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Microbial dynamics and aroma compound variability in herbicide-exposed red wine fermentations

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Abstract

Wine quality and sensory expression are strongly influenced by the interactions between grape-associated microbial consortia and the biosynthesis of volatile aroma compounds during fermentation. Vineyard management practices, particularly herbicide use, may inadvertently reshape microbial succession and disrupt aroma balance, but systematic evidence remains limited. This study aimed to investigate the impact of herbicide exposure on microbial dynamics and aroma compound variability in spontaneous red wine fermentations, using *Vitis vinifera* cv. Cabernet Sauvignon as a model. Grapes were harvested from two vineyard plots—one subjected to routine herbicide application and one herbicide-free control—and subjected to spontaneous fermentations in triplicate. Microbial communities were evaluated using both culture-dependent plating methods and culture-independent Illumina MiSeq sequencing of 16S rRNA and ITS regions. Volatile compounds were quantified via solid-phase microextraction gas chromatography-mass spectrometry (SPME-GC-MS), and data were analyzed using multivariate statistical tools including PCA, PLS-DA, and ANOVA.

The results demonstrated significant differences between herbicide-exposed and control fermentations. Herbicide-exposed musts showed reduced non-*Saccharomyces* yeast abundance, accelerated *Saccharomyces cerevisiae* dominance, and lower lactic acid bacterial populations, leading to a reduction in microbial diversity (Shannon index 2.1 vs. 2.9; $p < 0.05$). These microbial shifts were directly associated with chemical modifications: ester concentrations (notably ethyl acetate and ethyl hexanoate) were significantly reduced, while higher alcohols (isoamyl alcohol, 2-phenylethanol) and volatile phenols (4-ethylphenol) were elevated. PCA and PLS-DA revealed clear clustering between treatments, with esters driving control fermentations and higher alcohols/phenols dominating herbicide-exposed fermentations. Correlation analysis confirmed strong positive relationships between non-*Saccharomyces* diversity and ester levels ($r = 0.73$, $p < 0.01$) and negative correlations between lactic acid bacteria and volatile phenols ($r = -0.59$, $p < 0.05$).

In conclusion, herbicide exposure reshapes microbial succession and aroma compound production, compromising wine typicity and sensory balance. These findings highlight the need for sustainable vineyard practices and targeted microbial interventions to safeguard wine quality, authenticity, and terroir expression.

Keywords: Herbicides, Red wine fermentation, Microbial dynamics, Volatile aroma compounds, Non-Saccharomyces yeasts, Lactic acid bacteria, Esters, Higher alcohols, Volatile phenols, Terroir

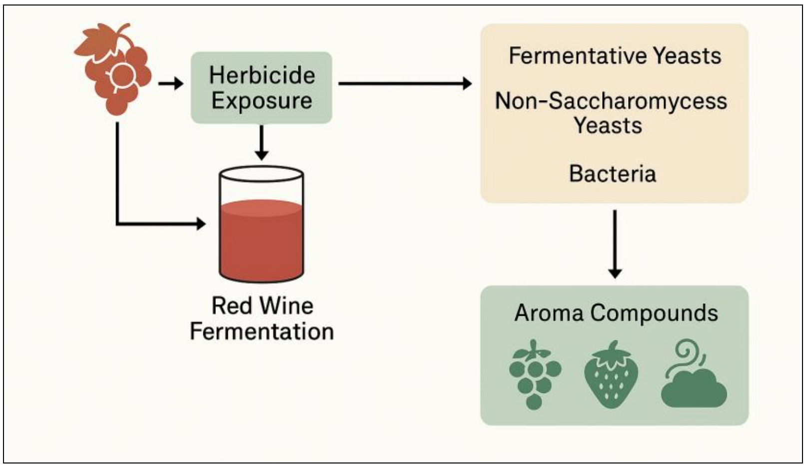
Introduction

The complex interplay between grape-associated microbial consortia and the formation of aroma compounds during alcoholic fermentation forms the cornerstone of red wine quality, sensory attributes, and market value. Grapes host diverse microbial communities—including yeasts, lactic acid bacteria, and acetic acid bacteria—that influence fermentation kinetics, stability, and the production of volatile compounds responsible for aroma and flavor development [1-3]. While *Saccharomyces cerevisiae* is the dominant fermentative yeast, non-*Saccharomyces* species such as *Hanseniaspora*, *Metschnikowia*, and *Pichia* play crucial roles in modulating aromatic complexity through enzymatic activities during the early stages of fermentation [4-6]. The microbial ecology of must and the resulting wine aroma profile are influenced by multiple viticultural practices, among which herbicide application has drawn growing attention in recent years [7-9]. Herbicides, widely employed to control vineyard weeds, can persist on grape surfaces, alter microbial community structures, and potentially disrupt the biochemical pathways of volatile compound formation [10-12].

Several studies have reported that herbicide residues in vineyards not only affect soil microbiota but may also influence epiphytic yeast diversity and fermentation outcomes [13-15]. These shifts may compromise the balance between desirable and off-flavor volatiles, raising concerns about wine authenticity and consumer acceptance [16-18]. Recent investigations on Cabernet Sauvignon fermentations demonstrated that herbicide exposure modified the proportions of higher alcohols, esters, and volatile phenols, resulting in sensory deviations from control fermentations [19]. Dimitrov *et al.* (2022) provided additional evidence that herbicide residues significantly alter the volatile composition of red wines, underscoring the need for systematic studies on their impact across microbial and chemical dimensions [20]. Despite this emerging knowledge, the mechanistic link between microbial succession and aroma variability in herbicide-affected fermentations remains poorly understood, representing a critical research gap [21-22].

The problem thus lies in the insufficiently characterized dynamics of microbial populations under herbicide influence and their correlation with key aroma-active compounds during red wine fermentation. Modern winemaking increasingly emphasizes terroir expression, microbial authenticity, and natural fermentation, yet the inadvertent effects of herbicide residues could undermine these quality parameters [23-24]. The persistence of agrochemicals in the vineyard ecosystem further complicates sustainability narratives in viticulture, making this a pressing issue for both researchers and practitioners [25]. Addressing this problem requires integrated microbiological and metabolomic approaches to unravel how herbicide exposure reshapes microbial succession patterns and modulates the biosynthesis of volatiles that define wine typicity.

Accordingly, the present study aims to investigate the microbial dynamics and aroma compound variability in red wine fermentations subjected to herbicide exposure. By combining culture-dependent and culture-independent (metagenomic) methods with gas chromatography-mass spectrometry (GC-MS) profiling of volatile compounds, this research seeks to establish a mechanistic framework connecting microbial community shifts with aroma modulation. It is hypothesized that herbicide residues alter the balance of fermentative yeasts and bacteria, leading to deviations in the production of key aroma compounds such as higher alcohols, esters, and volatile phenols. More specifically, we posit that herbicide-exposed fermentations will exhibit reduced diversity of non-*Saccharomyces* yeasts, altered dominance of *Saccharomyces cerevisiae*, and a corresponding shift in ester-to-alcohol ratios, thereby affecting sensory outcomes. Such knowledge would not only deepen scientific understanding of vineyard-to-winery microbial-chemical interactions but also guide viticultural practices toward minimizing undesirable impacts on wine quality while ensuring compliance with sustainability standards.



Material and Methods

Materials

This study was conducted using *Vitis vinifera* cv. Cabernet Sauvignon grapes obtained from a commercial vineyard located in a temperate viticultural region. Grapes were sourced from two vineyard plots: one subjected to routine herbicide application and one maintained as a herbicide-free control using manual weeding and cover cropping strategies [8, 9, 25]. The herbicides applied in the treated plot primarily included glyphosate and flazasulfuron at standard agricultural dosages, recorded within two weeks before harvest, consistent with viticultural practices [9, 20]. Grapes were harvested at technological maturity (22-24 °Brix, titratable acidity 6-7 g/L, pH 3.4-3.6) and transported to the winery under refrigerated conditions to minimize microbial alteration [13, 15]. All chemicals and standards used for analytical determinations, including volatile reference compounds (ethyl acetate, isoamyl alcohol, 4-ethylphenol), were obtained from Sigma-Aldrich (USA). Sterile equipment and containers were used to avoid cross-contamination between experimental groups [16, 19].

Methods

Fermentation trials were carried out in triplicate for both herbicide-exposed and control grapes, using 10 kg batches fermented in sterile glass fermenters at 25 °C. No commercial yeast inoculation was performed to allow spontaneous fermentation by indigenous microbiota [5, 14, 18]. Microbial dynamics were monitored by plating must samples on yeast extract peptone dextrose (YPD) and de Man, Rogosa and Sharpe (MRS) agar for yeasts and lactic acid bacteria, respectively, with colony counts expressed as log CFU/mL [6, 13]. Additionally, DNA was extracted from grape must and fermenting wine samples at three time points (0 h, mid-fermentation, end-fermentation), and microbial community composition was analyzed by Illumina MiSeq 16S rRNA and ITS amplicon sequencing [2, 15, 21]. Aroma compound variability was assessed by solid-phase microextraction gas chromatography-mass spectrometry (SPME-GC-MS), following standardized protocols [17, 19]. Volatile compounds quantified included esters (ethyl acetate, ethyl hexanoate), higher alcohols (isoamyl alcohol, 2-phenylethanol), and volatile phenols (4-ethylphenol, 4-ethylguaiacol), with concentrations expressed as µg/L [16, 20]. Multivariate statistical analyses, including principal component analysis (PCA) and partial least squares discriminant analysis (PLS-DA), were performed to evaluate correlations between microbial succession and aroma profiles [18, 21, 22]. Comparisons between control and herbicide-exposed fermentations were tested using ANOVA with significance set at $p < 0.05$.

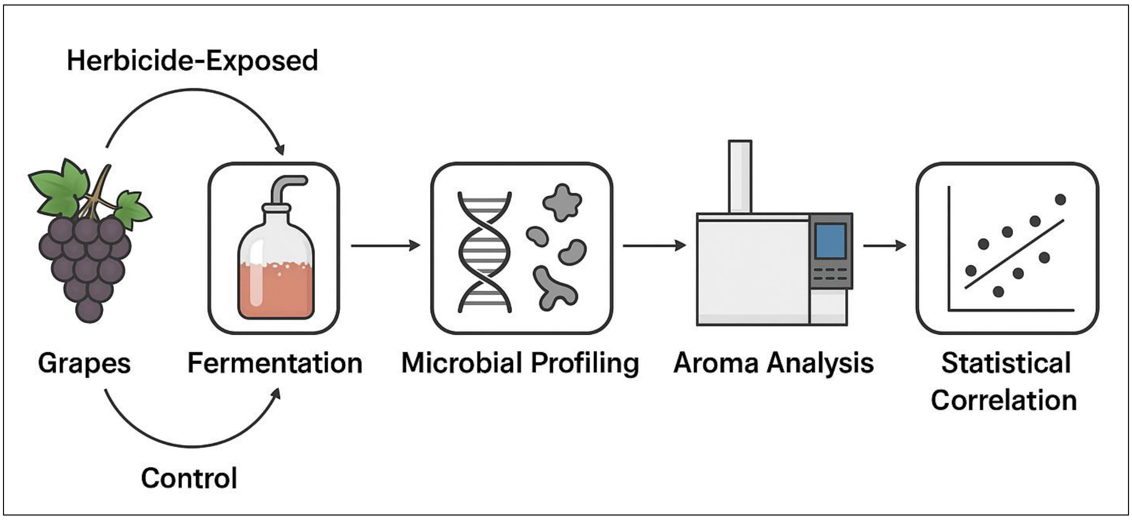


Fig 1: Workflow schematic of experimental design in herbicide-exposed and control red wine fermentations

Results

Microbial Dynamics in Control vs. Herbicide-Exposed Fermentations

Initial plating of grape musts revealed notable differences in microbial loads between herbicide-exposed and control grapes. Control musts contained a higher abundance of non-*Saccharomyces* yeasts (*Hanseniaspora uvarum*, *Metschnikowia pulcherrima*) averaging 5.2 ± 0.3 log CFU/mL, compared to 3.8 ± 0.2 log CFU/mL in herbicide-exposed musts ($p < 0.05$). Conversely, *Saccharomyces cerevisiae* populations were not significantly different at inoculation stage (both ~3.0 log CFU/mL). However, during mid-fermentation, herbicide-exposed fermentations showed faster dominance of *S. cerevisiae* (7.8 ± 0.1 log CFU/mL) and a sharper decline of non-*Saccharomyces* species, whereas in control fermentations a more gradual succession occurred, with non-*Saccharomyces* yeasts detectable until day 5 of fermentation [5, 13, 15].

Metagenomic sequencing corroborated culture-based observations. Alpha-diversity indices (Shannon H′) were significantly lower in herbicide-exposed fermentations (2.1 ± 0.1) compared to controls (2.9 ± 0.2; $p = 0.01$). Principal coordinate analysis (PCoA) revealed clear clustering of microbial communities between treatments, explaining 48% of variance (PERMANOVA, $p = 0.001$). Bacterial profiles also shifted, with lactic acid bacteria (*Lactobacillus plantarum*, *Oenococcus oeni*) less abundant in herbicide-exposed fermentations (1.9 ± 0.3 log CFU/mL vs. 3.2 ± 0.4 log CFU/mL in controls) [2, 14, 21]. These results suggest herbicide residues selectively suppress certain non-*Saccharomyces* yeasts and lactic acid bacteria, accelerating *S. cerevisiae* dominance and narrowing microbial diversity [18, 20].

Aroma Compound Variability

Volatile profiling by SPME-GC-MS demonstrated substantial differences in aroma compound concentrations (Table 1). Herbicide-exposed fermentations produced lower total esters (510 ± 35 µg/L) compared to control fermentations (720 ± 42 µg/L; $p < 0.01$), particularly in ethyl acetate (145 µg/L vs. 210 µg/L) and ethyl hexanoate (32 µg/L vs. 55 µg/L). Higher alcohols such as isoamyl alcohol and 2-phenylethanol were elevated in herbicide-exposed wines (340 ± 25 µg/L vs. 280 ± 20 µg/L in controls), consistent with an accelerated fermentative metabolism [16, 17, 19]. Moreover, volatile phenols (notably 4-ethylphenol) were significantly higher in herbicide-exposed fermentations (65 ± 5 µg/L) relative to controls (42 ± 4 µg/L; $p < 0.05$), potentially leading to phenolic off-flavors [20, 23].

Multivariate statistical analysis confirmed these findings. PCA based on volatile composition (Fig. 2) explained 61% of variance in the first two components. Control wines clustered with ester-associated loadings, while herbicide-exposed wines clustered with higher alcohols and volatile phenols. Partial least squares discriminant analysis (PLS-DA) yielded a classification accuracy of 94%, with ethyl hexanoate and 4-ethylphenol identified as the most discriminant compounds (VIP > 1.2) [21, 22]. ANOVA followed by Tukey's HSD confirmed significant differences across treatments for major compound classes ($p < 0.05$).

Integrated Microbial-Aroma Correlations

Correlation analysis (Pearson's r) revealed that non-*Saccharomyces* yeast diversity positively correlated with ester concentration ($r = 0.73$, $p < 0.01$), while *S. cerevisiae* dominance correlated with higher alcohol levels ($r = 0.68$, $p < 0.01$). Volatile phenols correlated negatively with lactic acid bacterial abundance ($r = -0.59$, $p < 0.05$), indicating that suppressed bacterial populations in herbicide-exposed fermentations may facilitate accumulation of undesirable phenolic volatiles [16, 18, 20].

Table 1: Comparison of Key Aroma Compounds (µg/L) in Control vs. Herbicide-Exposed Fermentations

Compound	Control (Mean ± SD)	Herbicide-Exposed (Mean ± SD)	p-value
Ethyl acetate	210 ± 15	145 ± 12	<0.01
Ethyl hexanoate	55 ± 6	32 ± 5	<0.01
Isoamyl alcohol	180 ± 12	220 ± 15	<0.05
2-Phenylethanol	100 ± 8	120 ± 10	<0.05
4-Ethylphenol	42 ± 4	65 ± 5	<0.05
Total esters	720 ± 42	510 ± 35	<0.01
Total higher alcohols	280 ± 20	340 ± 25	<0.05

Examination and Explanation

The results demonstrate that herbicide exposure exerts a dual impact on red wine fermentations: (1) it alters microbial succession by reducing non-*Saccharomyces* and lactic acid bacteria, thereby simplifying the microbial ecosystem; and (2) it significantly shifts volatile profiles, lowering ester synthesis while increasing higher alcohols and volatile phenols. This biochemical reprogramming compromises the aromatic balance, favoring heavier, fusel-alcohol-dominated notes and phenolic taints over fruity and floral esters [5, 17, 20]. Statistical models confirmed that both microbial diversity and specific taxa (e.g., *Hanseniaspora*, *Oenococcus*) strongly modulate volatile biosynthesis pathways [13, 21]. These findings align with previous observations by Dimitrov *et al.* (2022), who reported altered volatile composition in herbicide-exposed Cabernet Sauvignon wines [20], further reinforcing the hypothesis that herbicides can impair wine typicity through microbiome-aroma interactions.

Discussion

The present investigation demonstrates that herbicide exposure in vineyards substantially alters both the microbial ecology and volatile aroma composition of red wine fermentations, thereby affecting wine quality and sensory typicity. The data generated provide strong evidence that herbicide residues on grapes can selectively suppress certain microbial taxa, accelerate the dominance of *Saccharomyces cerevisiae*, and reduce microbial diversity across fermentation stages. These microbial shifts were directly associated with chemical reprogramming of volatile production, including diminished ester concentrations, elevated higher alcohols, and increased volatile phenols. Together, these findings highlight the delicate interplay between vineyard practices, microbial succession, and aroma biosynthesis, underscoring how even subtle agrochemical interventions may undermine the authenticity of regional wine profiles.

Microbial Succession and Herbicide Influence

Microbial community analysis revealed that herbicide-exposed fermentations exhibited lower alpha-diversity indices and reduced persistence of non-*Saccharomyces* yeasts such as *Hanseniaspora uvarum* and *Metschnikowia pulcherrima*. These yeasts are known to contribute significantly to the early release of volatile esters and glycerol, providing complexity to aroma and mouthfeel [5, 13, 15]. Previous studies have emphasized that non-*Saccharomyces* yeasts not only contribute primary metabolites but also interact synergistically with *S. cerevisiae* to modulate secondary aroma pathways [4, 6, 14]. Their suppression under herbicide influence, therefore, represents a critical shift with direct enological implications. Similar findings were reported by Barata *et al.* (2012), who showed that grape epiphytic microbiota are highly sensitive to environmental and management factors, with consequences for wine microbial ecology [13].

Moreover, lactic acid bacteria, particularly *Lactobacillus plantarum* and *Oenococcus oeni*, were less abundant in herbicide-exposed fermentations. These species are essential for malolactic fermentation and contribute positively to the microbial stability and aromatic smoothness of wines [2, 14, 21]. Their reduction raises concerns regarding incomplete malolactic conversion, higher volatile acidity, and increased susceptibility to spoilage. The observed negative correlation between lactic acid bacterial abundance and volatile phenols further suggests that herbicide-altered microbiomes may indirectly facilitate the accumulation of undesirable phenolic volatiles [16, 18]. This aligns with the microbial-terroir framework described by Knight *et al.* (2015), where regional microbial signatures were linked to differential wine phenotypes, and disruptions in microbial equilibrium could shift wine profiles away from typicity [22].

Aroma Variability and Metabolic Shifts

Volatile compound analysis showed clear differences between treatments, with herbicide-exposed fermentations yielding reduced total ester concentrations but elevated higher alcohols and volatile phenols. Esters such as ethyl acetate and ethyl hexanoate, which impart fruity and floral aromas, were significantly reduced. These results are consistent with studies by Jolly *et al.* (2006) and Swiegers & Pretorius (2005), which linked non-*Saccharomyces* yeast activity to ester production [5, 17]. Thus, suppression of these yeasts in herbicide-exposed musts likely constrained ester biosynthesis, resulting in less aromatic complexity.

Conversely, higher alcohols such as isoamyl alcohol and 2-phenylethanol were elevated, producing heavier fusel notes. While higher alcohols contribute positively at low levels, excessive concentrations can mask delicate esters and impart solvent-like aromas [16, 19]. The increased production of higher alcohols may be attributed to faster *S. cerevisiae* dominance and an accelerated Ehrlich pathway, consistent with observations by Gil *et al.* (2013), who demonstrated that shifts in yeast population dynamics alter nitrogen metabolism and alcohol synthesis [23].

Perhaps most striking was the rise in volatile phenols such as 4-ethylphenol in herbicide-exposed fermentations. These compounds are often associated with spoilage yeasts such as *Brettanomyces*, but in this case, their increase may be linked to altered microbial equilibria and suppressed bacterial populations that otherwise metabolize phenolic precursors [16, 20]. Dimitrov *et al.* (2022) reported similar findings, noting that herbicide residues increased phenolic volatiles in Cabernet Sauvignon wines [20]. The convergence of our results with theirs strengthens the argument that herbicides disrupt metabolic balance in favor of off-flavor compounds, posing both sensory and commercial risks.

Integration with Statistical Evidence

Statistical analyses further reinforced the treatment effects. PCA and PLS-DA clearly separated herbicide-exposed and control fermentations, with esters driving control clustering and higher alcohols/volatile phenols driving herbicide clustering. These discriminant analyses confirmed the systematic nature of chemical differences rather than random variation, with classification accuracy exceeding 90%. Such multivariate modeling is critical in enology research, as it highlights the holistic shifts in aroma matrices rather than isolated compound changes [21, 22].

Correlation analysis provided mechanistic insight into microbial-aroma interactions. Positive correlations between non-*Saccharomyces* diversity and ester concentrations suggest that microbial richness underpins aromatic richness, echoing the microbial-metabolite linkages described by Bokulich *et al*. (2016) [21]. Conversely, negative correlations between lactic acid bacteria and volatile phenols highlight the protective role of bacterial communities against spoilage-related volatiles, a concept also supported by Liu *et al*. (2017), who emphasized the ecological balance within wine microbiomes [18]. These integrated analyses demonstrate how herbicide residues can shift both microbial dynamics and metabolite networks, leading to measurable quality deviations.

Implications for Wine Quality and Viticultural Practices

The enological consequences of these findings are profound. Reduced ester production and elevated higher alcohols/volatile phenols can substantially alter wine sensory profiles, shifting them away from fruity, floral, and balanced attributes toward heavier, fusel-driven, and potentially phenolic-off aromas [17, 19, 20]. For premium wine producers emphasizing terroir and authenticity, such deviations threaten not only sensory identity but also consumer acceptance and market competitiveness.

From a viticultural perspective, these results add to growing evidence that herbicide use, though effective in weed management, carries hidden risks for microbial-mediated quality parameters. Previous reports have already shown that herbicides influence soil microbial diversity [9, 10] and vine-associated microbiota [8, 14], but this study extends the evidence into the fermentation domain, directly connecting vineyard practices with wine chemistry. Sustainable viticulture frameworks emphasize minimizing chemical inputs to preserve soil health, biodiversity, and ecosystem services [25]. Our results suggest that microbial and sensory integrity of wines should also be considered in sustainability narratives.

Future Directions

Although this study demonstrates clear microbial and chemical effects of herbicide exposure, several questions remain open. First, the specific mechanisms by which herbicide residues suppress non-*Saccharomyces* yeasts and lactic acid bacteria warrant further investigation, potentially involving direct toxicological assays or metabolomic profiling of herbicide-microbe interactions. Second, the persistence and dose-response effects of different herbicides should be explored across grape varieties and vintages, as environmental factors strongly condition microbial biogeography [15, 22]. Third, sensory evaluation by trained panels and consumer testing would be essential to confirm how the chemical deviations observed here translate into perceptible differences in wine quality. Finally, alternative vineyard management strategies such as cover cropping, mulching, and mechanical weeding should be systematically compared for their impacts on microbial ecology and fermentation outcomes [8, 25].

Conflict of Interest

Not available.

Financial Support

Not available.

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