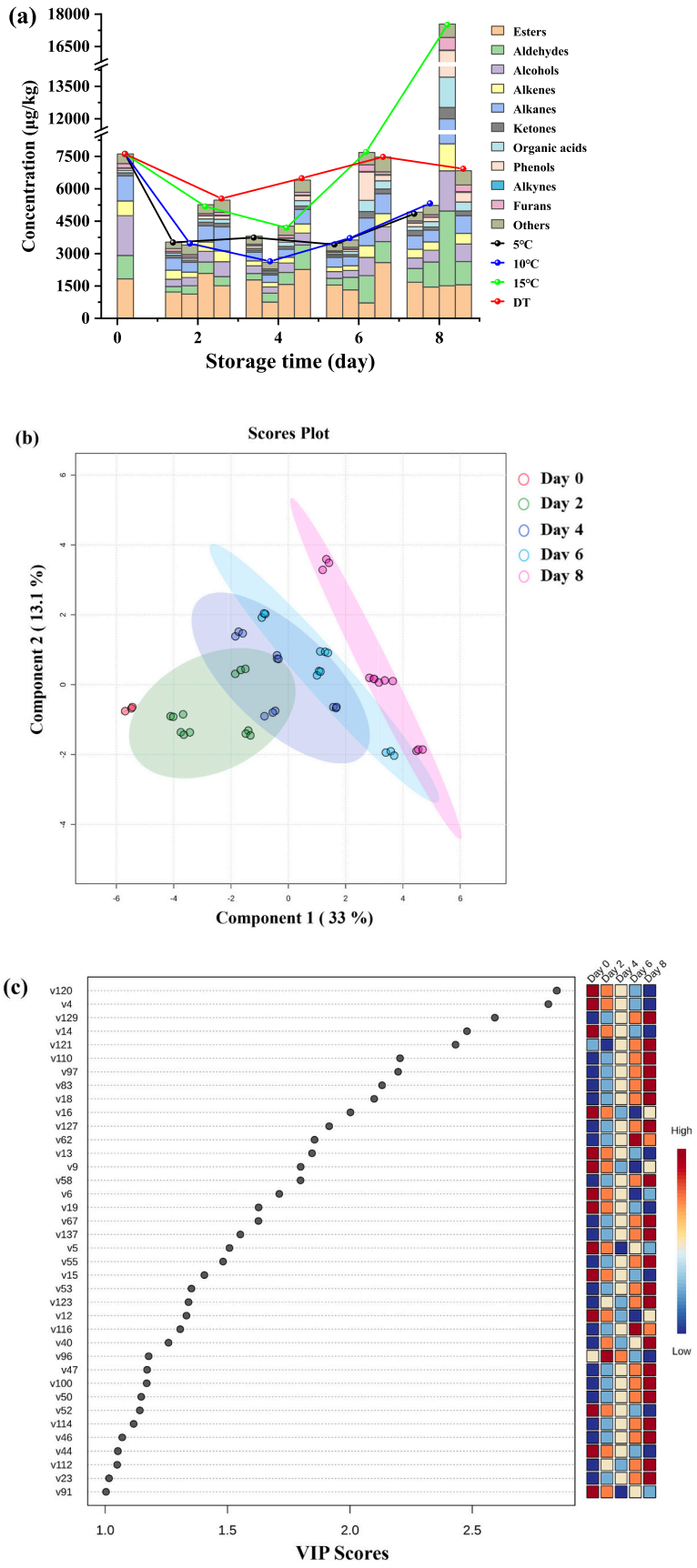

Fig. 4. (a) Changes in total concentration of VOCs in different chemical classes of fresh-cut chili peppers stored at different temperatures. (b) Partial least-squares discriminant analysis (PLS-DA) score plot of fresh-cut peppers stored at different temperatures (R2X = 0.614, R2Y = 0.381 and Q2 = 0.343). (c) Important volatile compounds (VIP >1.0) identified by PLS-DA based on GC–MS.

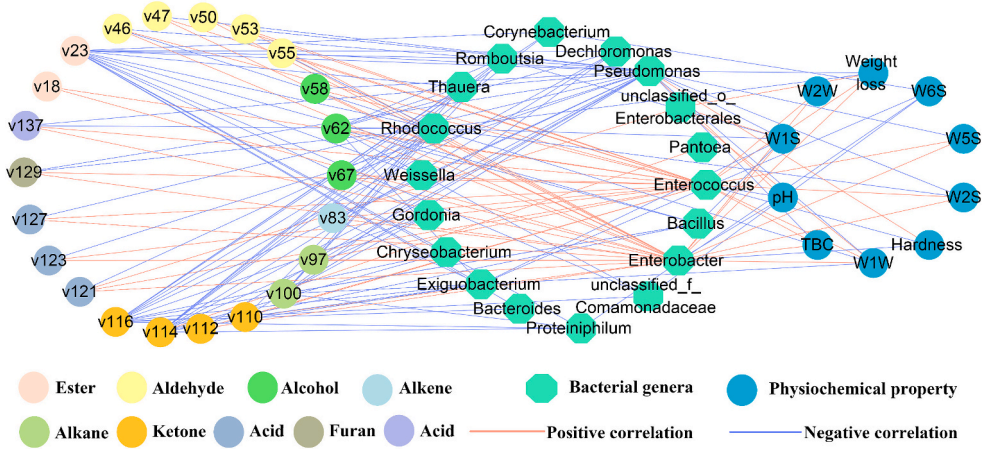

Fig. 5. The correlating network between bacterial communities and qualities of fresh-cut chili peppers. The left-hand circles represent differential volatile metabolites, the middle octagon represents the bacterial genera, and the right-hand circles represent physiochemical properties. The red and blue lines respectively represent the positive and negative correlation coefficients. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and 2 sensors (W1S, W1W). Previous studies showed that *Pantoea*, as spoilage bacteria, consisted of the two major genera in storing longan (Cai et al., 2022). *Pantoea* commonly existed in the fermentation process, which was correlated with the production of VOCs (Cai et al., 2022; Yang et al., 2020).

4. Conclusion

This study provided insights into the evolution of microbial community and quality attributes of fresh-cut chili peppers as affected by storage temperatures. Compared with fungi, the bacterial community was more susceptible to storage conditions during storage. In detail, dominant bacteria genera varied dramatically among different temperatures at the end of storage. *Pantoea* and *Enterobacter* dominated at low (5 °C) and high temperatures (15 °C), respectively. *Enterobacter* and *Rhodococcus* were the main genera at 10 °C and dynamic temperature. Based on the NMDS model, there was no significant variability in bacterial composition between different batches. The deterioration of physicochemical and flavor qualities accelerated with the increase in temperature, and low temperature effectively maintained the freshness of fresh-cut chili peppers. Additionally, 140 VOCs were determined in fresh-cut chili peppers. Twenty-two potential spoilage markers were screened through PLS-DA and VIP values. Correlation analysis showed that 2 bacterial genera (*Enterobacter*, *Enterococcus*) were highly associated with quality loss and spoilage markers of fresh-cut chili peppers. Elucidating the key spoilage microorganisms under different storage temperatures will benefit the development of effective strategies to preserve the quality and extend the shelf-life of fresh-cut fruit and vegetables.

CRediT authorship contribution statement

Zudi Li: Conceptualization, Methodology, Validation, Investigation, Data curation, Writing – original draft, Visualization. **Wenting Zhao:** Writing – review & editing, Conceptualization, Validation, Supervision, Funding acquisition. **Pan Wang:** Investigation, Formal analysis. **Shuang Zhao:** Investigation. **Dan Wang:** Writing – review & editing. **Xiaoyan Zhao:** Supervision, Funding acquisition.

Declaration of competing interest

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

Data availability

The authors do not have permission to share data.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foodchem.2024.139401.

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