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RESEARCH ARTICLE

Microbial and aroma characteristics of spontaneously fermented wine from organic grapes at the eastern foot of the Helan Mountain

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Highlights

- Organic managernent paractices enhance microbial diversity in grape must and wine.
- Organic management vineyard (OMV) fermentation leads to lower *Saccharomyces* dominance and higher yeast diversity.
- OMV spontaneous fermentation increases fermentative and varietal volatiles of wine.
- OMV wine boosted floral and sweet fruity aroma with nail polish and vegetal odors.
- OMV better suited spontaneous fermentation, producing complex-flavored wines.

Abstract

Organic management practices and spontaneous fermentations have become focal points in wine research due to increasing consumer interest in healthy foods and sustainable agriculture. In this study, 'Cabernet Sauvignon' grapes sourced from organic and conventional management vineyard (OMV/CMV) in the Ningxia region were subjected to spontaneous fermentation. The microbial, oenological, and aroma profiles of grape must and resulting wines were assessed using high-throughput sequencing (HTS), high-performance liquid chromatography (HPLC), gas chromatography with mass spectrometry (GC-MS), and sensory evaluations. Network analysis was applied to explore relationships among microorganisms, volatile compounds, and aroma attributes. Results showed that organic management significantly increased microbial species richness, α-diversity, and the variety and concentration of aroma compounds, favoring the production of natural wines with complex aroma profiles. Relative abundance of *Saccharomyces* in OMV reduced, promoting the prevalence of other yeast species during fermentation. Bacterial succession in wines from OMV remained stable, with *Pantoea* as the dominant genus. Among oenological parameters, OMV wines significantly induced glycerol content, while reduced total acidity, tartaric acid, and citric acid content. These wines exhibited significantly higher levels of fermentative (+16%) and varietal (+72%) volatiles, as well as enhanced floral and sweet fruity aromas, along with distinct nail polish and vegetal notes. Additionally, *Saccharomyces*, *Hanseniaspora*, *Metschnikowia*, and *Pantoea* were strongly correlated with specific volatile compounds and aroma characteristics. This study provides valuable data that can inform spontaneous fermentation practices and guide vineyard management for natural wine production.

Keywords: spontaneous fermentation, vineyard management, wine aroma, microbial community, *Saccharomyces cerevisiae*, volatile compounds

1. Introduction

Wine aroma is a defining element of wine quality and sensory profiles, shaped by the combined effects of fermentative and varietal aroma compounds. Fermentative aroma compounds, including higher alcohols, fatty acids, esters, and phenylethyl derivatives, arise primarily from microbial activity during fermentation, while varietal aroma compounds such as C6-compounds and terpenes originate from the grape itself. The

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conversion of grapes into wine is driven by complex microbial communities, including yeasts, bacteria, and filamentous fungi, which collectively influence the metabolic pathways responsible for flavor development (Wei *et al*. 2022). Spontaneous fermentation, which relies on indigenous microorganisms from grape skins, offers a pathway to enhance flavor complexity and express regional terroir, fostering distinctive wine styles (Mas and Portillo 2022).

Vineyard management practices, such as soil management, fertilizer application, irrigation, and pesticide use, directly affect the diversity of fungal communities on grape skins, microbial metabolic activity, and wine quality (Escribano-Viana *et al*. 2018; Perpetuini *et al*. 2022). Organic viticulture, which avoids synthetic chemicals, has gained prominence since the 1960s as a method to preserve regional microbial biodiversity and terroir expression (Brock *et al*. 2019; Doring *et al*. 2019). In contrast, conventional management permits the use of chemical fertilizers and pesticides, which can reduce microbial richness on grape surfaces (Pinto *et al*. 2014; Escribano-Viana *et al*. 2018). Biodynamic management, an extension of organic practices, is another environmentally sustainable approach to viticulture. This practice reduces adverse environmental impact by using specific fermented preparations and adhering to natural rhythms. Additionally, biodynamic viticulture requires producers to have advanced knowledge of vineyard management and the local ecosystem (Parpinello *et al*. 2015). While biodynamic practices extend organic principles through additional ecological interventions, organic management remains more widely adopted due to its practicality and alignment with sustainable goals.

Organic management practices can significantly alter grape-associated microbial communities, leading to distinct metabolic profiles in wine (Schmid *et al*. 2011). For instance, organic wines are often characterized by higher levels of compounds like ethyl acetate, diethyl succinate, and isoamyl acetate, whereas conventional wines may contain greater amounts of acetaldehyde (Maioli *et al*. 2021). Furthermore, sensory assessments have indicated that wines from conventional vineyards tend to exhibit more pronounced acidity and sweetness, while those from organic vineyards offer a fruitier aroma, enhanced purity of body, and a smoother mouthfeel (Xu *et al*. 2020).

Current research on spontaneously fermented wines and organic vineyards has primarily focused on individual aspects, such as yeast microbiota, volatile compounds, non-volatile compounds, or sensory quality (Laureati *et al*. 2014; Patrignani *et al*. 2017; Parpinello *et al*. 2019). However, an integrated understanding of how microbial communities influence aroma compounds in spontaneously fermented wines remains elusive. Specifically, it is still unclear whether organic and conventional vineyard practices provide equally favorable conditions for spontaneous fermentation and how specific microbial groups relate to the development of volatile profiles. This gap in knowledge highlights the need for a comprehensive and holistic approach to elucidate the complex interactions between vineyard practices, microbial communities, and wine aroma profiles.

This study addresses these gaps by analyzing microbial diversity, community succession, oenological parameters, volatile compounds and aroma characteristics of grape must and wine derived from spontaneous fermentation in both organic and conventional vineyards at the eastern foot of the Helan Mountain wine-producing region in Ningxia, China. Furthermore, a network analysis approach was used to identify associations among microorganisms, volatile compounds, and aroma attributes. Overall, the findings of this study offer important insights that can inform vineyard management strategies for spontaneous fermentation.

2. Materials and methods

2.1. Grape sampling

'Cabernet Sauvignon' grapes (*Vitis vinifera* L.) were sourced from two vineyards with different management practices at Xiban Winery (Qingtongxia region, Ningxia Hui Autonomous Region, China) in October 2022. The organic management vineyard (OMV) was designated as the experimental group, while the conventional management vineyard (CMV) served as the control group. Healthy grapes were manually harvested, destemmed, crushed and filled into sterilized fermentation tanks (1 L, with a working volume of 800 mL). Each tank was fitted with a fermentation lock to release carbon dioxide. The sugar content of the grape must from OMV and CMV was 246 and 260 g L^{-1}, respectively, while the acid content (expressed as tartaric acid) was 3.8 and 3.4 g L^{-1}, respectively. The 100-berry weights of the grape from OMV and CMV was 118 and 122 g, respectively. The pH values of the grape must from OMV and CMV was 3.4 and 3.5 g L^{-1}, respectively.

2.2. Laboratory-scale fermentation

Spontaneous fermentations were conducted in triplicate at 25°C using grape must from OMV and CMV, with no addition of sulfur dioxide or commercial yeast. Fermentation progress was monitored by daily measurement of residual sugar, with fermentation considered complete when sugar concentration fell below 2 g L^{-1}. Samples were collected at five key stages: Grape must (O-GM/C-GM, d 0), beginning of fermentation (O-BF/C-BF, approximately 10% sugar depletion), prophase fermentation (O-PF/C-PF, approximately 25% sugar depletion), mid-fermentation (O-MF/C-MF, approximately 50% sugar depletion), and ending of fermentation (O-EF/C-EF, residual sugar<2 g L^{-1}). Subsequently, all samples were centrifuged at 8,000×g for 15 min at 4°C. The resulting precipitates were collected for microbial community analysis *via* high-throughput sequencing (HTS), while supernatants were analyzed for oenological parameters and volatile compounds.

2.3. DNA extraction and sequencing

Total genomic DNA was extracted from all samples using the Fast DNA SPIN Kit (MP Biomedicals, USA), following the manufacturer's instructions. The extracted DNA integrity was verified using approximately 1% agarose gel electrophoresis (running at 5 V cm^{-1} for 20 min) (Lu *et al*. 2020). For fungal community analysis, the ITS2 region was amplified using the PCR primers ITS3_KYO2F (GATGAAGAACGYAGYRAA)

and ITS4_2409R (TCCTCCGCTTATTGATATGC). Meanwhile, bacterial communities were characterized by amplifying the V3–V4 regions of the 16S rRNA genes using the primers 341F (CCTACGGGNGGCWGCAG) and 806R (GGACTACHVGGGTATCTAAT). PCR amplicons were purified with AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, USA). Subsequently, paired-end sequencing was performed on the Illumina platform (Hiseq 2500, PE250). The sequences were clustered into operational taxonomic units (OTUs) at a similarity threshold of 97%, using UPARSE version 9.2.64 (Edgar 2010). The sequence with the highest abundance in each OTU was selected as the representative sequence. Finally, the classification information of each representative sequence was annotated using the SILVA database with the Mothur algorithm (Quast *et al*. 2013).

2.4. Analysis of oenological parameters

Oenological parameters, including residual sugar, ethanol, glycerol, total acidity, volatile acidity, pH, and organic acids (lactic acid, malic acid, citric acid, succinic acid, and tartaric acid) were measured. Residual sugar, glycerol, and organic acids were quantified using a Waters Alliance 2695 high-performance liquid chromatography (HPLC) system (Waters Corp, Milford, MA, USA), following previously reported methods (Li *et al*. 2024). Ethanol, total acidity, volatile acidity, and pH were determined using a Lyza 5000 wine analyzer (Anton Paar GmbH, Graz, Austria).

2.5. Volatile compound analysis

Volatile compounds in finished wines were analyzed using headspace solid-phase microextraction-gas chromatography-mass spectrometry (HS-SPME/GC-MS). The analysis was performed on a Shimadzu GC-MS-QP2020 system (Shimadzu Corporation, Japan), equipped with a DB-WAX column (60 m×0.25 mm×0.25 μm, Agilent Corporation, USA). Sample preparation was carried out as previously described (Kong *et al*. 2021). Volatiles were extracted using a DVB/CAR/PDMS SPME fiber (film thickness 120 μm, fiber length 20 mm, Supelco, Bellefonte PA, USA). The GC temperature program started at 40°C, increased to 160°C at 4°C min^{-1}, then to 220°C at 7°C min^{-1}, and held for 5 min. The ion source and transfer line temperatures were maintained at 200°C and 220°C, respectively. Ion-electron impact spectra at 70 eV were scanned in the range m/z 35–350 amu at 0.2 s intervals. Compounds were identified by comparing their retention times, retention indices, and mass spectra with their corresponding standards in the NIST17 mass spectral library (Appendix A). Quantification was performed using the internal standard method with 2-octanol as the internal standard.

2.6. Sensory analysis

Sensory analysis was conducted by a panel (9 females and 11 males) trained using a 54-Aroma Kit (Le Nez du Vin®, France). Wine samples were served in ISO standard tasting glasses and distributed randomly. Panelists were asked to evaluate each sample by selecting 4–6 aroma terms from the kit and rate their intensity on a five-point scale, where 1=very weak, 2=weak, 3=medium, 4=intense, and 5=very intense. The final aroma attributes of each sample were represented by "modified frequency" (MF) values, calculated according to previous study (Tao *et al*. 2009).

2.7. Statistical analysis

Data analysis was performed using SPSS 25.0 (IBM SPSS Inc., Chicago, IL, USA), with Tukey's HSD test (P<0.05) for one-way ANOVA. Microbial α-diversity was calculated using the OmicStudio tools (https://www.omicstudio.cn). Correlation networks among dominant fungal and bacterial taxa (GM: top ten in relative abundance), differential volatile compounds (OAV>0.1), and differential aroma attributes were constructed *via* Bioincloud tools (https://www.bioincloud.tech/) based on the strong correlation coefficients (Pearson correlation coefficient, $|r|$>0.5, P<0.05).

3. Results

3.1. Microbial species and community composition in grape must

Grape musts from OMV and CMV showed distinct microbial profiles. A total of 273 fungal OTUs and 1,308 bacterial OTUs were identified across all samples (Fig. 1-A and B). OMV contained 207 fungal species, while CMV contained 192 fungal species. Among these, 81 fungal species were unique to OMV, 66 were unique to CMV, and 126 were shared between the two vineyards (Fig. 1-A). Bacterial diversity showed a more pronounced divergence, with 1,105 species detected in OMV musts and 412 in CMV. Notably, 896 bacterial species were unique to OMV, 203 to CMV, and 209 were common to both (Fig. 1-B). The organic system supported 23% more unique fungal species and 341% more unique bacterial species than the conventional system.

Fungi and bacteria communities in grape musts from OMV and CMV exhibited distinct compositional profiles (Fig. 1-C and D). At the genus level, the top ten most abundant fungi included *Hanseniaspora*, *Cladosporium*, *Metschnikowia*, *Alternaria*, *Vishniacozyma*, *Aureobasidium*, *Citeromyces*, *Filobasidium*, *Saccharomyces*, and *Papiliotrema*. *Hanseniaspora* was predominantly enriched in OMV (44.89%),while *Metschnikowia* was more abundant in CMV (35.52%). For bacteria, the top ten most abundant genera were *Pantoea*, *Fructobacillus*, *Massilia*, *Pseudomonas*, *Gluconobacter*, *Sphingomonas*, *Hymenobacter*, *Nocardioides*, *Allorhizobium*, and *Variovorax*. *Pantoea* was enriched in both OMV (92.00%) and CMV (56.54%). These results reveal differences in microbial composition and community structure of grape must between the two vineyard management systems.

3.2. Microbial diversity and community composition during fermentation

Alpha diversity, which describes the complexity of microbial communities within a sample, is commonly assessed using species richness (the number of species) and species evenness (the distribution of species). The abundance-based coverage estimator (ACE) index mainly reflects species richness, with higher values indicating greater diversity. The Shannon index accounts for both species richness and

evenness, with higher values representing greater diversity. As shown in Fig. 2-A–D, the ACE index for fungi and bacteria was higher in grape musts from OMV compared to CMV, suggesting that OMV had a greater initial species richness. However, the Shannon index was higher in CMV, indicating that although OMV harbored more species, the microbial distribution was less even. During spontaneous fermentation, fungal and bacterial diversity declined significantly. By the end of fermentation, both fungal and bacterial communities in OMV maintained higher diversity compared to CMV. These results suggest that vineyard management practices influenced microbial succession and stability during fermentation.

The composition and succession of the dominant fungal and bacterial taxa (top 10) from the two vineyards were analyzed to track microbial dynamics during spontaneous fermentation (Fig. 3-A and B). In OMV, *Hanseniaspora* was the dominant fungal genus before fermentation and maintained a relatively stable abundance throughout the process. *Saccharomyces*, which initially accounted for only 1.17%, increased in relative abundance to 37.97% by the end of fermentation. In contrast, the relative abundances of *Cladosporium*, *Vishniacozyma*, and *Alternaria* gradually decreased. In CMV, *Metschnikowia* was the predominant genus before fermentation but declined rapidly during BF stage. *Saccharomyces* showed a substantial increase, particularly from PF to MF stage, and became the dominant genus during the MF stage, reaching 82.70% by the end of fermentation. The relative abundances of *Cladosporium* and *Alternaria* initially increased but later declined. Regarding bacterial communities, *Pantoea* was the dominant genus throughout fermentation in OMV, with a relative abundance ranging from 91.11 to 95.32%. In CMV, *Pantoea* was also predominant at the beginning of fermentation; however, *Fructobacillus* gradually became the dominant genus, reaching 69.32% by the end of fermentation, whereas *Pantoea* decreased to 26.41%.

3.3. Oenological parameters of wine samples

All fermentations were completed within 12 d, with residual sugar levels in the final wines ranging from 1.21 to 1.97 g L^{-1}. To investigate the influence of vineyard management on oenological parameters, an independent samples *t*-test was performed (Table 1). Among the 11 measured parameters,

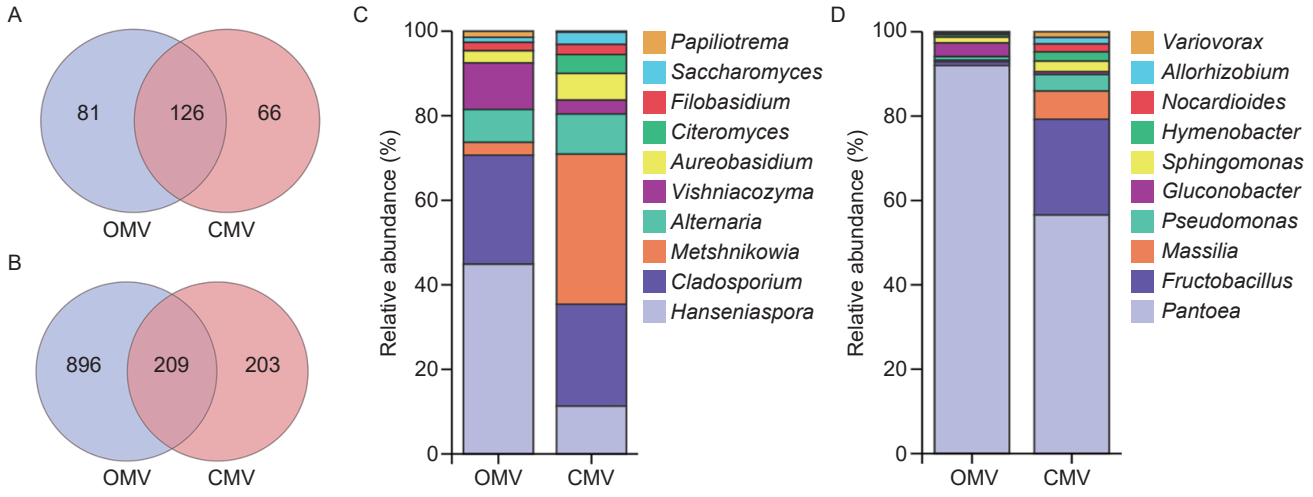


Fig. 1 Microbial species and community composition of grape must. Differences in OTU (fungi A, bacteria B). Community composition of fungi (C) and bacteria (D) at the genus level (showing top 10). OMV, organic management vineyard; CMV, conventional management vineyard.

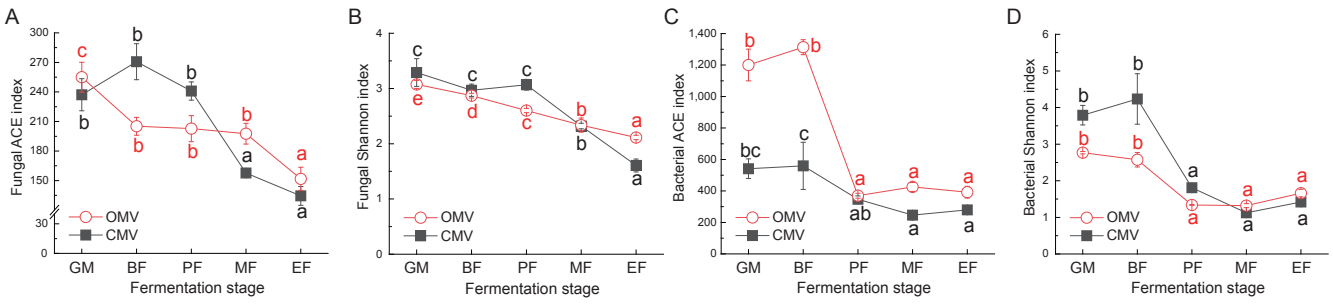


Fig. 2 Microbial diversity during fermentation. Different letters indicate the significance of differences between different groups. GM, grape must; BF, beginning of fermentation; PF, prophase fermentation; MF, mid-fermentation; EF, ending of fermentation. Data are mean±SE (*n*=3).

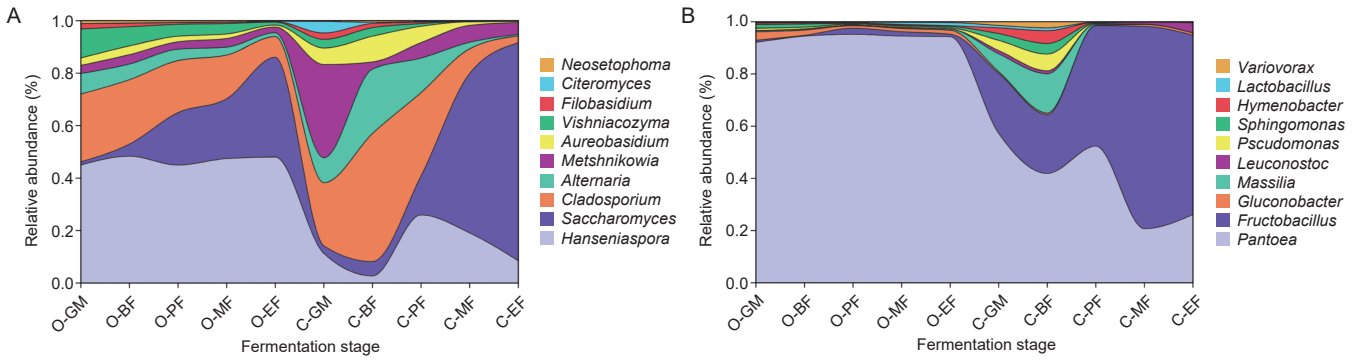


Fig. 3 Microbial community composition and succession. The relative abundance of dominant fungi (A) and bacteria (B) at the genus level during the fermentation process (showing top 10). GM, grape must; BF, beginning of fermentation; PF, prophase fermentation; MF, mid-fermentation; EF, ending of fermentation.

Table 1 Fermentation characteristics of wines from grape spontaneous fermentation[1)]

Parameters	OMV	CMV	*P*-value[2)]
Residual sugar (g L^{-1})	1.21±0.05	1.97±0.28	0.218
Ethanol (v/v %)	12.13±0.14	14.93±0.76	0.115
Glycerol (g L^{-1})	11.55±1.32	8.06±0.12	0.039*
Total acidity (g L^{-1})	5.45±0.22	7.65±0.05	0.001**
Volatile acidity (g L^{-1})	0.88±0.05	0.51±0.15	0.155
pH	3.84±0.04	3.69±0.01	0.125
Tartaric acid (g L^{-1})	2.86±0.09	3.39±0.08	0.008**
Malic acid (g L^{-1})	2.92±0.30	1.85±0.54	0.059
Lactic acid (g L^{-1})	2.12±0.18	2.57±0.17	0.071
Citric acid (g L^{-1})	0.23±0.03	0.66±0.04	0.002**
Succinic acid (g L^{-1})	0.75±0.04	0.47±0.22	0.313

[1)] OMV, organic management vineyard; CMV, conventional management vineyard.
[2)] *P*-values in the table indicate significant difference ($P<0.05$) by independent samples *t*-test. *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

glycerol content was significantly higher in OMV wines compared to CMV wines. In contrast, total acidity, tartaric acid, and citric acid levels were significantly lower in OMV wines. No significant differences were observed for the remaining parameters.

3.4. Volatile compounds and aroma characteristics of wines

A total of 38 volatile compounds were identified in wine samples, categorized into two major groups: fermentative volatiles and varietal volatiles. These included 9 higher alcohols, 14 esters, 2 phenylethyls, 4 fatty acids, 6 terpenes, and 3 C6 alcohols (Table 2). The total contents of fermentative and varietal volatiles were significantly higher in OMV wines compared to CMV wines. Specifically, the total content of fermentative volatiles (533,141 μg L^{-1}) was 16% higher, while that of varietal volatiles (1,903 μg L^{-1}) was 72% higher. Among individual volatile groups, OMV wines had significantly higher concentrations of ethyl acetate (+83.5%), acetates of higher alcohols (+257.2%), phenylethyls (+40.5%), C6 alcohols (+60.0%), and terpenes (+162.7%) compared to CMV wines. In contrast, the total content of fatty acid ethyl esters (–63.1%) was significantly lower in OMV wines than in CMV wines. No significant differences were observed in higher alcohols, other esters, and fatty acids.

To further assess the impact of vineyard management on volatile compounds, the odor activity value (OAV) was calculated to determine the contribution of each compound to wine aroma. OMV wines contained 14 compounds with OAV>1 and 12 compounds with OAV between 0.1 and 1, while CMV wines contained 12 compounds with OAV>1 and 11 compounds within the 0.1–1 range. These results indicate that organic management significantly affected the composition and concentration of aroma-active compounds in the wines. Fig. 4 shows the MF values of aroma characteristics in wine samples, including sweet fruity, acid fruity, berry, floral, vegetal, and nail polish odors. Significant differences were observed in all aroma attributes except for berry and vegetal aromas. OMV wine samples exhibited higher intensities of floral and sweet fruity aromas than CMV wines and were characterized by pronounced nail polish and vegetal odors.

3.5. Correlation among microorganisms, volatiles, and aroma attributes

Network analysis was conducted to explore the co-occurrence patterns among dominant fungal and bacterial taxa (GM: top ten in relative abundance), differential volatile compounds (OAV>0.1), and differential aroma attributes. Correlations were identified based on a Pearson correlation coefficient ($|r|>0.5$, $P<0.05$; Fig. 5). Among fungal genera, *Saccharomyces*, *Hanseniaspora*, and *Metschnikowia* exhibited strong correlations with volatile compounds and aroma characteristics. Notably, *Saccharomyces* showed a positive correlation with decanoic acid and ethyl butyrate but a negative correlation with α-terpineol and sweet fruity aroma. *Hanseniaspora* was positively correlated with ethyl acetate, sweet fruity aroma, 2-phenylethyl acetate, and nail polish aroma, but negatively correlated with acid fruity aroma. *Metschnikowia* was also positively correlated with decanoic acid and ethyl butyrate. For bacteria taxa, *Pantoea* was positively correlated with α-terpineol, 1-hexanol, 2-phenylethanol, and isoamyl alcohol.

Table 2 Volatile compounds of wines from grape spontaneous fermentation

RI[1)]	Compounds	Concentration (μg L^{-1})		*P*-value[2)]	Threshold	OAV[3)]		Odor description
		OMV	CMV			OMV	CMV	
	Fermentative volatiles	533,141±52,608	460,590±52,034	0.020*				
895	Ethyl acetate	123,887±17,893	67,529±7,801	0.007**	7,500 (Peng *et al*. 2013)	16.52±2.39	9.00±1.04	*Fruity*, *sweet*, *nail polish* (Peng *et al*. 2013; Swiegers *et al*. 2005)
	Acetates of higher alcohols	4,572±160	1,280±112	0.000***				
1,021	Isobutyl acetate	309±19	197±12	0.001**	1,600 (Peng *et al*. 2013)	0.19±0.01	0.12±0.01	Fruity, floral (Peng *et al*. 2013)
1,142	Isoamyl acetate	4,185±139	1,023±95	0.000***	30 (Peng *et al*. 2013)	139.51±4.63	34.10±3.17	Fruity, banana (Peng *et al*. 2013)
1,281	Hexyl acetate	78±2	60±6	0.007**	670 (Peng *et al*. 2013)	0.12±0.00	0.09±0.01	Fruity, pear, cherry (Peng *et al*. 2013)
	Higher alcohols	375,761±33,597	366,847±41,269	0.633				
1,120	Isobutyl alcohol	52,107±1,827	24,825±3,430	0.000***	40,000 (Peng *et al*. 2013)	1.30±0.05	0.62±0.09	Mild sweet, alcohol (Peng *et al*. 2013)
1,168	1-Butanol	1,142±77	4,294±676	0.014*	150,000 (Hu *et al*. 2018)	0.01±0.00	0.03±0.00	Fusel, spiritous (Swiegers *et al*. 2005)
1,225	Isoamyl alcohol	253,733±27402	219,493±12,163	0.119	30,000 (Peng *et al*. 2013)	8.46±0.91	7.32±0.41	Alcohol, bitter, nail polish (Peng *et al*. 2013)
1,548	2,3-Butanediol	68,734±4,280	118,190±24,997	0.028*	120,000 (Ma *et al*. 2017)	0.57±0.04	0.98±0.21	Butter, cheese (Ma *et al*. 2017)
1,464	1-Heptanol	22±9	22±1	0.948	1,000 (Peng *et al*. 2013)	0.02±0.01	0.02±0.00	Green, sweet (Peng *et al*. 2013)
1,609	1-Octanol	5.1±0.2	8.3±1.0	0.028*	120 (Peng *et al*. 2013)	0.04±0.00	0.07±0.01	Intense citrus, rose (Peng *et al*. 2013)
1,667	1-Nonanol	8.6±1.1	2.6±0.1	0.010*	600 (Peng *et al*. 2013)	0.01±0.00	0.00±0.00	Green, rose, orange (Peng *et al*. 2013)
1,768	1-Decanol	1.5±0.3	2.8±0.5	0.012*	400 (Peng *et al*. 2013)	0.00±0.00	0.01±0.00	Sweet, fruity, flowery, wax (Peng *et al*. 2013)
1,977	1-Dodecanol	9.0±0.1	9.1±0.3	0.474	1,000 (Ma *et al*. 2017)	0.01±0.00	0.01±0.00	Fruity in low concentration (Ma *et al*. 2017)
	Phenylethyls	19,099±501	13,589±1475	0.004**				
1,840	2-Phenylethyl acetate	401±45	165±10	0.001**	250 (Peng *et al*. 2013)	1.61±0.18	0.66±0.04	Flowery, fruity (Peng *et al*. 2013)
1,931	2-Phenylethanol	18,697±457	13,424±1465	0.004**	10,000 (Ma *et al*. 2017)	1.87±0.05	1.34±0.15	Floral, rose (Ma *et al*. 2017)
	Fatty acid ethyl esters	1,191±84	3,228±245	0.000***				
1,041	Ethyl butyrate	446±47	1,079±78	0.000***	20 (Peng *et al*. 2013)	22.28±2.33	53.93±3.89	Strawberry, fruity (Peng *et al*. 2013)
1,085	Ethyl isovalerate	9±3	14±3	0.128	3 (Hu *et al*. 2018)	3.12±0.98	4.65±1.00	Sweet fruity, apple (Ma *et al*. 2017)
1,241	Ethyl hexanoate	200±17	687±95	0.001**	5 (Peng *et al*. 2013)	39.99±3.43	137.40±18.90	Green apple, fruity, strawberry (Peng *et al*. 2013)
1,444	Ethyl heptanoate	1.4±0.6	1.8±0.6	0.519	220 (Peng *et al*. 2013)	0.01±0.00	0.01±0.00	Pineapple, fruity (Peng *et al*. 2013)
1,449	Ethyl octanoate	295±5	880±26	0.000***	5 (Waterhouse *et al*. 2016)	58.92±1.05	175.94±5.27	Fruity, pear, floral (Peng *et al*. 2013)
1,650	Ethyl decanoate	139±5	189±15	0.005**	200 (Peng *et al*. 2013)	0.69±0.03	0.95±0.08	Fruity, fatty, wax (Peng *et al*. 2013)
1,860	Ethyl dodecanoate	101±7	378±28	0.000***	1,500 (Ma *et al*. 2017)	0.07±0.00	0.25±0.02	Sweet, floral, fruity, cream Ma *et al*. 2017)
	Other esters	7,329±294	6,257±855	0.108				
1,351	Ethyl lactate	7,251±281	6,221±850	0.117	14,000 (Hu *et al*. 2018)	0.52±0.02	0.44±0.06	Lactic, raspberry (Ma *et al*. 2017)
1,706	Methyl Decanoate	2.7±0.1	2.4±0.2	0.088	1,200 (Peng *et al*. 2013)	0.00±0.00	0.00±0.00	Fruity, soap, waxy (Peng *et al*. 2013)
1,786	Diethyl succinate	75±13	34±5	0.007**	6,000 (Peng *et al*. 2013)	0.01±0.00	0.01±0.00	Light fruity; wine (Peng *et al*. 2013)
	Fatty acids	1,302±78	1,860±277	0.054				
1,671	Isobutyric acid	177±11	221±6	0.004**	200,000 (Guth 1997)	0.00±0.00	0.00±0.00	Cheese, rancid (Guth 1997)

(Continued on next page)

Table 2 (Continued from preceding page)

RI[1)]	Compounds	Concentration (μg L^{-1})		*P*-value[2)]	Threshold	OAV[3)]		Odor description
		OMV	CMV			OMV	CMV	
1,865	Hexanoic acid	238±16	357±7	0.000***	400 (Waterhouse *et al.* 2016)	0.59±0.04	0.89±0.02	Cheese, rancid (Ma *et al.* 2017)
2,080	Octanoic acid	764±46	1,027±206	0.097	500 (Peng *et al.* 2013)	1.53±0.09	2.05±0.41	Rancid, harsh (Peng *et al.* 2013)
2,293	Decanoic acid	123±5	255±58	0.017*	1,000 (Peng *et al.* 2013)	0.12±0.01	0.25±0.06	Fatty, unpleasant (Peng *et al.* 2013)
	Varietal volatiles	1,903±90	1,109±117	0.000***				
	C6 alcohols	1,573±74	983±101	0.001**				
1,358	1-Hexanol	1,283±49	739±76	0.000***	8,000 (Peng *et al.* 2013)	0.16±0.01	0.09±0.01	Green, fruity, sweet (Peng *et al.* 2013)
1,369	(*E*)-3-hexen-1-ol	58±2	21±3	0.000***	1,550 (Waterhouse *et al.* 2016)	0.04±0.00	0.01±0.00	Green, herb (Waterhouse *et al.* 2016)
1,393	(*Z*)-3-hexen-1-ol	232±23	224±22	0.661	400 (Ma *et al.* 2017)	0.58±0.06	0.56±0.06	Green, herb (Ma *et al.* 2017)
	Terpenes	331±17	126±16	0.000***				
1,563	Linalool	236±12	66±7	0.000***	25 (Peng *et al.* 2013)	9.42±0.48	2.66±0.27	Floral, fruity (Peng *et al.* 2013)
1,691	*α*-Terpineol	33±1	23±2	0.002**	250 Ma *et al.* 2017)	0.13±0.01	0.09±0.01	Sweet, mushroom (Ma *et al.* 2017)
1,778	Citronellol	22±1	9.1±0.4	0.000***	100 (Peng *et al.* 2013)	0.22±0.01	0.09±0.00	Green, rose (Peng *et al.* (2013)
1,796	Geraniol	23±2	13±4	0.022*	30 (Peng *et al.* 2013)	0.76±0.05	0.43±0.15	Citric (Peng *et al.* 2013)
1,830	*β*-Damascenone	14±0.4	3.6±0.7	0.000***	0.05 (Peng *et al.* 2013)	285.48±8.07	71.22±13.53	Floral, sweet, honey, apple (Peng *et al.* 2013)
1,927	*β*-Ionone	3.1±0.4	11±2	0.004**	0.09 (Peng *et al.* 2013)	34.14±4.78	120.18±24.24	Balsamic, rose, violet (Peng *et al.* 2013)

[1)] RI, retention index calculated by the DB-WAX column.
[2)] *P*-values in the table indicate significant difference ($P<0.05$) by independent samples *t*-test. *, ** and *** indicate significant differences at $P<0.05$, $P<0.01$, $P<0.001$.
[3)] OAV (odor activity value) equals the ratio of the aroma compound concentration to its odor threshold; OMV, organic management vineyard; CMV, conventional management vineyard.

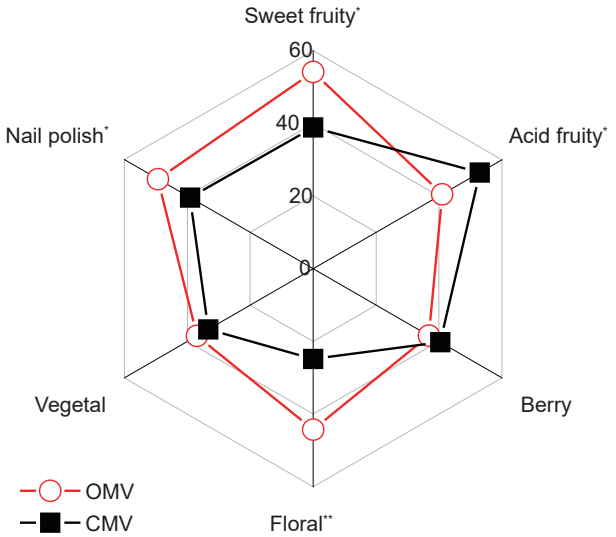


Fig. 4 Modified frequency (MF) values of aroma characteristics of wines. *Significant difference at 95% confidence level. OMV, organic management vineyard; CMV, conventional management vineyard.

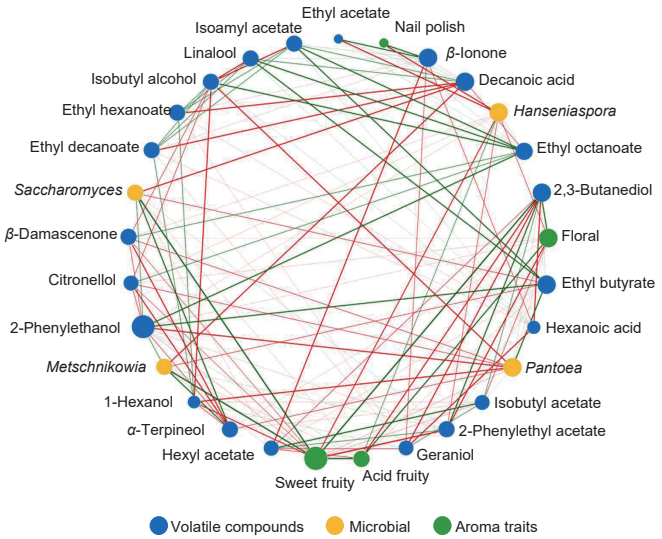


Fig. 5 Network analysis of microorganisms, volatile compounds and aroma attributes. The red and green lines refer to positive correlations ($r>0.5$ and $P<0.05$) and negative correlations ($r<-0.5$ and $P<0.05$), respectively.

4. Discussion

4.1. Microbial diversity in grape must

Microbial diversity on grape surfaces is shaped by multiple factors, including geography, climate, ultraviolet radiation, vintage, and grape variety. In addition to these environmental factors, vineyard management practices such as cultivation methods, pesticide application, and fungicide use also play a critical role in shaping microbial communities (Liu *et al*. 2019). Even within the same wine-producing region, differences in vineyard management can lead to distinct microbial profiles, which can influence fermentation kinetics and wine quality throughout fermentation. Grape must from OMV typically had a more diverse microbial community than that from CMV. This difference is likely due to the absence of chemical treatments, which can reduce microbial diversity and alter community composition (Escribano-Viana *et al*. 2018).

Several studies have reported variations in fungal and bacterial populations between organic and conventional vineyards. For instance, Grangeteau *et al*. (2017) found that organic vineyards had a higher prevalence of *Basidiomycota*, particularly *Cryptococcus*, whereas conventional vineyards were dominated by *Saccharomyces*, *Metschnikowia*, and *Hanseniaspora*. Bagheri *et al*. (2015) reported that biodynamic vineyards exhibited greater species richness and diversity of *Hanseniaspora* yeast. However, recent findings by Bunbury-Blanchette *et al*. (2024) suggested that while vineyard management does not necessarily affect overall yeast diversity or species richness, it significantly influences yeast community composition. In terms of bacterial populations, Vrublevskaya *et al*. (2023) reported that dominant genera such as *Pantoea*, *Bacillus*, *Pseudomonas*, and *Staphylococcus* are common across both biodynamic and conventional vineyards.

4.2. Microbial diversity and community dynamics during fermentation

As fermentation progresses, shifts in fungal and bacterial communities occur, leading to a decline in microbial diversity. In both vineyard types, α-diversity of fungal and bacterial communities decreased significantly during fermentation. Xu *et al*. (2020) reported a more pronounced reduction in microbial diversity in organic vineyard fermentations compared to conventional ones, suggesting that different vineyard management practices influence microbial succession. At the beginning of spontaneous fermentation, *Hanseniaspora* dominated in organic vineyard fermentations, while *Metschnikowia* was more prevalent in conventional vineyards. Several non-*Saccharomyces* yeasts, including *Metschnikowia*, *Candida*, *Hanseniaspora*, *Pichia*, and *Kluyveromyces*, typically initiate fermentation, contributing to early-stage metabolic activity before being outcompeted (Capozzi *et al*. 2015). As fermentation progressed, *Saccharomyces* gradually became dominant, likely due to its greater tolerance to high ethanol content, low oxygen availability, and high fermentation temperatures (Pinto *et al*. 2015). Comparative studies on yeast succession in organic and conventional fermentations have consistently shown that *Hanseniaspora* dominates early fermentation, while *Saccharomyces* rapidly increases in abundance. At the end of fermentation, the relative abundance of *Saccharomyces* was higher in organic vineyards (99.96%) than in conventional vineyards (79.94%) (Xu *et al*. 2020). In this study, we observed that the relative abundance of *Saccharomyces* in organic vineyard fermentations was significantly lower compared to conventional vineyards at the end of fermentation. This difference may be due to the stronger persistence of non-*Saccharomyces* yeasts in the organic vineyard, which could outcompete *S. cerevisiae* by rapidly depleting nutrients and occupying favorable ecological niches earlier in fermentation (Mas and Portillo 2022). The prolonged presence of these non-*Saccharomyces* species may have contributed to a different fermentation trajectory, potentially influencing the final wine composition.

4.3. Association between microorganisms and wine metabolites

The metabolic composition of wine is closely linked to the microbial communities involved in fermentation. The growth, activity, and interactions of yeast and bacteria influence key oenological parameters, including sugar consumption, acid metabolism, and the production of secondary metabolites. Perpetuini *et al*. (2022) reported that wines from organic vineyards generally had higher residual sugar and lower alcohol content than those from conventional vineyards, while other oenological parameters showed no significant differences. In this study, OMV wines had higher glycerol contents but lower total acidity, tartaric acid, and citric acid levels compared to CMV wines. These differences may be attributed to the higher abundance of *Hanseniaspora* in organic vineyards fermentations, this yeast is known to enhance glycerol production and reduce acidity (Hong and Park 2013). Beyond primary metabolites, differences in volatile composition and aroma profiles were also evident between organic and conventional vineyard wines. Perpetuini *et al*. (2022) found that wines from organic vineyards had higher ester content and were associated with floral, herbaceous, and spicy aromas. Similarly, in this study, OMV wines had significantly higher total contents of ethyl acetate, acetates of higher alcohols, phenylethyls, C6 alcohols, and terpenes, contributing to more pronounced floral and sweet fruity aromas compared to CMV wines.

Microorganisms contribute to the complexity of wine flavor, regulation of metabolic products and aroma characteristics through interactions (Liu *et al*. 2017). In this study, *Saccharomyces*, *Hanseniaspora*, *Metschnikowia*, and *Pantoea* showed significant positive correlations with various volatile compounds and aroma characteristics. Wei *et al*. (2022) identified *Starmerella*, *Saccharomyces*, *Hanseniaspora*, *Alternaria*, *Gluconobacter*, and *Tatumella* as key microbial taxa associated with certain volatile metabolites. Among these, *Hanseniaspora* is known for its high production of acetate esters, particularly ethyl acetate (Viana *et al*. 2008). While ethyl acetate can contribute fruity notes to wines at moderate concentrations, excessive levels (≥100 mg L^{-1}) impart undesirable solvent-like or nail polish aromas (Hu *et al*. 2018). The concentration of ethyl acetate in OMV wines

has been found to exceed the acceptable limits, reaching levels as high as 124 mg L^{-1}. This excess is likely due to the higher abundance and persistence of *Hanseniaspora* in OMV wines, which drives the observation of pronounced nail polish aroma. This off-flavor can not only negatively impact the overall sensory experience of the wine but also suppress the other esters and volatile compounds, overshadowing the perception of other desirable wine characteristics (Ruiz *et al*. 2019). *Metschnikowia* known for its elevated extracellular enzyme activity, plays a role in increasing ester compound production, which enhances fruity aromas (Morata *et al*. 2019). In addressing off-flavor formation, *Metschnikowia fructicola* has been effectively employed to significantly reduce the production of ethyl acetate by *Hanseniaspora uvarum* (Johnson *et al*. 2020). *Pantoea* was positively correlated with higher alcohols, ester compounds, and fatty acids, all of which influence wine aroma and mouthfeel (Zhang *et al*. 2022). Additionally, certain microbial species, though not directly involved in fermentation, produce metabolites or enzymatic activities that indirectly shape wine aroma and sensory characteristics (Verginer *et al*. 2010; Romano *et al*. 2022; Li *et al*. 2025).

5. Conclusion

In conclusion, OMV grape must had higher microbial diversity and richness than CMV grape must, although evenness was lower. Similarly, microbial diversity remained higher in spontaneously fermented OMV wines than in CMV wines. Wines from OMV contained greater amounts of glycerol, fermentative volatiles, and varietal aroma compounds, contributing to more pronounced floral and sweet fruity aromas. However, OMV wines also exhibited distinct nail polish and vegetal notes, likely influenced by differences in microbial composition. Network analysis revealed strong correlations between key microbial genera, such as *Saccharomyces*, *Hanseniaspora*, *Metschnikowia*, and *Pantoea*, and specific volatile compounds and aroma characteristics. These findings suggest that grapes from organic vineyards may be particularly well-suited for spontaneous fermentation, producing wines with greater complexity and distinctive sensory attributes. This study provides valuable insights into how vineyard management practices influence microbial succession during fermentation and their impact on wine composition and quality. Further work will investigate the potential of microbial tools to modulate microbial communities, thereby optimizing wine flavor profiles and reducing the occurrence of off-flavors.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this manuscript, the authors used Kimi to assist in improving the clarity and readability of the language. All content generated was carefully reviewed and revised by the authors as necessary, and the authors take full responsibility for the final content of the article.

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