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Review

Advances in the Ester Accumulation and Regulation in Grape Berries and Wine

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Abstract

Esters are pivotal volatile compounds that shape the floral and fruity attributes of grape berries and wine. In the case of sustainable viticultural system, understanding the formation and regulation of esters is essential for optimizing aroma quality under variable environmental conditions and reducing reliance on intensive cultivation inputs. In this review, the following aspects are comprehensively analyzed: (1) the biosynthetic pathways of esters in grape berries and wine; (2) the main environmental factors affecting ester accumulation in grape berries include light, moisture, temperature, and soil fertility; (3) the impacts of yeast strain selection, inoculation protocols, and post-fermentation processes, such as barrel aging and bottle storage, on ester composition. By integrating biochemical insights with viticultural and enological strategies, this review aims to provide references for developing sustainable approaches to regulate the esters biosynthesis and enhance the aroma quality of grapes and wine.

Keywords: esters; grape; wine; biosynthesis; regulation

1. Introduction

Grape berries contain a variety of aroma compounds, mainly including esters, aldehydes, alcohols, terpenes, norisoprenoids, and methoxypyrazines. Among these, esters, which mainly composed of ethyl esters of organic acids, acetates of higher alcohols, and ethyl esters of fatty acids [1], are widely recognized as key contributors to the characteristic aromatic profiles of different grape varieties. *Vitis labrusca* grapes and *Vitis labrusca* × *Vitis vinifera* hybrids typically exhibit higher ester levels, contributing floral and fruity characteristics [2]. In these varieties and hybrids of *V. vinifera* or *V. amurensis*, esters such as ethyl acetate, ethyl butanoate, ethyl 2-butenoate, ethyl hexanoate and ethyl 2-hexenoate are key contributors to their distinctive strawberry-like notes [3]. Methyl anthranilate, also known as methyl aminobenzoate, imparts 'foxy' aroma to grapes, and it is a characteristic aroma component unique to *V. labrusca* grapes [4–6]. In other grape varieties, fewer esters are detected, and their concentrations are generally below sensory thresholds. Consequently, most esters that contribute to wine aroma are formed during alcoholic fermentation and

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wine aging. In wine, esters constitute one of the most abundant classes of volatile compounds after alcohols and acids [7], and they are the major contributors to fruity and floral aromas [8]. Previous studies have shown that ethyl octanoate and ethyl hexanoate are the most odor-active compounds in Vidal blanc and Riesling table wines and icewines [9]. In addition, isopentyl acetate, phenethyl acetate, ethyl butyrate, ethyl hexanoate, ethyl octanoate, ethyl lactate, and ethyl decanoate have been identified as major impact odorants in Chardonnay dry white wines from Changli County [10]. During the fermentation process, esters are primarily synthesized by *Saccharomyces cerevisiae*, while non-*Saccharomyces* yeasts also contribute, enhance aromatic complexity of wine. Fermentation parameters such as temperature, pH, oxygen availability, and sulfur dioxide addition further modulate ester formation [11–13].

Recent advances in analytical chemistry and molecular biology have deepened our understanding of the diversity, biosynthesis, and regulation of esters in grapes and wine. High-resolution mass spectrometry has enabled more precise profiling of ester compositions, while genomics and molecular biology techniques have revealed regulatory mechanisms that govern ester production in berries and during fermentation. This review summarizes current progress in elucidating ester biosynthesis in grape berries and wine and highlights the environmental, agronomic, and enological factors that influence their formation. The goal is to provide a foundation for developing effective strategies aligned with sustainable viticulture principles to regulate ester accumulation and enhance the aroma quality of grapes and wine.

2. Esters in Grapes and Wine

2.1. Biosynthesis of Esters

In grape berries, ester accumulation patterns vary among different grape varieties. In Cabernet Sauvignon grapes, C6 esters, including (*Z*)-3-hexenyl acetate and (*Z*)-3-hexenyl butanoate, accumulated during early berry development but were undetectable after véraison [14]. In contrast, in *Vitis labrusca* and hybrids of *Vitis labrusca* × *V. vinifera*, esters such as ethyl acetate, ethyl butanoate, ethyl (*E*)-crotonate, ethyl hexanoate, ethyl 2-hexenoate, and n-propyl acetate, and methyl anthranilate increased steadily from véraison to pre-harvest stages [15,16].

Esters are formed through the conjugation of alcohols and acyl-CoAs, which can be derived from fatty acids via β-oxidation and lipoxygenase (LOX) pathways or from amino acid metabolism. Fatty acids act as precursors for straight-chain fatty esters through the β-oxidation and lipoxygenase pathways. In the LOX pathway, linoleic acid and linolenic acid are catalyzed by LOX to produce 9-hydroperoxides or 13-hydroperoxides, which are then cleaved by hydroperoxide lyase (HPL) to yield C6 and C9 aldehydes [17]. These aldehydes are subsequently reduced to the corresponding alcohols by alcohol dehydrogenase (ADH), and esterified by alcohol acyltransferase (AAT) to form straight-chain esters [14]. When amino acids serve as precursors, they are first transaminated by aminotransferase (AST) to produce branched-chain α-keto acids, which are decarboxylated by α-ketoacid decarboxylase to generate branched-chain aldehydes. These aldehydes are further reduced by ADH to branched-chain alcohols, which are then esterified by AAT, giving rise to branched-chain aliphatic esters [18]. Incubation with exogenous L-Leu and L-Phe has been shown to enhance the accumulation of 3-methylbutyl acetate and 2-phenylethyl acetate in grape berries, respectively [19]. Different grape AAT genes exhibit specific substrate selectivity. In Concord grapes, the alcohol acyltransferase AMAT demonstrates selective activity, with its enzyme activity, protein abundance, and gene expression tightly coordinated during ripening, paralleling the accumulation of anthranilic acid and methyl anthranilate [16]. In *Vitis vinifera*, Maoz et al. identified a novel *VvAAT2* gene capable of catalyzing the

formation of volatile esters with the utilization of benzyl alcohol, 2-phenylethanol, hexanol or 3-methylbutanol [19].

Over 150 esters have been detected in wine, most of which are formed during fermentation, whereas only minor amounts are present in grape berries prior to fermentation [20]. In wine, esters are mainly formed enzymatically during fermentation under the action of yeast, although some esters are formed chemically during aging and storage via esterification between alcohol and acids under low pH conditions [21]. Enzymatic ester synthesis is mediated by esterases, lipases, and AAT in wine. Esterases and lipases, as serine hydrolases, can catalyze both ester synthesis and hydrolysis depending on physicochemical conditions, whereas alcohol acetyltransferases exclusively catalyze ester formation [21]. Overexpression of the alcohol acetyltransferase gene (ATF1) of *S. cerevisiae* has been shown to increase the levels of ethyl acetate, iso-amyl acetate, and 2-phenylethyl acetate in wine [22].

2.2. Odor Characteristics of Esters

Esters contribute a wide range of sensory attributes to grape berries and wine (Table 1). For instance, several esters, including ethyl butyrate, ethyl butanoate, ethyl valerate, ethyl hexanoate, ethyl octanoate, and ethyl 3-hydroxybutyrate, display high odor activity values in grapes or wine and play important roles in shaping overall aroma profiles [23,24]. Among them, ethyl butyrate and ethyl hexanoate impart fruity aromas such as strawberry and green apple notes [25–27], and they are recognized as key aroma-active esters in Black Beet, Jingya, and Jumeigui grapes [28]. Ethyl butanoate contributes floral, fruity, red berry, apple, and banana notes [29–31]. Ethyl valerate provides fruity, orange, and mint notes [23]. Ethyl octanoate imparts pineapple, pear, floral, brandy, and red berry notes [23,28]. Ethyl 3-hydroxybutyrate provides grape, coconut, caramel, red berry, and wine-like aromas [23,28,30]. In Kyoho grapes, ethyl acetate is the major contributor to pulp aroma [28]. However, when presents at high concentrations, particularly above 12 mg/L, ethyl acetate can negatively affect wine quality by imparting varnish or nail polish-like aromas [32]. In addition, isobutyl propionate provides a rum-like aroma, whereas ethyl lactate is associated with a pungent odor [33]. Yeast-derived esters such as ethyl anthranilate and ethyl cinnamate exhibit sweet fruity, grapey, cinnamon, sweet-balsamic, plum, and cherry-like aromas [34].

Table 1. Odor descriptions of esters.

Matrix	Esters	Odor Descriptions	References
Wine	Benzyl acetate	Fresh, boiled vegetable	[35]
Grape	Butyl acetate	Fruity, sweet, ripe banana, pear	[36]
Grape	Butyl lactate	Green, fruity, lactonic, winey	[36]
Grape	(*E*)-2-ethyl butenoate	Musty, pungent, onion	[36]
Grape and wine	Ethyl 2-methylbutanoate	Apple skin, pineapple skin, and unripe plum skin, fruity, strawberry, blackberry	[29,30,32,33]
Wine	Ethyl 2-methylpropanoate	Sweet, rubber, blackberry	[30,35]
Grape and wine	Ethyl 3-hydroxybutyrate	Grape, coconut, caramel, red berry, wine	[23,28,30]
Wine	Ethyl 9-decenoate	Fruity	[35]
Grape and wine	Ethyl acetate	Pineapple, fruity solvent, anise, balsamic, celery, varnish, nail polish	[28,29,32]
Grape and wine	Ethyl anthranilate	Sweet, sweet-fruity, grape-like odor	[34,37]
Wine	Ethyl benzoate	Heavy, floral, fruity	[35]
Grape and wine	Ethyl butanoate	Floral, fruity, red berry, apple, banana	[29–31]
Wine	Ethyl butyrate	Sour fruit, apple, strawberry, and sweet fruit	[23,25]
Grape	Ethyl cinnamate	Cinnamon like, sweet-balsamic, sweet-fruity, plum, cherry-like flavor	[34]
Wine	Ethyl decanoate	Grape, floral, soap	[31,35]

Table 1. *Cont.*

Matrix	Esters	Odor Descriptions	References
Wine	Ethyl dodecanoate	Leaf	[35]
Wine	Ethyl formate	Green apple	[31]
Grape and wine	Ethyl heptanoate	Fruit, brandy, wine, rose	[28,29,35]
Wine	Ethyl hexanoate	Green apple, fruity, strawberry, anise, flowery	[23,25–27,34]
Grape	Ethyl isobutyrate	Strawberry	[29]
Wine	Ethyl isovalerate	Apple, fruity	[38]
Wine	Ethyl lactate	Pungent odor	[33]
Wine	Ethyl myristate	Floral, honey	[35]
Grape and wine	Ethyl octanoate	Pineapple, pear, floral, brandy, red berry	[23,28]
Grape and wine	Ethyl pentanoate	Grass, yeast, fruit	[28,35]
Wine	Ethyl phenylacetate	Fruit, sweet	[35]
Grape	Ethyl propionate	Pineapple, blackberry, banana, apple	[28,29,32]
Wine	Ethyl valerate	Fruity, orange, mint	[23]
Grape	Ethyl acetate	Vegetable oil	[29]
Wine	(*E*)-3-Hexenyl acetate	Sweet, Green, Sharp-fruity	[35]
Wine	(*Z*)-3-Hexenyl acetate	Green, banana	[35]
Grape	Hexyl acetate	Apple, pear, flora, green, cherry	[28]
Wine	Isoamyl acetate	Banana, pear, fruity, sweet	[25,26,31]
Grape	Isoamyl butyrate	fruity, green, sweet	[36]
Wine	Isobuty lacetate	Banana, fruity	[31]
Wine	Isobutyl butyrate	Pineapple, grape skin aromas, and etheric notes	[33]
Wine	Isobutyl propionate	Rum and pineapple aromas	[33]
Wine	Methyl benzoate	Wintergreen, almond	[23]
Wine	Methyl hexanoate	Fruit, fresh, sweet	[35]
Wine	Methyl octanoate	Orange	[35]
Wine	Methyl salicylate	Pepper, mint	[35]
Wine	2-Methylpropyl acetate	Fruit, apple, banana, fruity, lychee	[35,37]
Wine	3-Methylbutyl acetate	Fruity, Banana	[35,37]
Wine	3-Mercaptohexan-1-ol acetate	Tropical, passion fruit	[39]
Grape	Methyl anthranilate	Floral, sweety, foxy	[16,40]
Wine	Phenethyl acetate	Rose, honey, tobacco	[35]
Wine	2-Phenyl acetate	Rose, honey, flowery	[38]
Wine	2-Phenylethyl acetate	Flowery, rose, fruity	[34]
Wine	*β*-phenylethyl acetate	Honey, fruity, floral	[41]
Grape and wine	Propyl acetate	Fruity scent	[28,31,33]

3. Factors Influencing the Ester Content During Grape Development and Ripening

3.1. Light

Light is a crucial environmental factor affecting the biosynthesis and accumulation of esters in grape berries. Light quality, UV radiation, and sunlight exposure all playing significant roles in determining ester content in both grape berries and the resulting wine. Manipulation of light quality environment through supplemental lighting has been shown to positively affect ester accumulation. For example, applications of red, blue, white, and combined red-blue light increased total ester contents, especially ethyl acetate, in three table grape varieties [42]. Compared with natural light, blue and red light increased total ester contents in 'Kyoho' grape berries, while the concentrations of ethyl acetate, n-propyl acetate, and butyric acid ethyl ester were significantly higher under white light and a red-to-blue light ratio of 1:2 [43]. However, current studies on the effects of light on ester formation are restricted to a limited number of grape varieties. Further research focusing on the most widely cultivated varieties is therefore required to obtain more representative and generalizable conclusions.

In wines produced from grapes grown under black, red, and white shading nets, ethyl acetate, hexanedioic acid dioctyl ester, hexyl acetate, geranyl acetate, and ethyl heptanoate

were present at higher levels than in the control. Different esters respond distinctly to UV treatments. The levels of fatty acid-derived esters, including 2-butoxyethyl acetate and (*Z*)-3-hexen-1-ol, significantly decreased in grape berries under attenuated UV radiation in the field [44]. These effects depend on the phenological stage, with UV reduction from véraison to harvest resulting in a greater decrease in ester composition than UV reduction from fruit set to the onset of véraison. In a potted vine experiment, enhanced UV-B radiation lowered the concentrations of branched-chain fatty acids esters including ethyl isobutyrate and ethyl isovalerate in grape berries relative to UV block treatment [45]. Decreases in ethyl hexanoate, ethyl octanoate, ethyl nonanoate, and ethyl decanoate was also observed in Pinot noir wine produced from berries subjected to the UV transmission treatment [46]. Sunlight exposure through shoot positioning and limited basal leaf removal reduced the concentration of ethyl 2-methylpropanoate while increasing ethyl vanillate [46]. In a two-year study, grape berries grown under a black light-selective sunshade net exhibited higher contents of total esters, ethyl acetate, isoamyl acetate, and ethyl octanoate, whereas the effects of red and white nets on ester concentrations varied depending on the season [47]. The synthesis of esters in harvested grape berries was inhibited in stripe, brown, and two-layered bags with light transmittances of 15%, 5%, and 0%, respectively [48].

3.2. Moisture

Moisture availability during berry development strongly influences ester composition in wine. Moderate water deficits during berry development generally enhance ester accumulation, while excessive water stress reduces it. Irrigating at 60% of the estimated crop evapotranspiration (ETc) reduced ester contents in the resulting wine, whereas moderate water deficits at 70% and 80% ETc led to an overall increase in ester concentrations [49]. Under reduced irrigation, elevated levels of isoamyl acetate, ethyl acetate, ethyl butanoate, ethyl hexanoate, ethyl decanoate, ethyl pentanoate, ethyl isobutyrate, and ethyl isovalerate were observed, along with decreased levels of phenylethyl acetate and ethyl cinnamate [45]. In a two-year study evaluating multiple irrigation regimes, the most severe water deficit resulted in the lowest ester concentrations in wine [50].

3.3. Temperature

Temperature is key driver of grape growth and ripening. Variations in temperature significantly affect the sugar accumulation, acidity, pH, phenolic compounds, esters, and other aroma-related metabolites. In grape berries from vineyards with different accumulated growing degree days (GDDs), both the rate of ester accumulation and their final concentrations varied substantially [51]. However, current studies on the effects of temperature on ester formation remain limited in number.

3.4. Soil Fertility

Soil fertility is the primary factor influencing ester contents in grape berries and wine. Soil composition is associated with the aroma of wines. Cabernet Sauvignon wines produced from potassium-rich Bom Retiro soils exhibited higher concentrations of acetate esters [52]. Increased ester concentrations have also been reported in aged Riesling wines following nitrogen fertilization [53]. Wines from vines treated with N fertilization contained higher levels of ethyl decanoate, ethyl butyrate, and ethyl isovalerate compared with the control [54]. Combined usage of magnesium and plant growth regulator of 6-benzylaminopurine increased relative ester contents in grapes [55]. Foliar fertilizers offer a strategy to reduce overall fertilizer usage and improve nutrient uptake efficiency. Foliar applications of urea combined with S and of Basfoliar Algae to 'Cabernet Sauvignon' grapevines led to an increase in ethyl hexanoate, ethyl octanoate, and ethyl decanoate in wines [56]. Higher levels of alcohols and aldehydes in grapes under foliar nitrogen

application may contribute to this increase in ester formation [57]. Foliar fertilization of potassium increased ethyl isobutyrate, butyl acetate, ethyl hexanoate, hexyl acetate, and methyl salicylate in the pulp juice of 'Hanxiangmi' table berries [58]. However, traditional foliar fertilizers are susceptible to photolysis and evaporation loss. For this reason, Ma et al. evaluated various foliar fertilizer adjuvants combined with potassium dihydrogen phosphate to improve grape quality and provided an efficient and low-cost foliar fertilizer adjuvant application scheme [59]. The extensive application of synthetic chemical fertilizers in horticulture has created environmental concerns, including groundwater pollution, soil salinization, and increased greenhouse gas emissions [60]. As an alternative, inoculation of the plant growth-promoting rhizobacterium *Streptomyces saraceticus* strain 31 into the rhizosphere of 'Benifuji' grapevines improved soil fertility by increasing organic matter, phosphorus, potassium, and nitrate nitrogen, and enhanced the accumulation of esters such as ethyl acetate, ethyl-2-methylbutyrate, ethyl propionate, ethyl butyrate, isopentyl acetate, ethyl caproate, and diethyl succinate [61].

3.5. Viticultural Practices

Viticultural practices such as cluster thinning are common and straightforward practices used to enhance the quality of grapes. These practices significantly increased total ester contents in 'Jumeigui' table grapes [62]. Rain-shelter cultivation, widely adopted in regions with high rainfall, also influenced ester formation. Grapes grown under rain-shelter conditions contained higher concentrations of fatty acid-derived esters, including ethyl hexanoate, hexyl acetate, and ethyl octanoate [63]. This increase may be associated with elevated fatty acid levels induced by rain-shelter treatment. Several studies have demonstrated that leaf removal exerts significant yet highly vintage-dependent effects on ester accumulation in grapes and wines. In Cabernet Sauvignon berries, a three-year investigation revealed pronounced interannual variability in straight-chain aliphatic esters, with leaf removal modulating the composition and concentration of acetate and ethyl esters in a timing- and year-dependent manner [64]. Similarly, in Shiraz wines, apical and basal defoliation across two vintages showed limited and inconsistent impacts on ester profiles, although apical defoliation at véraison significantly reduced multiple ethyl and acetate esters in the 2010–2011 vintage, with much weaker effects observed in 2015–2016 [65]. In contrast, studies on Merlot wines reported a marked increase in total ester abundance following leaf removal, with ethyl esters being particularly positively affected [66]. Nevertheless, available evidence regarding the effects of viticultural practices on ester metabolism is still scarce, and additional studies involving diverse practices and grape varieties are required to draw more generalizable conclusions.

4. Factors Influencing Ester Synthesis During the Winemaking Process and Storage

4.1. Yeasts

In winemaking, yeasts are typically classified into *Saccharomyces cerevisiae* and non-*Saccharomyces cerevisiae* species, both of which play essential roles in determining the composition and concentration of ester compounds in wine. *Saccharomyces cerevisiae* has been widely studied and used in winemaking due to its high fermentation efficiency, strong ethanol production capacity, efficient conversion of diverse sugars, and consistent production [67]. Different *Saccharomyces cerevisiae* strains can produce distinct ester profiles [68,69]. These differences are reflected in their capacities to produce ethyl esters and acetate esters under comparable fermentation conditions. For instance, Chardonnay wines fermented with individual or mixed Burgundian *S. cerevisiae* strains (C2 and C6) showed intermediate levels of ethyl and acetate esters compared with those produced using industrial strains

such as Blanc, Elegance, Fusion, CY3079, ICV-D254, and X16 [68]. Cabernet franc wines fermented with CSM contained higher levels of esters than those fermented with EC 1118 or FX10 [70]. In sparkling wine production, flocculent strains such as F6789, F6030, and FI were reported to generate the highest levels of ethyl esters after three months of aging, with ester concentrations increasing further after six months [69]. Collectively, these studies demonstrate that ester formation in wine is strongly strain dependent, and that the influence of S. cerevisiae on ester composition may further interact with grape variety and winemaking conditions.

In recent years, non-*Saccharomyces cerevisiae* such as *Torulaspora delbrueckii*, *Lachancea thermotolerans*, *Metschnikowia pulcherrima*, and *Pichia kluyveri* have attracted considerable attention for their ability to enhance flavor complexity and improve overall wine quality [71]. Their effects on ester formation in mixed cultures with *S. cerevisiae*, compared with pure *S. cerevisiae* fermentations, are summarized in Table 2. Among them, the genus *Metschnikowia* is particularly well studied due to its widespread distribution and significant influence on winemaking [72]. Although *M. pulcherrima* produces esters less efficiently than *S. cerevisiae* in monoculture, sequential inoculation of *M. pulcherrima* and *S. cerevisiae* at a 1:1 ratio can significantly increase total esters and phenylethyl acetate [73,74]. Furthermore, increasing the proportion of *M. pulcherrima* in simultaneous or sequential inoculation (10:1) further increased the concentrations of ethyl acetate, isoamyl acetate, and ethyl lactate in wine [75]. *Pichia kluyveri* is recognized as an efficient ester producer because it exhibits esterase activity that promotes ester formation [76]. A 9:1 SIM of *Pichia kluyveri* and *S. cerevisiae* significantly increased 3-mercaptohexyl acetate, a highly aromatic compound contributing passion fruit or sassafras-like notes [77]. SEQ at a 1:1 ratio of *Pichia kluyveri* and *S. cerevisiae* increased total esters, as well as ethyl acetate, isoamyl acetate, ethyl octanoate, ethyl caprate, phenethyl acetate, and ethyl dodecanoate [78]. The strain PK-19 has been shown to significantly increase ethyl lactate and ethyl succinate [79]. *P. kluyveri* also possessed the ability to increase isobutyl acetate, isoamyl acetate, and 2-phenylethyl acetate in mixed fermentation [80]. For *Torulaspora delbrueckii*, SEQ with *S. cerevisiae* generally results in higher contents and a wide variety of esters than the SIM, thereby enhancing aroma diversity and intensifying fruity and flowery attributes [81]. Zhang et al. reported that the metabolites produced by *T. delbrueckii* promoted the formation of ethyl octanoate and ethyl decanoate, potentially through the upregulation of the acyltransferase gene EEB1 in *S. cerevisiae* [82]. Certain *Hanseniaspora* species also contribute positively to wine flavor and quality. For instance, an increase in total esters was observed in wines fermented by 1:1 SEQ of *Hanseniaspora vineae*/*S. cerevisiae* or *Hanseniaspora opuntiae*/*S. cerevisiae* [83].

Table 2. Effects of mixed non-*Saccharomyces cerevisiae* and *Saccharomyces cerevisiae* cultures on esters in wine compared with pure *Saccharomyces cerevisiae* fermentation.

Mixed Cultures	Modality	Inoculation Ration	Impact on Wine Esters	Ref.
Metschnikowia pulcherrima/*S. cerevisiae*	SEQ	1:1	Increased total esters and 2-phenylethyl acetate	[73]
	SEQ	1:1	Increased 2-phenylethyl acetate	[74]
	SEQ	1:1	Increased ethyl acetate, ethyl propanoate, 2-methylpropyl acetate, ethyl butanoate, and ethyl hexanoate	[84]
	SIM	10:1	Increased total esters, ethyl acetate, 2-phenethyl acetate, isoamyl acetate, ethyl butanoate, ethyl lactate, and ethyl phenylacetate. Decreased hexyl acetate, ethyl hexanoate, ethyl octanoate, and ethyl decanoate.	[75]
	SEQ	10:1	Increased total esters, ethyl acetate, 2-phenethyl acetate, isoamyl acetate, hexyl acetate, and ethyl lactate. Decreased ethyl hexanoate and ethyl octanoate.	[75]

Table 2. *Cont.*

Mixed Cultures	Modality	Inoculation Ration	Impact on Wine Esters	Ref.
Pichia kluyveri/*S. cerevisiae*	SIM	9:1	Increased 3-mercaptohexyl acetate	[77]
	SEQ	1:1	Increased total esters, ethyl acetate, isoamyl acetate, ethyl octanoate, ethyl caprate, phenethyl acetate, and ethyl dodecanoate	[78]
	SEQ	1:1	Increased ethyl lactate and ethyl succinate	[79]
	SEQ/SIM	1:1	Increased isobutyl acetate, isoamyl acetate, and 2-phenylethyl acetate	[80]
Torulaspora delbrueckii/*S. cerevisiae*	SIM	10:1	Increased ethyl decanoate and isoamyl octanoate	[81]
	SEQ	10:1	Increased isoamyl acetate, ethyl dodecanate, ethyl heptanoate, ethyl octanoate, ethyl nonanoate, ethyl decanoate, isoamyl octanoate, diethyl succinate, methyl octanoate, and isopentyl hexanoate	[81]
	SIM	10:1	Increased total esters, ethyl butanoate, ethyl decanoate, isoamyl acetate, phenylethyl acetate, ethyl propanoate, ethyl isobutanoate, ethyl trans-2-hexenoate, propyl acetate, isobutyl acetate, and butyl acetate	[85]
	SEQ	10:1	Increased isoamyl acetate, ethyl propanoate, ethyl isobutanoate, ethyl 2-methylbutanoate, ethyl trans-2-hexenoate, ethyl dihydrocinnamate, propyl acetate, and isobutyl acetate	[85]
	SEQ	1:1	Increased total esters, ethyl butanoate, ethyl hexanoate, ethyl octanoate, ethyl decanoate, ethyl hexadecanoate, isoamyl acetate, hexyl acetate, ethyl acetate, methyl octanoate, isopentyl Hexanoate, Isoamyl octanoate	[86]
Hanseniaspora vineae/*S. cerevisiae*	SEQ	1:1	Increased total esters, ethyl acetate, isoamyl acetate, and 2-phenylethyl acetate	[83]
Hanseniaspora opuntiae/*S. cerevisiae*	SEQ	1:1	Increased total esters, isoamyl acetate, and 2-phenylethyl acetate	[83]
	SIM	10:1	Increased ethyl acetate, 2-phenylethyl acetate, 2-methylbutyl acetate, and ethyl propionate Decreased isoamyl acetate, ethyl butyrate, and ethyl decanoate	[87]
Hanseniaspora guilliermondii/*S. cerevisiae*	SIM	10:1	Increased ethyl acetate, isoamyl acetate, 2-phenylethyl acetate, 2-methylbutyl acetate, hexyl acetate, and ethyl butyrate	[87]
Hanseniaspora uvarum/*S. cerevisiae*	SIM	10:1	Increased ethyl acetate, isoamyl acetate, 2-phenylethyl acetate, hexyl acetate, and ethyl propionate	[87]
	SEQ	1:1	Increased ethyl acetate	[88]
	SIM	1:2	Increased isoamyl acetate, ethyl octanoate, and ethyl decanoate	[89]
	SEQ	1:2	Increased ethyl acetate, isobutyl acetate, isoamyl acetate, hexyl acetate, 2-phenylethyl acetate, and ethyl decanoate	[89]

SIM, simultaneous inoculation; SEQ, sequential inoculation.

4.2. Fermentation Conditions

During fermentation, factors such as temperature, pH, oxygen availability, and sulfur dioxide (SO_2) additions exert significant influences on the composition and concentration of ester compounds in wine.

Temperature is one of the most critical parameters influencing ester formation, as it directly affects yeast growth, enzymatic activity, and the balance between ester synthesis and hydrolysis. In general, lower temperatures promote ester accumulation. For example, fermentations conducted at 15 °C yielded higher concentrations of ethyl esters than those carried out at 28 °C [90,91]. Du et al. suggested that the enhanced production of ethyl acetate and ethyl butyrate at lower temperatures may result from the stimulation of enzymes involved in their metabolic pathways [11]. Similarly, Merlot wines fermented at 15 °C showed higher total ester concentrations compared with those fermented at 25 °C [92]. However, low fermentation temperature, such as 12 °C, has been reported to reduce the formation of acetate esters relative to fermentations at 28 °C [91].

pH also affects ester formation. Wines with a pH of 3.2 have been reported to exhibit higher concentrations of ethyl acetate than wines with pH 3.6 or 3.8 [93]. This phenomenon may be related to changes in the ester-producing activity of lactic acid bacteria during

malolactic fermentation under different pH conditions [13]. However, the underlying mechanisms remain incompletely understood and require further investigation.

Oxygen serves as an essential nutritional factor in wine fermentation, as it participates in yeast growth and the synthesis of unsaturated fatty acids, both of which can influence the aromatic composition of wine [94]. The effects of oxygen on esters are complex and depend on several factors, including the timing and amount of oxygen introduced, inoculation protocol, fermentation conditions, yeast species, and wine type. Valero et al. found that wines fermented with initial oxygenation exhibited higher levels of major esters than those produced without oxygenation, likely due to reduced yeast growth under oxygen-limited conditions [95]. Varela et al. reported that initial oxygen supplementation increased the production of acetate esters but decreased ethyl esters [96]. A similar pattern was observed in sequential fermentations involving *H. vineae* and *S. cerevisiae*, where initial oxygen aeration boosted *H. vineae* populations and prolonged its coexistence with *S. cerevisiae*, resulting in higher acetate ester levels but lower ethyl ester levels [97].

Sulfur dioxide is one of the most versatile and efficient additives in winemaking, owing to its antiseptic and antioxidant properties. Its presence can markedly influence ester formation during fermentation. Wines fermented with SO_2 exhibited higher levels of ethyl octanoate and diethyl succinate but lower levels of ethyl acetate, ethyl lactate, and isoamyl lactate compared with those produced without SO_2 [98]. Additionally, SO_2 addition has been reported to enhance the levels of ethyl hexanoate and ethyl octanoate [12]. More recent work also reported moderate increases in total ester content in wines produced with SO_2 supplementation [99].

4.3. Barrel Aging and Bottle Storage

Oak barrel aging and bottle storage are traditional and widely used practices in winemaking, particularly for red wine, due to their benefits on flavor development, aromatic complexity, color stabilization, bitterness reduction, and astringency modulation [100,101]. During aging and storage, ester composition evolves mainly through chemical hydrolysis and esterification reactions, gradually approaching equilibrium with their corresponding alcohols and acids. Although esters are typically produced in excess by the end of fermentation, they gradually undergo hydrolysis during aging and storage to achieve chemical equilibrium with their corresponding acids and alcohols.

The evolution of esters during barrel aging reflects interactions between the wine matrix and wood-derived compounds, as well as oxygen transfer through the barrel. The evolution of esters during barrel aging varies with the wine matrix, wine–wood contact time, wood or oak species, geographical origin, toasting intensities, and aging conditions [102]. For example, red wines aged in cherry barrels contained higher levels of ethyl benzoate, methyl benzoate, methyl vanillate, methyl syringate, and benzyl salicylate compared with those aged in chestnut, acacia, ash, or oak barrels [103]. In French and American oak barrels, ethyl esters of straight-chain fatty acids and higher alcohol acetates generally decreased with prolonged aging, although their evolution also depended on the toasting intensity of the oak [100]. Wines aged in French oak were found to contain higher levels of ethyl lactate than those aged in American oak [104]. Furthermore, the development of isoamyl acetate, ethyl butyrate, and ethyl hexanoate during aging was affected by wine turbidity [105].

Ester composition also changes continuously during bottle storage due to ongoing hydrolysis and esterification reactions [106]. These changes are influenced by storage time, temperature, bottle position, closure type, and light exposure. Generally, ethyl esters of branched acids tend to increase, whereas acetate esters and ethyl esters of fatty acids tend to decline during bottle storage. Previous studies reported decreases in isoamyl acetate and ethyl 4-hydroxybutyrate, accompanied by increases in ethyl lactate, diethyl succinate,

ethyl monosuccinate, and diethyl malate with prolonged storage [107]. Consistently, ethyl butyrate, ethyl lactate, and diethyl succinate increased, while isoamyl acetate decreased after 12 months of bottle aging [108]. Increases in ethyl acetate and ethyl lactate have also been documented during storage [109]. Temperature plays a crucial role in modulating ester stability during bottle aging, as it directly affects hydrolysis and esterification rates. Ideally, wines should be stored in cool cellars or temperature-controlled environments maintained at 15–20 °C [110]. The evolution of ester composition during bottle storage is mainly governed by temperature-dependent chemical reactions, including ester hydrolysis and esterification, as well as by the redox environment of the wine. Chilled storage at 5 °C effectively prevent the loss of fruity ethyl esters and acetates during bottle storage compared with storage under uncontrolled temperature conditions [107]. In contrast, higher temperatures accelerate both ester hydrolysis and esterification reactions [39]. Additionally, bottle storage without sulfites further accelerated the hydrolysis of acetate esters [111].

5. Prospects

Despite considerable progress has been made in characterizing ester production during grape development, fermentation, aging, and bottle storage, many aspects of their formation, transformation, and preservation from vineyard to bottle remains insufficiently resolved. Future research should clarify the metabolic pathways linking amino acids and fatty acids to specific esters, elucidate the biochemical and microbial mechanisms through which environmental factors and viticultural practices influence ester accumulation, and further define how non-*Saccharomyces* species interact with *S. cerevisiae* to modulate ester production. Developing predictive models that integrate fermentation variables such as temperature, oxygen management, pH, and SO_2 will be essential for improving control over ester dynamics. In addition, barrel aging and bottle storage reshape ester profiles through hydrolysis and esterification reactions driven by wood species, toasting intensity, wine turbidity, storage temperature, closure type, and light exposure, yet the underlying mechanisms remain to be clarified. These efforts will provide a more integrated understanding of ester formation from vineyard to bottle, support the development of sustainable winemaking practices, and ultimately enhance grape and wine quality.

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References

1. Díaz-Maroto, M.C.; Schneider, R.; Baumes, R. Formation pathways of ethyl esters of branched short-chain fatty acids during wine aging. *J. Agric. Food Chem.* **2005**, *53*, 3503–3509. [CrossRef] [PubMed]
2. Yang, C.; Wang, Y.; Wu, B.; Fang, J.; Li, S. Volatile compounds evolution of three table grapes with different flavour during and after maturation. *Food Chem.* **2011**, *128*, 823–830. [CrossRef]
3. Yang, C.; Wang, Y.; Liang, Z.; Fan, P.; Wu, B.; Yang, L.; Wang, Y.; Li, S. Volatiles of grape berries evaluated at the germplasm level by headspace-SPME with GC–MS. *Food Chem.* **2009**, *114*, 1106–1114. [CrossRef]
4. Power, F.B. Examination of authentic grape juices for methyl anthranilate 1. *J. Agric. Res.* **1923**, *23*, 47–53.

5. Fuleki, T. The Vineland Grape Flavor Index—A new objective method for the accelerated screening of grape seedlings on the basis of flavor character. *Vitis* **1982**, *21*, 111–120.
6. Holley, R.W.; Stoyla, B.; Holley, D. The identification of some volatile constituents of Concord grape juice a. *J. Food Sci.* **1955**, *20*, 326–331. [CrossRef]
7. Ou, C.; Du, X.; Shellie, K.; Ross, C.; Qian, M.C. Volatile Compounds and Sensory Attributes of Wine from Cv. Merlot (*Vitis vinifera* L.) Grown under Differential Levels of Water Deficit with or without a Kaolin-Based, Foliar Reflectant Particle Film. *J. Agric. Food Chem.* **2010**, *58*, 12890–12898. [CrossRef]
8. Gürbüz, O.; Rouseff, J.M.; Rouseff, R.L. Comparison of aroma volatiles in commercial Merlot and Cabernet Sauvignon wines using gas chromatography–olfactometry and gas chromatography–mass spectrometry. *J. Agric. Food Chem.* **2006**, *54*, 3990–3996. [CrossRef]
9. Bowen, A.J.; Reynolds, A.G. Odor potency of aroma compounds in Riesling and Vidal blanc table wines and icewines by gas chromatography–olfactometry–mass spectrometry. *J. Agric. Food Chem.* **2012**, *60*, 2874–2883. [CrossRef]
10. Li, H.; Tao, Y.-S.; Wang, H.; Zhang, L. Impact odorants of Chardonnay dry white wine from Changli County (China). *Eur. Food Res. Technol.* **2008**, *227*, 287–292. [CrossRef]
11. Du, Q.; Ye, D.; Zang, X.; Nan, H.; Liu, Y. Effect of low temperature on the shaping of yeast-derived metabolite compositions during wine fermentation. *Food Res. Int.* **2022**, *162*, 112016. [CrossRef]
12. Coetzee, C.; Lisjak, K.; Nicolau, L.; Kilmartin, P.; du Toit, W.J. Oxygen and sulfur dioxide additions to Sauvignon blanc must: Effect on must and wine composition. *Flavour Fragr. J.* **2013**, *28*, 155–167. [CrossRef]
13. Pérez-Martín, F.; Seseña, S.; Izquierdo, P.M.; Palop, M.L. Esterase activity of lactic acid bacteria isolated from malolactic fermentation of red wines. *Int. J. Food Microbiol.* **2013**, *163*, 153–158. [CrossRef]
14. Kalua, C.M.; Boss, P.K. Evolution of volatile compounds during the development of Cabernet Sauvignon grapes (*Vitis vinifera* L.). *J. Agric. Food Chem.* **2009**, *57*, 3818–3830. [CrossRef]
15. Qian, X.; Liu, Y.; Zhang, G.; Yan, A.; Wang, H.; Wang, X.; Pan, Q.; Xu, H.; Sun, L.; Zhu, B. Alcohol acyltransferase gene and ester precursors differentiate composition of volatile esters in three interspecific hybrids of Vitis labrusca × V. Vinifera during berry development period. *Food Chem.* **2019**, *295*, 234–246. [CrossRef] [PubMed]
16. Wang, J.; De Luca, V. The biosynthesis and regulation of biosynthesis of Concord grape fruit esters, including 'foxy'methylanthranilate. *Plant J.* **2005**, *44*, 606–619. [CrossRef] [PubMed]
17. Reynolds, A.G. (Ed.) 11—Viticultural and vineyard management practices and their effects on grape and wine quality. In *Managing Wine Quality*, 2nd ed.; Woodhead Publishing: Shaxton, UK, 2022; pp. 443–539.
18. Mamede, M.E.; Pastore, G.M. Study of methods for the extraction of volatile compounds from fermented grape must. *Food Chem.* **2006**, *96*, 586–590. [CrossRef]
19. Maoz, I.; Rikanati, R.D.; Schlesinger, D.; Bar, E.; Gonda, I.; Levin, E.; Kaplunov, T.; Sela, N.; Lichter, A.; Lewinsohn, E. Concealed ester formation and amino acid metabolism to volatile compounds in table grape (*Vitis vinifera* L.) berries. *Plant Sci.* **2018**, *274*, 223–230. [CrossRef] [PubMed]
20. González-Barreiro, C.; Rial-Otero, R.; Cancho-Grande, B.; Simal-Gándara, J. Wine aroma compounds in grapes: A critical review. *Crit. Rev. Food Sci. Nutr.* **2015**, *55*, 202–218. [CrossRef]
21. Sumby, K.M.; Grbin, P.R.; Jiranek, V. Microbial modulation of aromatic esters in wine: Current knowledge and future prospects. *Food Chem.* **2010**, *121*, 1–16. [CrossRef]
22. Lilly, M.; Lambrechts, M.G.; Pretorius, I.S. Effect of increased yeast alcohol acetyltransferase activity on flavor profiles of wine and distillates. *Appl. Environ. Microbiol.* **2000**, *66*, 744–753. [CrossRef]
23. Chang, E.-H.; Jeong, S.-M.; Hur, Y.-Y.; Koh, S.-W.; Choi, I.-M. Changes of volatile compounds in Vitis labrusca 'Doonuri'grapes during stages of fruit development and in wine. *Hortic. Environ. Biotechnol.* **2015**, *56*, 137–144. [CrossRef]
24. Yang, C.; Fan, X.; Lao, F.; Huang, J.; Giusti, M.M.; Wu, J.; Lu, H. A comparative study of physicochemical, aroma, and color profiles affecting the sensory properties of grape juice from four Chinese *Vitis vinifera* × *Vitis labrusca* and *Vitis vinifera* grapes. *Foods* **2024**, *13*, 3889. [CrossRef]
25. Kong, C.-L.; Li, A.-H.; Su, J.; Wang, X.-C.; Chen, C.-Q.; Tao, Y.-S. Flavor modification of dry red wine from Chinese spine grape by mixed fermentation with Pichia fermentans and S. cerevisiae. *LWT* **2019**, *109*, 83–92. [CrossRef]
26. Sánchez-Palomo, E.; Delgado, J.; Ferrer, M.; Viñas, M.G. The aroma of La Mancha Chelva wines: Chemical and sensory characterization. *Food Res. Int.* **2019**, *119*, 135–142. [CrossRef]
27. Siebert, T.E.; Barter, S.R.; de Barros Lopes, M.A.; Herderich, M.J.; Francis, I.L. Investigation of 'stone fruit'aroma in Chardonnay, Viognier and botrytis Semillon wines. *Food Chem.* **2018**, *256*, 286–296. [CrossRef]
28. Wu, Y.; Duan, S.; Zhao, L.; Gao, Z.; Luo, M.; Song, S.; Xu, W.; Zhang, C.; Ma, C.; Wang, S. Aroma characterization based on aromatic series analysis in table grapes. *Sci. Rep.* **2016**, *6*, 31116. [CrossRef] [PubMed]
29. Wang, W.-N.; Qian, Y.-H.; Liu, R.-H.; Liang, T.; Ding, Y.-T.; Xu, X.-L.; Huang, S.; Fang, Y.-L.; Ju, Y.-L. Effects of table grape cultivars on fruit quality and aroma components. *Foods* **2023**, *12*, 3371. [CrossRef] [PubMed]

30. Robinson, A.L.; Boss, P.K.; Solomon, P.S.; Trengove, R.D.; Heymann, H.; Ebeler, S.E. Origins of grape and wine aroma. Part 1. Chemical components and viticultural impacts. *Am. J. Enol. Vitic.* **2014**, *65*, 1–24. [CrossRef]
31. Romano, P.; Braschi, G.; Siesto, G.; Patrignani, F.; Lanciotti, R. Role of yeasts on the sensory component of wines. *Foods* **2022**, *11*, 1921. [CrossRef]
32. Ruiz, J.; Kiene, F.; Belda, I.; Fracassetti, D.; Marquina, D.; Navascués, E.; Calderón, F.; Benito, A.; Rauhut, D.; Santos, A. Effects on varietal aromas during wine making: A review of the impact of varietal aromas on the flavor of wine. *Appl. Microbiol. Biotechnol.* **2019**, *103*, 7425–7450. [CrossRef]
33. Cao, W.; Shu, N.; Wen, J.; Yang, Y.; Jin, Y.; Lu, W. Characterization of the key aroma volatile compounds in nine different grape varieties wine by headspace gas chromatography–ion mobility spectrometry (HS-GC-IMS), odor activity values (OAV) and sensory analysis. *Foods* **2022**, *11*, 2767. [CrossRef]
34. Swiegers, J.; Bartowsky, E.; Henschke, P.; Pretorius, I. Yeast and bacterial modulation of wine aroma and flavour. *Aust. J. Grape Wine Res.* **2005**, *11*, 139–173. [CrossRef]
35. Zhang, S.; Petersen, M.A.; Liu, J.; Toldam-Andersen, T.B. Influence of pre-fermentation treatments on wine volatile and sensory profile of the new disease tolerant cultivar Solaris. *Molecules* **2015**, *20*, 21609–21625. [CrossRef]
36. Feng, T.; Sun, J.; Song, S.; Wang, H.; Yao, L.; Sun, M.; Wang, K.; Chen, D. Geographical differentiation of Molixiang table grapes grown in China based on volatile compounds analysis by HS-GC-IMS coupled with PCA and sensory evaluation of the grapes. *Food Chem. X* **2022**, *15*, 100423. [CrossRef]
37. Zhao, P.; Gao, J.; Qian, M.; Li, H. Characterization of the key aroma compounds in Chinese Syrah wine by gas chromatography-olfactometry-mass spectrometry and aroma reconstitution studies. *Molecules* **2017**, *22*, 1045. [CrossRef]
38. Styger, G.; Prior, B.; Bauer, F.F. Wine flavor and aroma. *J. Ind. Microbiol. Biotechnol.* **2011**, *38*, 1145. [CrossRef]
39. Makhotkina, O.; Kilmartin, P.A. Hydrolysis and formation of volatile esters in New Zealand Sauvignon blanc wine. *Food Chem.* **2012**, *135*, 486–493. [CrossRef]
40. Sale, J.; Wilson, J. Distribution of volatile flavor in grapes and grape juices. *J. Frankl. Inst.* **1926**, *202*, 663–664. [CrossRef]
41. Carpena, M.; Fraga-Corral, M.; Otero, P.; Nogueira, R.A.; Garcia-Oliveira, P.; Prieto, M.A.; Simal-Gandara, J. Secondary aroma: Influence of wine microorganisms in their aroma profile. *Foods* **2020**, *10*, 51. [CrossRef] [PubMed]
42. Zhang, J.; Li, W.; Zhang, P.; Zhang, X.; Wang, J.; Wang, L.; Chen, K.; Fang, Y.; Zhang, K. Effect of supplementary light with different wavelengths on anthocyanin composition, sugar accumulation and volatile compound profiles of grapes. *Foods* **2023**, *12*, 4165. [CrossRef]
43. Dong, T.; Hao, T.; Zhang, P.; Hakeem, A.; Zhao, P.; Song, S.; Ren, Y.; Chen, Y.; Jia, H.; Fang, J. A comprehensive evaluation of different responses of supplementary light qualities on physiological and biochemical mechanisms of 'Kyoho' grape. *Sci. Hortic.* **2024**, *333*, 113261. [CrossRef]
44. Liu, D.; Gao, Y.; Li, X.-X.; Li, Z.; Pan, Q.-H. Attenuated UV radiation alters volatile profile in Cabernet Sauvignon grapes under field conditions. *Molecules* **2015**, *20*, 16946–16969. [CrossRef]
45. Zhu, Y.; Sun, M.; Harrison, R.; Jordan, B.; Creasy, G.; Hofmann, R. Effects of UV-B and water deficit on aroma precursors in grapes and flavor release during wine micro-vinification and consumption. *Foods* **2022**, *11*, 1336. [CrossRef]
46. Song, J.; Smart, R.; Wang, H.; Dambergs, B.; Sparrow, A.; Qian, M.C. Effect of grape bunch sunlight exposure and UV radiation on phenolics and volatile composition of *Vitis vinifera* L. cv. Pinot noir wine. *Food Chem.* **2015**, *173*, 424–431. [CrossRef]
47. Ju, Y.; Francoise, U.; Li, D.; Zhang, Y.; Liu, B.; Sun, M.; Fang, Y.; Wei, X. Effect of light-selective sunshade net on the quality and aromatic characteristics of Cabernet Sauvignon grapes and wine: Exploratory experiment on strong solar irradiance in northwestern China. *Food Chem. X* **2023**, *17*, 100510. [CrossRef]
48. Ma, Z.; Yang, S.; Mao, J.; Li, W.; Li, W.; Zuo, C.; Chu, M.; Zhao, X.; Zhou, Q.; Chen, B. Effects of shading on the synthesis of volatile organic compounds in 'Marselan' grape berries (*Vitis vinifera* L.). *J. Plant Growth Regul.* **2021**, *40*, 679–693. [CrossRef]
49. Ju, Y.-L.; Liu, M.; Tu, T.-Y.; Zhao, X.-F.; Yue, X.-F.; Zhang, J.-X.; Fang, Y.-L.; Meng, J.-F. Effect of regulated deficit irrigation on fatty acids and their derived volatiles in 'Cabernet Sauvignon' grapes and wines of Ningxia, China. *Food Chem.* **2018**, *245*, 667–675. [CrossRef]
50. Talaverano, I.; Ubeda, C.; Cáceres-Mella, A.; Valdés, M.E.; Pastenes, C.; Peña-Neirae, Á. Water stress and ripeness effects on the volatile composition of Cabernet Sauvignon wines. *J. Sci. Food Agric.* **2017**, *98*, 1140–1152. [CrossRef]
51. Pedneault, K.; Dorais, M.; Angers, P. Flavor of cold-hardy grapes: Impact of berry maturity and environmental conditions. *J. Agric. Food Chem.* **2013**, *61*, 10418–10438. [CrossRef] [PubMed]
52. Falcão, L.D.; De Revel, G.; Perello, M.-C.; Riquier, L.; Rosier, J.-P.; Uberti, A.A.A.; Bordignon-Luiz, M.T. Volatile profile characterization of young Cabernet-Sauvignon wines from a new grape growing region in Brazil. *Oeno One* **2008**, *42*, 133–145. [CrossRef]
53. Webster, D.R.; Edwards, C.G.; Spayd, S.E.; Peterson, J.C.; Seymour, B.J. Influence of vineyard nitrogen fertilization on the concentrations of monoterpenes, higher alcohols, and esters in aged riesling wines. *Am. J. Enol. Vitic.* **1993**, *44*, 275–284. [CrossRef]

54. Miliordos, D.E.; Kanapitsas, A.; Lola, D.; Goulioti, E.; Kontoudakis, N.; Leventis, G.; Tsiknia, M.; Kotseridis, Y. Effect of nitrogen fertilization on Savvatiano (*Vitis vinifera* L.) grape and wine composition. *Beverages* **2022**, *8*, 29. [CrossRef]
55. Wang, Q.; Yang, Y.; Wang, H.; Hou, Y.; Xia, Z. Effects of plant growth regulators on magnesium absorption and fruit quality in "*Vitis vinifera* cv. Shine-Muscat" grape. *J. Plant Growth Regul.* **2025**, *44*, 4054–4072. [CrossRef]
56. Gutiérrez-Gamboa, G.; Garde-Cerdán, T.; Carrasco-Quiroz, M.; Martínez-Gil, A.M.; Moreno-Simunovic, Y. Improvement of wine volatile composition through foliar nitrogen applications to 'Cabernet Sauvignon' grapevines in a warm climate. *Chil. J. Agric. Res.* **2018**, *78*, 216–227. [CrossRef]
57. Cheng, X.; Ma, T.; Wang, P.; Liang, Y.; Zhang, J.; Zhang, A.; Chen, Q.; Li, W.; Ge, Q.; Sun, X.; et al. Foliar nitrogen application from veraison to preharvest improved flavonoids, fatty acids and aliphatic volatiles composition in grapes and wines. *Food Res. Int.* **2020**, *137*, 109566. [CrossRef]
58. Chen, T.; Xu, T.; Shen, L.; Zhang, T.; Wang, L.; Chen, Z.; Wu, Y.; Yang, J. Effects of girdling and foliar fertilization with K on physicochemical parameters, phenolic and volatile composition in 'Hanxiangmi' table grape. *Horticulturae* **2022**, *8*, 388. [CrossRef]
59. Ma, M.; Ma, X.; Ma, Z.; Wang, T.; Li, Y.; Mao, J.; Chen, B. Effects of foliar fertilizer additives on grape fruit quality and endogenous hormones in leaves. *BMC Plant Biol.* **2025**, *25*, 516. [CrossRef]
60. Phogat, V.; Skewes, M.; Cox, J.; Sanderson, G.; Alam, J.; Šimůnek, J. Seasonal simulation of water, salinity and nitrate dynamics under drip irrigated mandarin (*Citrus reticulata*) and assessing management options for drainage and nitrate leaching. *J. Hydrol.* **2014**, *513*, 504–516. [CrossRef]
61. Ma, C.; Li, Y.; Tian, S.; Wang, R.; Wang, C. Impact of the plant growth-promoting Rhizobacterium Streptomyces saraceticus strain 31 on berry quality of 'Benifuji' grape: Improvements through the reconfiguration of fine root morphology and vessel anatomy. *HortScience* **2024**, *59*, 1077–1087. [CrossRef]
62. Xi, X.; Zha, Q.; He, Y.; Tian, Y.; Jiang, A. Influence of cluster thinning and girdling on aroma composition in 'Jumeigui' table grape. *Sci. Rep.* **2020**, *10*, 6877. [CrossRef]
63. Gao, Y.; Li, X.-X.; Han, M.-M.; Yang, X.-F.; Li, Z.; Wang, J.; Pan, Q.-H. Rain-shelter cultivation modifies carbon allocation in the polyphenolic and volatile metabolism of *Vitis vinifera* L. chardonnay grapes. *PLoS ONE* **2016**, *11*, e0156117. [CrossRef]
64. Li, Z.; Yang, D.; Guan, X.; Sun, Y.; Wang, J. Changes in Volatile Composition of Cabernet Sauvignon (*Vitis vinifera* L.) Grapes under Leaf Removal Treatment. *Agronomy* **2023**, *13*, 1888. [CrossRef]
65. Zhang, P.; Wu, X.; Needs, S.; Liu, D.; Fuentes, S.; Howell, K. The influence of apical and basal defoliation on the canopy structure and biochemical composition of *Vitis vinifera* cv. Shiraz grapes and wine. *Front. Chem.* **2017**, *5*, 48. [CrossRef]
66. Cincotta, F.; Verzera, A.; Prestia, O.; Tripodi, G.; Lechhab, W.; Sparacio, A.; Condurso, C. Influence of leaf removal on grape, wine and aroma compounds of *Vitis vinifera* L. cv. Merlot under Mediterranean climate. *Eur. Food Res. Technol.* **2022**, *248*, 403–413. [CrossRef]
67. Adebami, G.E.; Kuila, A.; Ajunwa, O.M.; Fasiku, S.A.; Asemoloye, M.D. Genetics and metabolic engineering of yeast strains for efficient ethanol production. *J. Food Process Eng.* **2022**, *45*, e13798. [CrossRef]
68. Saberi, S.; Cliff, M.; Van Vuuren, H. Impact of mixed S. cerevisiae strains on the production of volatiles and estimated sensory profiles of Chardonnay wines. *Food Res. Int.* **2012**, *48*, 725–735. [CrossRef]
69. Di Gianvito, P.; Perpetuini, G.; Tittarelli, F.; Schirone, M.; Arfelli, G.; Piva, A.; Patrignani, F.; Lanciotti, R.; Olivastri, L.; Suzzi, G.; et al. Impact of *Saccharomyces cerevisiae* strains on traditional sparkling wines production. *Food Res. Int.* **2018**, *109*, 552–560. [CrossRef]
70. Lan, Y.; Wang, J.; Aubie, E.; Crombleholme, M.; Reynolds, A. Effects of frozen materials other than grapes on red wine volatiles. mitigation of floral taints by yeast strains. *Am. J. Enol. Vitic.* **2022**, *73*, 125–141. [CrossRef]
71. Jolly, N.P.; Varela, C.; Pretorius, I.S. Not your ordinary yeast: Non-Saccharomyces yeasts in wine production uncovered. *FEMS Yeast Res.* **2014**, *14*, 215–237. [CrossRef]
72. Vicente, J.; Ruiz, J.; Belda, I.; Benito-Vázquez, I.; Marquina, D.; Calderón, F.; Santos, A.; Benito, S. The genus metschnikowia in enology. *Microorganisms* **2020**, *8*, 1038. [CrossRef]
73. Rodríguez, M.E.; Lopes, C.A.; Barbagelata, R.J.; Barda, N.B.; Caballero, A.C. Influence of Candida pulcherrima Patagonian strain on alcoholic fermentation behaviour and wine aroma. *Int. J. Food Microbiol.* **2010**, *138*, 19–25. [CrossRef]
74. Ruiz, J.; Belda, I.; Beisert, B.; Navascués, E.; Marquina, D.; Calderón, F.; Rauhut, D.; Santos, A.; Benito, S. Analytical impact of *Metschnikowia pulcherrima* in the volatile profile of Verdejo white wines. *Appl. Microbiol. Biotechnol.* **2018**, *102*, 8501–8509. [CrossRef]
75. Zhang, B.-Q.; Shen, J.-Y.; Duan, C.-Q.; Yan, G.-L. Use of indigenous *Hanseniaspora vineae* and *Metschnikowia pulcherrima* co-fermentation with *Saccharomyces cerevisiae* to improve the aroma diversity of Vidal Blanc icewine. *Front. Microbiol.* **2018**, *9*, 2303. [CrossRef] [PubMed]
76. Vicente, J.; Calderón, F.; Santos, A.; Marquina, D.; Benito, S. High potential of Pichia kluyveri and other Pichia species in wine technology. *Int. J. Mol. Sci.* **2021**, *22*, 1196. [CrossRef] [PubMed]

77. Anfang, N.; Brajkovich, M.; Goddard, M.R. Co-fermentation with Pichia kluyveri increases varietal thiol concentrations in Sauvignon Blanc. *Aust. J. Grape Wine Res.* **2009**, *15*, 1–8. [CrossRef]
78. Gao, M.; Hu, J.; Wang, X.; Zhang, H.; Du, Z.; Ma, L.; Du, L.; Zhang, H.; Tian, X.; Yang, W. Effects of Pichia kluyveri on the flavor characteristics of wine by co-fermentation with *Saccharomyces cerevisiae*. *Eur. Food Res. Technol.* **2023**, *249*, 1449–1460. [CrossRef]
79. Guan, X.; Li, Y.; Ma, W.; Zhang, J.; Tao, Y. Fermentation biological protection and aroma characteristics of selected non-Saccharomyces yeasts in wine fermentation. *Food Biosci.* **2025**, *68*, 106707. [CrossRef]
80. Li, Y.; Xu, L.; Sam, F.E.; Li, A.; Hu, K.; Tao, Y. Improving aromatic higher alcohol acetates in wines by co-fermentation of Pichia kluyveri and *Saccharomyces cerevisiae*: Growth interaction and amino acid competition. *J. Sci. Food Agric.* **2024**, *104*, 6875–6883. [CrossRef]
81. Zhang, B.-Q.; Luan, Y.; Duan, C.-Q.; Yan, G.-L. Use of Torulaspora delbrueckii co-fermentation with two *Saccharomyces cerevisiae* strains with different aromatic characteristic to improve the diversity of red wine aroma profile. *Front. Microbiol.* **2018**, *9*, 606. [CrossRef]
82. Zhang, B.; Yu, C.; Wang, M.; Zhao, X.; Lin, L.; Yan, G.; Zhang, C. Investigation of novel metabolites generated by Torulaspora delbrueckii to promote the aroma biosynthesis in *Saccharomyces cerevisiae* during wine fermentation. *LWT* **2024**, *211*, 116816. [CrossRef]
83. del Fresno, J.M.; Escott, C.; Carrau, F.; Herbert-Pucheta, J.E.; Vaquero, C.; González, C.; Morata, A. Improving aroma complexity with *Hanseniaspora* spp.: Terpenes, acetate esters, and safranal. *Fermentation* **2022**, *8*, 654. [CrossRef]
84. Varela, C.; Sengler, F.; Solomon, M.; Curtin, C. Volatile flavour profile of reduced alcohol wines fermented with the non-conventional yeast species *Metschnikowia pulcherrima* and Saccharomyces uvarum. *Food Chem.* **2016**, *209*, 57–64. [CrossRef] [PubMed]
85. Renault, P.; Coulon, J.; de Revel, G.; Barbe, J.-C.; Bely, M. Increase of fruity aroma during mixed T. delbrueckii/S. cerevisiae wine fermentation is linked to specific esters enhancement. *Int. J. Food Microbiol.* **2015**, *207*, 40–48. [CrossRef]
86. Zhang, B.; Liu, H.; Xue, J.; Tang, C.; Duan, C.; Yan, G. Use of Torulaspora delbrueckii and *Hanseniaspora vineae* co-fermentation with *Saccharomyces cerevisiae* to improve aroma profiles and safety quality of Petit Manseng wines. *LWT* **2022**, *161*, 113360. [CrossRef]
87. Badura, J.; Kiene, F.; Brezina, S.; Fritsch, S.; Semmler, H.; Rauhut, D.; Pretorius, I.S.; von Wallbrunn, C.; van Wyk, N. Aroma profiles of *Vitis vinifera* L. cv. Gewürztraminer must fermented with co-cultures of *Saccharomyces cerevisiae* and seven *Hanseniaspora* spp. *Fermentation* **2023**, *9*, 109. [CrossRef]
88. Li, Y.-Q.; Hu, K.; Xu, Y.-H.; Mei, W.-C.; Tao, Y.-S. Biomass suppression of *Hanseniaspora uvarum* by killer *Saccharomyces cerevisiae* highly increased fruity esters in mixed culture fermentation. *LWT* **2020**, *132*, 109839. [CrossRef]
89. Hu, K.; Jin, G.-J.; Xu, Y.-H.; Tao, Y.-S. Wine aroma response to different participation of selected *Hanseniaspora uvarum* in mixed fermentation with *Saccharomyces cerevisiae*. *Food Res. Int.* **2018**, *108*, 119–127. [CrossRef]
90. Molina, A.M.; Swiegers, J.H.; Varela, C.; Pretorius, I.S.; Agosin, E. Influence of wine fermentation temperature on the synthesis of yeast-derived volatile aroma compounds. *Appl. Microbiol. Biotechnol.* **2007**, *77*, 675–687. [CrossRef]
91. Gamero, A.; Tronchoni, J.; Querol, A.; Belloch, C. Production of aroma compounds by cryotolerant Saccharomyces species and hybrids at low and moderate fermentation temperatures. *J. Appl. Microbiol.* **2013**, *114*, 1405–1414. [CrossRef]
92. Massera, A.; Assof, M.; Sari, S.; Ciklic, I.; Mercado, L.; Jofré, V.; Combina, M. Effect of low temperature fermentation on the yeast-derived volatile aroma composition and sensory profile in Merlot wines. *LWT* **2021**, *142*, 111069. [CrossRef]
93. Knoll, C.; Fritsch, S.; Schnell, S.; Grossmann, M.; Rauhut, D.; du Toit, M. Influence of pH and ethanol on malolactic fermentation and volatile aroma compound composition in white wines. *LWT—Food Sci. Technol.* **2011**, *44*, 2077–2086. [CrossRef]
94. Tarko, T.; Duda-Chodak, A.; Sroka, P.; Siuta, M. The impact of oxygen at various stages of vinification on the chemical composition and the antioxidant and sensory properties of white and red Wines. *Int. J. Food Sci.* **2020**, *2020*, 7902974. [CrossRef]
95. Valero, E.; Moyano, L.; Millan, M.C.; Medina, M.; Ortega, J.M. Higher alcohols and esters production by *Saccharomyces cerevisiae*. Influence of the initial oxygenation of the grape must. *Food Chem.* **2002**, *78*, 57–61. [CrossRef]
96. Varela, C.; Torrea, D.; Schmidt, S.; Ancin-Azpilicueta, C.; Henschke, E.P. Effect of oxygen and lipid supplementation on the volatile composition of chemically defined medium and Chardonnay wine fermented with *Saccharomyces cerevisiae*. *Food Chem.* **2012**, *135*, 2863–2871. [CrossRef] [PubMed]
97. Yan, G.; Zhang, B.; Joseph, L.; Waterhouse, A.L. Effects of initial oxygenation on chemical and aromatic composition of wine in mixed starters of *Hanseniaspora vineae* and *Saccharomyces cerevisiae*. *Food Microbiol.* **2020**, *90*, 103460. [CrossRef]
98. Herraiz, T.; Martin-Alvarez, P.J.; Reglero, G.; Herraiz, M.; Cabezudo, M.D. Differences between wines fermented with and without sulphur dioxide using various selected yeasts. *J. Sci. Food Agric.* **1989**, *49*, 249–258. [CrossRef]
99. Martín-García, F.J.; Palacios-Fernández, S.; López de Lerma, N.; García-Martínez, T.; Mauricio, J.C.; Peinado, R.A. The effect of yeast, sugar and sulfur dioxide on the volatile compounds in wine. *Fermentation* **2023**, *9*, 541. [CrossRef]
100. González-Centeno, M.R.; Chira, K.; Teissedre, P.L. Ellagitannin content, volatile composition and sensory profile of wines from different countries matured in oak barrels subjected to different toasting methods. *Food Chem.* **2016**, *210*, 500–511. [CrossRef]

101. Echave, J.; Barral, M.; Fraga-Corral, M.; Prieto, M.A.; Simal-Gandara, J. Bottle aging and storage of wines: A review. *Molecules* **2021**, *26*, 713. [CrossRef]
102. Cameleyre, M.; Lytra, G.; Schütte, L.; Vicard, J.-C.; Barbe, J.-C. Oak wood volatiles impact on red wine fruity aroma perception in various matrices. *J. Agric. Food Chem.* **2020**, *68*, 13319–13330. [CrossRef]
103. De Simón, B.F.; Martínez, J.; Sanz, M.; Cadahía, E.; Esteruelas, E.; Muñoz, A.M. Volatile compounds and sensorial characterisation of red wine aged in cherry, chestnut, false acacia, ash and oak wood barrels. *Food Chem.* **2014**, *147*, 346–356. [CrossRef]
104. Cerdán, T.G.; Rodríguez Mozaz, S.; Ancín Azpilicueta, C. Volatile composition of aged wine in used barrels of French oak and of American oak. *Food Res. Int.* **2002**, *35*, 603–610. [CrossRef]
105. Moreno, N.J.; Azpilicueta, C.A. The development of esters in filtered and unfiltered wines that have been aged in oak barrels. *Int. J. Food Sci. Technol.* **2006**, *41*, 155–161. [CrossRef]
106. Ramey, D.D.; Ough, C.S. Volatile ester hydrolysis or formation during storage of model solutions and wines. *J. Agric. Food Chem.* **1980**, *28*, 928–934. [CrossRef]
107. Pérez-Coello, M.; González-Viñas, M.; Garcıa-Romero, E.; Dıaz-Maroto, M.; Cabezudo, M. Influence of storage temperature on the volatile compounds of young white wines. *Food Control* **2003**, *14*, 301–306. [CrossRef]
108. Recamales, Á.F.; Gallo, V.; Hernanz, D.; González-Miret, M.L.; Heredia, F.J. Effect of time and storage conditions on major volatile compounds of Zalema white wine. *J. Food Qual.* **2011**, *34*, 100–110. [CrossRef]
109. Cassino, C.; Tsolakis, C.; Bonello, F.; Gianotti, V.; Osella, D. Wine evolution during bottle aging, studied by 1H NMR spectroscopy and multivariate statistical analysis. *Food Res. Int.* **2019**, *116*, 566–577. [CrossRef]
110. Scrimgeour, N.; Nordestgaard, S.; Lloyd, N.; Wilkes, E. Exploring the effect of elevated storage temperature on wine composition. *Aust. J. Grape Wine Res.* **2015**, *21*, 713–722. [CrossRef]
111. Pati, S.; Crupi, P.; Savastano, M.L.; Benucci, I.; Esti, M. Evolution of phenolic and volatile compounds during bottle storage of a white wine without added sulfite. *J. Sci. Food Agric.* **2020**, *100*, 775–784. [CrossRef]

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