



## Yeast fermented alcoholic fruit beverages: A systematic review

Wenjia He <sup>a,b,c</sup>, Tiantian Dong <sup>a</sup>, Yiwei Zhang <sup>a</sup>, Maaria Kortensniemi <sup>b</sup>, Shuxun Liu <sup>d</sup>,  
Yuting Ding <sup>a,e</sup>, Xuxia Zhou <sup>a</sup>, Oskar Laaksonen <sup>b</sup>, Baoru Yang <sup>b,\*</sup>

<sup>a</sup> Key Laboratory of Green, Low-carbon and Efficient Development of Marine Fishery Resources, National R&D Branch Center for Pelagic Aquatic Products Processing (Hangzhou), College of Food Science and Technology, Zhejiang University of Technology, Hangzhou, 310014, China

<sup>b</sup> Food Sciences, Department of Life Technologies, University of Turku, Turun Yliopisto, FI-20014, Finland

<sup>c</sup> Zhejiang Gu Yue Long Shan Shaoxing Wine Co., Ltd, Beihai Bridge, Yuecheng District, Shaoxing, 312000, China

<sup>d</sup> Zhejiang Key Laboratory of Food Microbiology and Nutritional Health, College of Food Science and Biotechnology, Zhejiang Gongshang University, Hangzhou, 310014, China

<sup>e</sup> Food Science Research Institute of Zhangzhou, Zhangzhou, 363000, China

### ARTICLE INFO

#### Keywords:

Alcoholic fruit beverages  
Fermentation  
Comprehensive processing procedure  
Yeast strains  
Flavor compounds

### ABSTRACT

Yeast-driven alcoholic fermentation is widely applied to process fruits into value-added beverages. Fruit genotypes, yeast strains, and beverage production methods significantly influence the diversity and quality of alcoholic beverages. Traditionally, *Saccharomyces cerevisiae* is regarded as the most commercially important yeast in the alcoholic beverage production markets, whereas other *Saccharomyces* and non-*Saccharomyces* is considered to be either harmful or useless. However, the interest of applying these yeasts in numerous innovative yeast fermented alcoholic fruit-based beverages is growing due to their advantageous flavor attributions. In this review, the strategies for enhancing volatile properties and aroma and flavor complexity of alcoholic beverage fermentation were critically examined with a special emphasis on fruit types and yeast strains, as well as their impacts on the quality of alcoholic beverages. The current challenges and future prospects were also discussed on the development of desirable alcoholic beverage production.

### 1. Introduction

AFBs are medium-alcoholic beverages, typically containing 1.2–14 vol% alcohol, produced through yeast fermentation of non-grape fruit materials. The definition excludes mixed beverages, i.e., those produced by blending fruit juice with distilled alcohol, and is strictly limited to the beverages derived from fermentation of fruit materials and their processed juices. These innovative AFBs have attracted growing attention from young and middle-aged consumers worldwide, due to their moderate alcohol content, rich flavors, and diverse nutrient composition (Tan et al., 2024). Moreover, the global beverage industry has correspondingly expanded the production of AFBs with healthier nutrients

and natural flavors to meet this growing demand (Jagtap & Bapat, 2015; Zhu et al., 2023). The development of AFBs provides sustainability benefits, such as enhancing the value-added potential of fruits, reducing post-harvest waste, and mitigating imbalances between fruit production and market demands. Globally, pome fruits like apples and pears dominate the fruit-derived alcoholic drink market alongside grape wines, while other fruits like stone fruits, citrus fruits, tropical or exotic fruits also play important roles in the production of AFBs. For example, in the Northern American and European countries, strawberries, peaches, and plums are commonly utilized to ferment AFBs (Tarko & Duda, 2024), whereas tropical and subtropical fruits like lychee and citrus fruits are popular in the Asian countries. Meanwhile, African

**Abbreviations:** AFBs, alcoholic fruit beverages; VOCs, volatile organic compounds; *S. cerevisiae*, *Saccharomyces cerevisiae*; *S. bayanus*, *Saccharomyces bayanus*; *S. paradoxus*, *Saccharomyces paradoxus*; *S. mikatae*, *Saccharomyces mikatae*; *S. kudriavzevii*, *Saccharomyces kudriavzevii*; *S. capensis*, *Saccharomyces capensis*; *S. uvarum*, *Saccharomyces uvarum*; MCFAs, medium-chain fatty acids; *C. zemplinina*, *Candida zemplinina*; *H. spp.*, *Hanseniaspora spp.*; *H. osmophila*, *Hanseniaspora osmophila*; *H. uvarum*, *Hanseniaspora uvarum*; *K. marxianus*, *Cluyveromyces marxianus*; *K. pastoris*, *Komagataella pastoris*; *M. pulcherrima*, *Metschnikowia pulcherrima*; *L. thermotolerans*, *Lachancea thermotolerans*; *P. membranaefaciens*, *Pichia membranaefaciens*; *P. kluyveri*, *Pichia kluyveri*; *Starm. bacillaris*, *Starmerella bacillaris*; *Schizo. spp.*, *Schizosaccharomyces spp.*; *Schizo. pombe*, *Schizosaccharomyces pombe*; *T. delbrueckii*, *Torulaspora delbrueckii*; *T. quercuum*, *Torulaspora quercuum*; *Z. spp.*, *Zygosaccharomyces spp.*; *Z. bailii*, *Zygosaccharomyces bailii*; *Z. rouxii*, *Zygosaccharomyces rouxii*; YAN, yeast assimilable nitrogen.

\* Corresponding author.

E-mail address: [baoru.yang@utu.fi](mailto:baoru.yang@utu.fi) (B. Yang).

<https://doi.org/10.1016/j.fbio.2026.108351>

Received 13 November 2025; Received in revised form 20 January 2026; Accepted 21 January 2026

Available online 22 January 2026

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producers prefer to use local specialty fruits like sand apple to produce traditional AFBs with stable and low-price supply (Tarko & Duda, 2024).

Alcoholic fermentation process is biologically complex, and yeast strains play a key role in shaping the flavor characteristics of final AFBs. During the alcoholic fermentation process, yeasts transform the fruit sugars like fructose, sucrose, and glucose into carbon dioxide, ethanol, as well as various secondary metabolites, such as volatile secondary metabolites and functional nutrients (Al Daccache et al., 2020). This favorable biochemical transformation can significantly enhance the flavor and taste complexity and provide high health benefits in the final AFBs like antimicrobial, antioxidant, and anti-inflammatory properties (Gutiérrez-Escobar et al., 2021; Yuan et al., 2024). The types and concentrations of these bioactive substances have been demonstrated to directly affect the physicochemical and organoleptic properties in the production of AFBs. For example, ethanol could not only provide alcohol attributes in AFBs, but also interacts with other metabolite components and affect the flavor perceptions. Phenolic compounds contribute to the organoleptic properties and quality of AFBs, primarily as the appearance, bitterness, and especially astringency. The organic acids like citric, tartaric, and malic acids contribute to the acidity and refreshing mouthfeel of AFBs. An appropriate acidity level could effectively harmonize the mouthfeel of AFBs and are essential during the maturation process of AFBs (Feitosa et al., 2023; Zeng et al., 2025). Therefore, the optimization of fermentation conditions is essential to produce high-quality AFBs with desirable flavors and functional attributes.

The AFB fermentation procedure primarily consists of three key steps, including raw materials selection, fermentation process control, and post-fermentation treatment, as shown in Fig. 1. First, the selection of high-quality fruit cultivars with proper maturity and free of pest and diseases are crucial to ensure the overall quality of AFBs (Gong et al., 2017; Qi et al., 2017; Wei et al., 2019). The fruits undergo cleaning, coring or peeling, crushing, and squeezing, followed by filtration to remove impurities. Enzymatic treatments, like the pectinase and cellulase hydrolysis are then applied to enhance the juice yield and clarity (Espejo, 2021). The acidity and sugar levels of fruit juice are then added to adjust the fermentation condition of yeast strains and balance the taste and flavor profiles. Next, the selected yeast strains are inoculated into the prepared juices for the further temperature-controlled fermentation (Masella et al., 2025). Fermentation temperature is typically

maintained at 20–28 °C, and the pH at 3.0–4.0. The fermentation conditions would be changed based on the carbohydrate concentrations to ensure the growth of yeast strains and the stable production of flavor compounds. Typically, the fermentation temperature needs to be strictly controlled for a stable fermentation process. Excessively high temperatures may cause bacterial contamination or flavor deterioration, while excessively low temperatures would slow the fermentation speed (Liu et al., 2018). The duration of fermentation mainly depends on the sugar levels of used fruit juices and the targeted alcoholic contents of the AFBs, and the fermentation cycle varies from a few days to several weeks (Ferremi Leali et al., 2024). Throughout this process, regular monitoring of sugar level, alcoholic content, and pH value is crucial, as these factors directly influence the microbial activity, fermentation efficiency, and final product quality. After fermentation, the beverage is separated from the sediment, mainly yeast residue and fruit pomace, through decanting or filtration (Guerrini et al., 2019). The AFBs are then stored and aged under a constant temperature for several months to develop their flavor complexity. During the aging process, periodic chemical and sensory analyses are conducted to guarantee the quality of AFBs.

This current review summarizes the latest research progress on flavor-active substances as well as their sensory active properties of AFBs, with particular emphasis on the different fruit types and yeast metabolic activities. The application of *S. cerevisiae*, *Saccharomyces non-cerevisiae*, and non-*Saccharomyces* in shaping the chemical composition and organoleptic properties of AFBs is reviewed, highlighting the strain specific metabolism and the product typicity. This review aims to elucidate the potential utilization of yeast strains in AFBs fermentation and establish a theoretical stand for flavor enhancement and ultimately improve the overall quality of AFBs.

## 2. Volatile organic compounds in AFBs

It is essential to understand the knowledge of aroma and flavor properties that determined, or enhanced the overall organoleptic quality of AFBs. In general, the perception of aroma and flavor properties in the alcoholic beverages could be resulted from the volatile organic compounds (VOCs) as well as the sensory receptors in human beings. Furthermore, the VOCs exist in the “good alcoholic beverage” product are complex and subtle. However, not all the VOCs are considered as

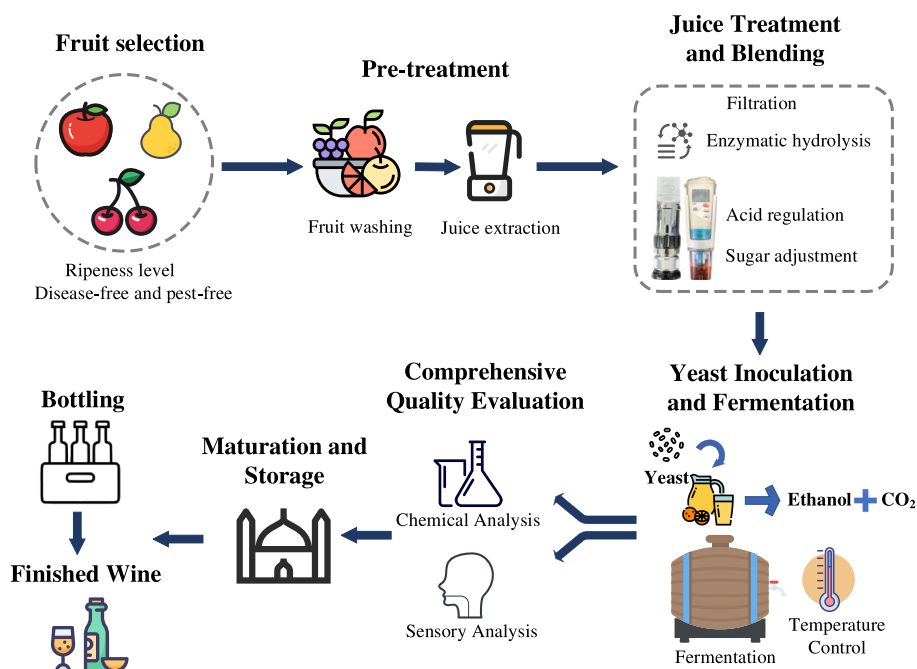


Fig. 1. Alcoholic fermentation process of yeast fermentation beverages.

odor-active compounds, only those present in concentrations above their sensory perception threshold contribute significantly to the aroma profiles of AFBs (Plutowska & Wardencki, 2008). The interactions among different volatiles and non-volatiles, including synergistic and antagonistic interactions, also determined the mouthfeel and taste perception of AFBs. The alcoholic beverages with single and strong flavor notes are usually not appreciated by the consumers (Lesschaeve, 2007). Therefore, the determination of principal VOCs in AFBs, especially those with the perceived sensorial attributes, is one of the long-standing goals of fruit beverage research. The VOCs could be categorized as the following groups: higher alcohols, esters, aldehydes, ketones, volatile acids, and other volatiles (terpenes and sulfur compounds) (Aith Barbará et al., 2020; Issa-Issa et al., 2020; Tian et al., 2021), as shown in Fig. 2. Moreover, the VOCs could also be divided into primary, secondary, and tertiary VOCs, depending on whether these compounds are originated from the fruit tissue or they are produced from microorganism, like yeast fermentation (Liu, Huang, & Lian, 2023). Most of the VOCs originate from the fruit tissue. For example, the major VOCs of ripe apples are esters and alcohols, accounting for 78–92 % and 6–16 %, respectively. Butyl acetate, hexyl acetate, hexan-1-ol, and butan-1-ol are also demonstrated as the dominant VOCs in ripe apple fruits (Dixon & Hewett, 2000; Setford et al., 2017; Yang et al., 2021). Minor VOCs such as ketones, aldehydes, and terpenoids have also been identified in ripe apple fruits. In the ripe pear (*Pyrus* spp.) fruit tissues, esters are detected as the major VOCs, accounting for 60–99 % of the total headspace vapors, followed by alcohols (1.5–4 % of total headspace vapors), primarily ethyl acetate, butyl acetate, nonan-1-ol, and heptan-1-ol. Moreover, minor VOCs like alkanes, ketones, aldehydes, and volatile acids have also been detected at the pear fruits (Chen et al., 2018).

### 2.1. Higher alcohols

Higher alcohols play a decisive role in shaping the flavor properties of AFBs. The major higher alcohols and their structural formulas are clearly shown in Fig. 2, including 2-methylpropan-1-ol, 4-methylpentan-1-ol, 2-methylbutan-2-ol, 3-methylbutan-1-ol, 2-phenylethanol, hexan-

1-ol, phenyl-1-methanol, and methylsulfanylpropan-1-ol. Previous study has demonstrated that the effect of higher alcohols on AFBs was highly dependent on the aromatic background. Among which, 3-methylbutan-1-ol and 2-methylpropan-1-ol were reported to contribute mostly to the aroma profiles, while methylsulfanylpropan-1-ol and 2-phenylethanol have also been demonstrated to show a less influence on the overall aroma profile (de-la-Fuente-Blanco et al., 2016). Some higher alcohols, such as 1-hexanol and 1-octanol, could strongly influence the aroma profiles of AFBs even with relatively low levels, whereas benzyl alcohol requires excessive higher concentrations to be perceived by human beings. Low concentrations ( $\leq 300$  mg/L) of higher alcohols could provide complex and pleasant aroma to the AFBs, whereas exceeded higher alcohols ( $>400$  mg/L) would ruin the overall sensory experience and even pose serious health risks to human beings (Tarko & Duda, 2024; Xu et al., 2025). Additionally, those branched chain amino acid derived higher alcohols usually contributes solvent or fusel odors, i. e., methionine derivative (3-methylthio-1-propanol) contributes boiled potato odors to AFBs (Cordente et al., 2021). The high levels of higher alcohols existed in the AFBs production could be achieved by controlled fermentation conditions, which helps in enhancing the overall quality of AFBs. For example, a constant fermentation temperature at 25 °C can be useful in increasing the contents of higher alcohols, as well as lowering the pH values of fermentation system further promotes the synthesis of higher alcohols (Tarko & Duda, 2024).

Ehrlich pathway (amino acid metabolism) and Harris pathway (monosaccharide metabolism) are the two major biosynthesis routes for higher alcohol production, with Harris pathway contributing approximately 75 % of the total yield. Detailed information of the Harris pathway is listed in Fig. 3, which synthesizes higher alcohols by first metabolizing sugars into pyruvate. Subsequently, pyruvate is found to interact with the amino acids to generate  $\alpha$ -keto acids, and this undergo the decarboxylation mechanism for improving the production levels of aldehydes. These aldehyde compounds are then reduced to yield the final higher alcohols. The Ehrlich synthesis pathway synthesizes higher alcohols by the deamination of amino acids into  $\alpha$ -keto acids, followed by their decarboxylation to form aldehydes (Gu et al., 2020). The production of higher alcohols can be affected by diversified factors,

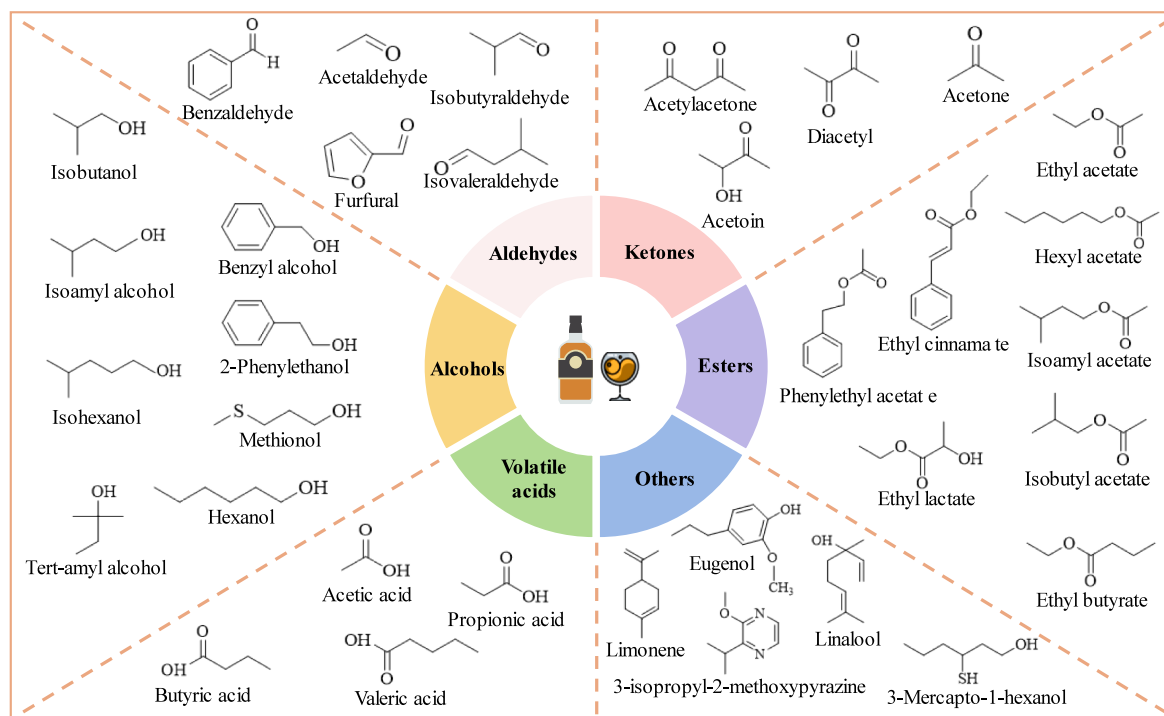
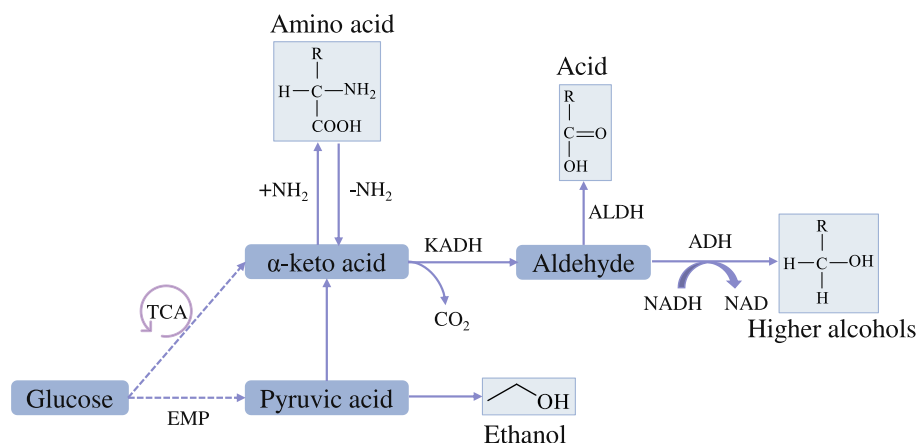


Fig. 2. Main volatile organic compounds in yeast fermented alcoholic fruit beverages.



**Fig. 3.** Metabolic pathway of higher alcohol biosynthesis during sugar fermentation and amino acid catabolism (TCA, tricarboxylic acid cycle; EMP, Embden Meyerhof Parnas pathway; KADH,  $\alpha$ -ketoglutarate dehydrogenase; ALDH, aldehyde dehydrogenase; ADH, alcohol dehydrogenase). Adapted from Hazelwood et al., 2008; Yan et al., 2022.

including yeast strain selections, YAN types, and carbohydrate concentrations in the fermentation substances (Hirst & Richter, 2016; Huang et al., 2023). Therefore, the optimization of yeast strains, nitrogen supply, and carbohydrate composition can effectively regulate the types and concentrations of higher alcohols and finally enhance organoleptic quality and safety. For example, insufficient nitrogen supply can prevent the metabolic conversion of keto acids to amino acids, thereby increasing the levels of higher alcohols during yeast fermentation process. Increasing the nitrogen supply could decrease the accumulation levels of higher alcohols, as most of keto acids would transfer into their corresponding amino acids (Klosowski et al., 2015). Importantly, higher alcohols serve as key aroma compounds and they are essential precursors for ester biosynthesis.

## 2.2. Esters

Esters are synthesized by the reaction between hydroxyl groups of alcohols/phenols and the carboxyl group of organic acids, represent one of the most significant classes of VOCs in AFBs (Ruiz et al., 2019). The most important ester compounds are listed clearly in Fig. 2. Among which, ethyl esters are the predominant compounds, which directly contributed to the fruity aroma profile of AFBs. Esters with relative low concentrations ( $\leq 100$  mg/L) usually give a desirable and fruity note to AFBs, however, excessive concentration may impart a nail varnish-like aroma (Sumbly et al., 2010). The characteristic fruity aroma of AFBs, especially prominent in the young wines, are predominantly attributed from the key ester classes, including ethyl esters of C4–C10 organic acids, ethyl esters of straight-chain fatty acids (C12–C18), and higher alcohol acetates (Tan et al., 2024). Notably, the sensory profile shifts with increasing hydrocarbon chain length of ester compounds. For example, a more soap-like flavor occurs at the length of hydrocarbon chain (C10, C12, and C14), the C16 and C18 fatty acid hydrocarbon chains would result in a lard-like note to AFBs.

The production of esters is highly influenced by a variety of factors, including fruit materials, fermentation processes, and environmental conditions (Ji et al., 2023). Only a small number of esters originate directly from fruit materials and present in the juice sample before beverage fermentation. And most of esters are formed via enzymatic esterification of higher alcohols together with organic acids (Liu, Huang, & Lian, 2023). It should be noted that the fermentation parameters affecting higher alcohol synthesis also modulate ester formation. Ester production is particularly sensitive to yeast-derived enzymatic activities, such as those of alcohol acetyltransferases, as well as to alcohol availability and intracellular acetyl-CoA levels (Valero et al., 2002). Some of the ester compositions change during the storage of AFBs,

mainly involving the esterification of branched-chain esters and hydrolysis of highly concentrated straight-chain esters (Rózański et al., 2020). In addition, microbial composition also significantly influences the ester production, with distinct yeast species exhibiting varied enzymatic capabilities for ester synthesis.

## 2.3. Aldehydes and ketones

Only low concentrations of aldehydes and ketones are presented in AFBs, but these compounds contain significantly low olfactory thresholds and play a significant role in the distinctive sensory profiles of AFBs. Aldehydes and ketones originate from the fruit juices, such as *n*-hexanal, 2-hexenal, 2-nonanone, and  $\beta$ -cyclocitral, which impart grassy and fruity notes (Abouelenein et al., 2023). However, the contents of aldehydes and ketones significantly changed during the fermentation of AFBs, which reduces the grassy note and harmonizes the flavor profile of AFBs (Lei et al., 2024). The dynamic changes of aldehydes and ketones during the fermentation and storage duration of alcoholic beverages significantly affect the overall quality of AFBs. For example, the concentrations of acetoin and benzaldehyde increase at the beginning of fermentation stage, and rapidly decrease during the storage period (Roustan & Sablayrolles, 2002). Furfural has been reported to further accumulate during storage, and enhance the sensory properties of AFBs (Song et al., 2017). Aldehydes are primarily derived from the amino acid transamination or decomposition pathways (Schober et al., 2023). The inherent reactivity of aldehydes is chemically more active due to the presence of carbonyl functional groups, which can be easily degraded into higher alcohols or oxidized into carboxylic acids. Most of the aldehydes, such as benzaldehyde, acetaldehyde, 2-methylpropanal, 3-methylbutanal, and furan-2-carbaldehyde, have relatively low thresholds and are important for the fresh aroma of AFBs. Acetaldehyde is one of the most important aldehydes during AFBs fermentation, with distinct green apple odor and significantly imparts to the freshness of AFBs. In contrast, benzaldehyde imparts distinct almond and cherry kernel notes, while furan-2-carbaldehyde often contributes to caramel or baked bread odors of AFBs (Chu & Yaylayan, 2008). These flavor compounds play a crucial role in shaping the complex aging characteristics of AFBs. Compared to aldehydes, ketones are much less abundant in AFBs, but still, these flavor compounds are important for the wine aroma profiles. Pentane-2,4-dione, butane-2,3-dione, propanone, and 3-hydroxy-2-butanone are the most commonly occurring ketones in AFBs (Geithe et al., 2017).

#### 2.4. Volatile acids

Volatile acids typically remain at low concentrations in the standard AFBs, and these compounds mainly originate from free volatile acids and their salt conjugates (Stanzer et al., 2023). The volatile acid concentration is primarily determined by the raw fruit materials used in the production, when the fresh and high-quality materials are employed, the resulted AFBs consequently exhibit lower volatile acid levels. Improper selection of temperature and pH values also affect the yeast fermentation and lead to high production of volatile acids in the AFBs (Giannattasio et al., 2013). Lencioni et al. (2018) has demonstrated that the mixed fermentation with both *Saccharomyces* and non-*Saccharomyces* yeast (*Z. florentina* and *Starm. bacillaris*) could significantly decrease the volatile acid contents in grape wines. Acetic acid is one of the most important volatile acids and the content of acetic acid is commonly used to determine the contamination status during the fermentation process. In a normal grape wine, the content of acetic acid usually varies from 0.2 to 0.6 g/L. The maximum acceptable limit for the volatile acidity in most of AFBs is settled as 1.2 g/L, and excessive quantities of volatile acids typically lead to a spoilage characteristic and unpleasant vinegar aroma to AFBs (Vilela-Moura et al., 2011). However, in some types of alcoholic beverages like ice wines, the maximum limitation of volatile acidity is 35 milliequivalents, which is equal to 2.1 g/L acetic acid (Zgardan et al., 2023).

#### 2.5. Other minor VOCs

In addition to the above-mentioned volatile compounds, terpenes and sulfur compounds are also commonly appeared in AFBs. Terpenes and sulfur compounds always show special aromatic and sensorial characteristics and represented as the primary sources of many strong odorants (Sánchez-Rodríguez et al., 2019). The formation of terpenes usually appear during the growth of fruit materials and fermentation process. However, the sulfur compounds are not naturally presented in the fruit materials, and they are always formed during the yeast fermentation process (Wedler et al., 2015). Volatile sulfur compounds are always divided into two major groups, including high volatile sulfurs (such as methyl mercaptan, ethyl mercaptan, and carbon disulfide) and low volatile sulfur compounds. The high volatile sulfur group is mainly synthesized during yeast fermentation through the assimilative reduction of sulfate, which is always associated with the undesirable odors like rotten eggs, onions, and garlic-like notes. The second group is known as “fruity volatile sulfur compounds”, which gives tropical fruit flavors to the AFBs, such as passion fruit and citrus-like notes (Duarte et al., 2010; Jiang & Zhang, 2018).

### 3. Influence of fruit materials on AFB quality

Still, the history of AFBs is relatively short unlike the grape wines, but these products are still gaining consistent popularity worldwide because of their pleasant taste (Gustavsen & Rickertsen, 2024). The overall quality of final AFBs is strongly affected by utilized fruit varieties, especially the bioactive nutrients and sensory profiles of fruit cultivars. Beverage and wine producers prefer to use the specialty fruit cultivars with optimal sugar levels and phenolic maturity to produce AFBs, such as specialty wine/beverage used grapes (Sabir et al., 2010). However, unlike the well-developed grape wine-making system, there are limited developed specialty fruit varieties with differential utilization, like fruit juice and alcoholic beverage production. Thus, researchers have been exploring alternative fruit approaches to produce AFBs with acceptable consumer preferences. In recent years, large amounts of fruit categories have been employed in AFBs production, including pome fruits (e.g., apple cider and pear wine), stone fruits (e.g., cherry wine and plum wine), citrus fruits (e.g., citrus wine), kiwifruits (e.g., kiwifruit wine), and tropical or exotic fruits (e.g., lychee, pineapple, and sweet melon wines). These fruit-based alcoholic beverages

exhibit distinctive sensory characteristics, thereby imparting more complex and unique flavor profiles to the modern fruit wines.

#### 3.1. Pome fruits

As two of the most economically important fruits in the *Rosaceae* family, apples and pears contain widely cultivation and highly consumption in the world. Apples are widely recognized for their health benefits and appealing taste, with the popular proverb “an apple a day keeps the doctor away” being embraced by the consumers. Similarly, pears are valued for their delicate peel, abundant juiciness, pleasing flavor properties, and high nutritional contents (Wei & Wang, 2013). The chemical composition and concentration of apples and pears vary among different cultivars and tissues. Flavonols represent the predominant class of phenolic compounds in most of apples and pears. A notable example is the apple cultivar ‘Hillwell’, a Braeburn clone, in which flavonols account for 51 % of the total phenolic contents (Carbone et al., 2011; Duralija et al., 2021). When compared with the white-fleshed apples or pears, those red-fleshed fruits exhibit significantly higher phenolic concentrations, particularly in anthocyanins and dihydrochalcones (Bars-Cortina et al., 2017; Galvis Sánchez et al., 2003). The synthesis of volatile metabolites continues until the fruit variety is fully ripened; overripe apples and pears contain higher volatile compounds whereas unripe fruits contain higher phenolic compounds in the fruit flesh (Hagen et al., 2007). The yeast fermented alcoholic beverages made from apples and pears contained clear fruity aroma and mild acidity with relatively low alcoholic contents.

#### 3.2. Stone fruits

Lychee (*Litchi chinensis*) is one of the most popular fruits worldwide, belongs to the family of *Sapindaceae*, which is commercially prized for its exotic fragrance, succulent aril, and nutritional values. Nowadays, lychee fruits are widely grown in several tropical and subtropical regions. Lychee exhibits notable bioactivities, including anti-inflammatory and antioxidant properties, while also provides high levels of organic acids, vitamin C, and soluble solids (Koul & Singh, 2017). Currently, fresh consumption remains the primary method of lychee utilization, mainly due to its heat sensitivity, seasonality, high sugar content, and short shelf-life. Fresh lychees are characterized by their vibrant, visually distinctive skin and translucent, sweet flesh. However, the bright color of lychee is highly perishable due to the post-harvest browning (polyphenol oxidation), rapidly deteriorating their appearance and market values (Passafiume et al., 2023). According to statistics, over 20 % of annual lychee production is lost to post-harvest rot and deterioration, which seriously restricts the production and development of lychee. The main lychee processing products existed in the market are lychee juice, dried lychee, lychee wine, canned lychee, and lychee vinegar. Among these, lychee wine is the most advantageous processed products in the lychee industry because of its exotic aroma, elevated sugar content, and low acid content (Pareek, 2016). The large amounts of flavonoid originated from the lychee fruits could significantly improve the blood circulation, potentially mitigating the arteriosclerosis and anti-aging effects (Anjum et al., 2017; Chen & Liu, 2016; Wu et al., 2023).

Cherry (*Prunus* spp.) is the smallest member of the stone fruit family, which comprises more than a hundred species that belonging to two distinct groups, sweet cherry and sour or tart cherry (Blando et al., 2004). The sweetness of cherry fruits mainly derives from glucose and fructose, while the acidity of cherry primarily originates from the presence of malic acid (organic acid). The sweet cherries contain higher amounts of monosaccharides than the sour cherries (13 g/100 g vs. 8 g/100 g) (Kim et al., 2005). Cherries contain both water-soluble vitamins (C and B) and fat-soluble vitamin compounds (A, E, and K) as well as some carotenoids, like  $\beta$ -carotene, lutein, and zeaxanthin. In addition, cherries contain high amounts of anthocyanins, including derivatives of

cyanidins, pelargonidins, and peonidins, which impart the charming red colors and nutritious functionality to the fruit wine products. Other phenolic compounds, like hydroxycinnamates, flavan-3-ols, and flavonols, have been also detected in several previous cherry research (Sun et al., 2011; Xiao et al., 2015; Yang et al., 2024). Among these phenolic compounds, *p*-coumaroylquinic acid and neochlorogenic acid are the predominant compounds appeared in both sweet and sour cherries (Blando & Oomah, 2019). These nutrient levels are highly affected by the maturity of different cultivars, the cultivation environment, and the harvest season, which play a crucial role in the fermentation performance and flavor of the final products in the fruit wine brewing.

### 3.3. Citrus fruits

Citrus fruits (*Citrus* spp.) are one of the most important fruit crops throughout the world, which is broadly planted in the tropical and subtropical areas. The annual output of citrus fruits is roughly 161.8 million tons (Pereira Gonzatto & Scherer Santos, 2023), including oranges, tangerines, and grapefruits. These fruits are widely processed into fruit juices, fruit wines, and fruit jams due to their distinctive bioactive substances, such as flavonoids, phenolic acids, carotenoids, and volatile essential oils with antioxidant, anti-inflammatory, and antibacterial activities (Bi et al., 2019; Gorinstein et al., 2001). The selection of citrus fruits is crucial for improving the sensory and nutritional values of the final processed products. As for the AFBs production, the inherent attributes, like pH value, sugars, soluble solids, titratable acidity, and vitamin C, were the principal factors for the final wine brewing (Belo et al., 2018). The abundant levels of volatile compounds like limonene and linalool play a vital role in the flavor hierarchy, which exhibit fresh, floral, and fruity notes to the citrus wines.

### 3.4. Kiwifruit

Kiwifruit (*Actinidia chinensis*) is well-known as the “King of Vitamin C” as it contains abundant concentrations of bioactive compounds, like carbohydrates, dietary fibers, vitamins, minerals, amino acids, polyphenols, and organic acids (Huang, Fan, et al., 2024; Richardson et al., 2018). The global kiwifruit cultivation gradually expanded during the last decades, mainly driven by the growing demand in the emerging markets. However, kiwifruit is highly sensitive to elevated temperatures and moist environments and spoils quickly (2–3 d) at room temperature (Rajan et al., 2024). Production of kiwifruit-based alcoholic beverages could significantly reduce the numbers of wasted edible kiwifruits by processing these fruits into value-added AFBs. However, previous studies have demonstrated that fermented kiwifruit wine was more prone to contain excessive high levels of higher alcohol compounds (Huang, Fan, et al., 2024). It is important to note that the quality of fruit material has an important influence on the aroma profiles of the kiwifruit wine, especially the higher alcoholic compositions. Gao et al. (2024) have investigated that the effects of fruit juice, fruit pulp, and pulp with skin fermentation on the aroma profiles of the final kiwifruit wines. The results demonstrated that the fruit pulp fermentation showed higher amounts of esters, aldehydes, and terpenoids in the final kiwifruit wines, whereas the peel pulp showed highest amounts of total VOCs, volatile acids, and ketones. The solid particles in the fermentation materials notably influenced the aroma and organoleptic quality, proper clarification process can reduce the turbidity and optimize the fermentation environment and resulted in lower amounts of higher alcohols, such as 3-methyl-1-butanol and 2-methyl-1-propanol (Marsili et al., 2025).

### 3.5. Tropical/exotic fruits

Pineapple (*Ananas comosus*) is the third most important tropical fruit with unique juiciness and tropical flavors after banana and citrus (Hossain, 2016). Most of the pineapple fruits are consumed fresh,

cooked, juiced as they are highly perishable and seasonal. Pineapple is rich in calcium, potassium, carbohydrate, crude fiber, vitamin C, and mineral as well as low fat and sodium, which are beneficial for the human digestion and balanced nutrition (Hossain et al., 2015). Pineapple is an ideal ingredient for fruit wine brewing as it contains moderate amounts of sugars and organic acids, strong aroma complexity, and high nutritional values. The moderate sugars and organic acids could effectively support the stability of fermentation system, which helps to avoid the bacterial contamination (Boondaeng et al., 2022). The unique aroma in the pineapple fruit is mainly derived from esters (ethyl acetate and ethyl butyrate), terpenes (linalool and  $\alpha$ -terpineol), and sulfur-containing compounds (methanethiol) (Dellacassa et al., 2017).

Sweet melon (*Cucumis melo*) is a member of the *Cucurbitaceae* family, which is cultivated worldwide because of its wide adaptability to differential soil types and temperature ranges, and they are highly prized for the sweetness, fragrance, and pulp consistency. There existed various melon botanical varieties based on the different morphological, physiological, and organoleptic properties. Sweet melon contains over 90 % water and is also rich in phytochemicals, and fermentation of sweet melon wine could solve the contamination problems during sweet melon transportation. *S. cerevisiae* has been applied to ferment melon wine with supplemented sucrose and organic acids to obtain a dry melon-based wine with strong fruity notes and an alcohol content of 10 % vol, which was documented by Salas-Millán et al. (2022). A notable feature of melon-based alcoholic wines is the abundant levels of fatty acid ethyl esters together with satisfactory sensory tastes, which presents as the primary volatile compounds.

## 4. Role of yeast strains in fermentation and flavor development

Historically, the AFBs was fermented through a spontaneous process driven by a diverse community of indigenous microorganism with different *Saccharomyces* and non-*Saccharomyces* yeasts. The quality of AFBs can be enhanced by applying controlled fermentation technology, where the application of *S. cerevisiae* was introduced and widely accepted at the beginning of 1970s. From 1980s, wine-makers started to investigate and analyze the positive effect of other *Saccharomyces* and non-*Saccharomyces* yeast strains and their application in fruit wine making. The researchers found that the utilization of these yeasts could provide an increased aroma complexity with proper inoculation and fermentation status, both with single and mixed inoculations. However, the other *Saccharomyces* and non-*Saccharomyces* yeasts contained poor fermentation ability together with a slower fermentation rate and a lower tolerance to the extreme environments compared with *S. cerevisiae*. Thus, it is crucial to select correct yeast strains in the innovative fermentation and thus the quality of AFBs can be optimally improved, including the stability, freshness and organoleptic quality of AFBs (Morata et al., 2023). It should be noticed that the yeast role is to convert the sugars into ethanol and other metabolites, and the suitable yeast selection should follow the next criteria. First, yeast should increase the aroma complexity by producing esters and higher alcohols; second, enhance the contents of polyalcohols, such as glycerol and 2, 3-butanediol, and release more polysaccharides and mannoproteins. Then, the yeast should not degrade the phenolic compounds existed in the fruit tissue, and help increase the stability of phenolic compounds by stabilizing the colloidal compounds in AFBs.

### 4.1. *Saccharomyces cerevisiae*

*S. cerevisiae* are ascosporogenous yeasts and largely utilized in the commercial wine fermentations. *S. cerevisiae* strains have a strong fermentative power under harsh environment conditions, for example, low pH values, low oxygen availability, high ethanol concentration, and high sulfur dioxide concentration (Da Silva Fernandes et al., 2022). Simultaneously, *S. cerevisiae* dominated in the later stages of fermentation as it contains strong sugar metabolism ability, high cell density, and



**Table 1**Effects of *Saccharomyces* yeast strains on the volatile organic compounds (VOCs) of alcoholic apple and pear beverages.

Yeast species	Products	Fermentation type <sup>a</sup>	Main effects on the volatile organic compounds (VOCs) <sup>b</sup>	Practical Implication	References
<i>Saccharomyces bayanus</i>	Apple cider	Pure	Free hydroxycinnamic acids†	Enhance oxidative stability and adds structural bitterness	Laaksonen et al. (2017)
	Apple wine	Pure	Malic acid†, carbonyl compounds†	Promote sensory freshness and complex oxidative notes	Satora et al. (2018)
	Apple wine	SimF SC	Ethanol†, methanol†, volatile esters†, volatile acids†	Strengthen overall aroma intensity and body thickness	Satora et al. (2018)
	Apple wine	Pure	Hexanoic acid†, octanoic acid†	Develop characteristic creamy and waxy notes	Liu et al., 2022
	Apple wine	SeqF TD	Ester†, ethyl esters†	Significantly intensify fruity bouquet perception	Liu et al., 2022
<i>Saccharomyces capensis</i>	Apple wine	Pure	Ethyl acetate†, isobutyl acetate†, acetaldehyde↓, isobutanol†, amyl alcohols†.	Reduce oxidative off-flavors and increases fruity complexity	Satora et al. (2016)
<i>Saccharomyces cerevisiae</i>	Apple wine	Pure	Acetaldehyde†	Provide fresh green apple traits or sherry-like notes	Lorenc et al., 2025; Satora et al., 2016
	Apple cider	Pure	Ethyl acetate†, higher alcohols†, acetic acid†	Increase brewing complexity but requires solvent-note control	He et al. (2021)
	Pear cider	Pure	Volatile acids†, ethyl ester†	Enhance flavor persistence and perceived acidity	Zhang et al. (2024)
<i>Saccharomyces paradoxus</i>	Pear cider	SimF SB	Acetaldehyde↓, diacetyl↓, 1-propanol†, 3-methyl-1-butanol↓	Eliminate unpleasant buttery off-odors for a cleaner profile	Guerrini et al. (2023)
	Apple wine	Pure	Volatile acidity↓	Prevent vinegar spoilage and enhances mouthfeel purity	Satora et al. (2018)
	Apple wine	Pure	Isobutanol↓, amyl alcohols↓.	Mitigate chemical-like roughness and highlights natural fruit	Satora et al. (2016)
<i>Saccharomyces uvarum</i>	Apple wine	SimF SC	Ethanol†, methanol†, volatile esters†, volatile acids†	Maximize alcohol yield and enriches aromatic breadth	Satora et al. (2018)
	Apple cider	Pure	2-Phenylethanol†	Impart elegant rose and honey floral notes	Lorenzini et al. (2019)

<sup>a</sup> SimF SC: simultaneous fermentation with *Saccharomyces cerevisiae*, SeqF TD: sequential fermentation with *Torulaspora delbrueckii*, SimF SB: simultaneous fermentation with *Starmerella bacillaris*.

<sup>b</sup> Compared to unfermented: † increase; ‡ decrease; VOCs: volatile organic compounds.

notes to the final fermented products (Lukić et al., 2024). *S. paradoxus* can produce more glycerol when compared with *S. cerevisiae*, however, the AFBs fermented by *S. paradoxus* has shown lower ethanol and acetic acid contents (Orlić et al., 2010).

*S. bayanus* is another hybrid yeast of *S. cerevisiae*, *S. eubayanus*, and *S. uvarum* that are commonly utilized in AFBs (Ono et al., 2020). The unique Lg-ATF1 gene exists in *S. bayanus* could enhance the synthesize ability of acetate esters in cold environment as it encodes the alcohol acetyltransferase with broader specificity for higher alcohol substrates when compared with *S. cerevisiae* (Verstrepen et al., 2003). The optimal growth temperature of *S. bayanus* ranges from 10 °C to 21 °C. It can ferment melibiose but not lactose or starch. Pogorzelski et al. (2007) reported that the pure fermentation of *S. bayanus* in pear AFB was able to result in high levels of ethanol with a value at 16.5 %vol. High amounts of glycerol, succinic acid, and malic acid were also produced in this pear alcoholic beverage when compared with alcoholic beverages fermented with *S. cerevisiae*. *S. bayanus* was able to enhance the amounts of malic acid and carbonyl compounds, as reported by Satora et al. (2018). Gamero et al. (2014) reported that *S. bayanus* fermentation could synthesize high levels of esters (ethyl lactate, 2-phenylethyl acetate, and some other acetate esters) but low levels of higher alcohols (2-methyl-1-propanol, 3-methyl-1-butanol, and normal amyl alcohol). Januszek et al. (2020) demonstrated that fermentation of *S. bayanus* provide high levels of acetate esters except for ethyl acetate. The spontaneous fermentation of *S. bayanus* and *S. cerevisiae* can result in more acetaldehyde and fusel alcohols. It should be noted that the methanol was also found at a high level when compared with the single fermentation of *S. cerevisiae*. This can be resulted from the high activity of  $\beta$ -glucosidase existed in the *S. bayanus*, and thus, more VOCs in glycosidic forms released. Co-fermentation of *S. bayanus* and other non-conventional yeasts can also improve the esters and reduce the volatile acids when compared with the single fermentation of *S. bayanus*.

*S. bayanus* var. *uvarum* is another well-characterized member in the genus *Saccharomyces* and often recognized as *S. uvarum*. *S. uvarum*

produces extremely low volatile acidity under low-temperature fermentation by preferentially directing acetyl-CoA towards the biosynthesis of medium-chain fatty acids to maintain membrane fluidity rather than converting into acetic acid (Coral-Medina et al., 2022). *S. uvarum* has the capacity to ferment glucose, sucrose, melibiose, and maltose, but it is unable to ferment lactose (Almeida et al., 2014; Pogorzelski et al., 2007). In comparison to *S. cerevisiae*, the inoculation of *S. uvarum* in grape wines led to a decrease in the contents of acetic acid and increase the contents of glycerol and succinic acid (Masneuf-Pomarède et al., 2010). Similar with *S. bayanus*, the application of *S. uvarum* in alcoholic apple beverages could lead to high amounts of acetate esters. Notably, the inoculation of *S. uvarum* could also increase the levels of higher alcohols (Lorenzini et al., 2019).

#### 4.3. Non-Saccharomyces yeast

The non-*Saccharomyces* yeasts are also largely utilized in the fermentation of AFBs, such as *C. zemplinina*, *H. osmophila*, *H. uvarum*, *K. marxianus*, *M. pulcherrima*, *L. thermotolerans*, *P. membranaefaciens*, *P. kluyveri*, *Starm. bacillaris*, *Schizo. pombe*, *T. delbrueckii*, *T. quercuum*, *Z. bailii*, and *Z. rouxii* (Bruner & Fox, 2020). The effects of representative non-*Saccharomyces* yeasts on VOCs in apple wines and pear wines are summarized in Table 2. Furthermore, a broader overview of yeast strain-dependent modulation of VOC profiles across different alcoholic fruit beverages is provided in Table 3.

*C. zemplinina* is a prominent non-*Saccharomyces* yeast species extensively utilized in the processes of AFBs, and its growth dynamics and persistence during fermentation are highly affected by the multiple environmental and biochemical factors, like temperature, pH, ethanol contents, sulfur dioxide levels, and nutrient availability. This yeast is firstly isolated from grape must with abundant sugar contents, like ripe grape, overripe grape, and cooked grapes, as well as in botrytized grape must. Mills et al. (2002) found that the utilization of *C. zemplinina* in the fermentation of sweet grape wine led to similar glycerol and acetic acid

**Table 2**Effects of non-*Saccharomyces* yeasts on the volatile organic compounds (VOCs) of alcoholic apple and pear beverages.

Yeast species	Products	Fermentation type <sup>a</sup>	Main effects on the volatile organic compounds (VOCs) <sup>b</sup>	Practical Implication	References
<i>Candida zemplinina</i>	Pear wine	Pure	VOCs↓	Suitable for neutral base wines to maintain raw material purity	Wei et al. (2019)
<i>Hanseniaspora osmophila</i>	Apple cider	Pure	Volatile acids↓, acetate esters↓, benzyl alcohol↑	Reduce pungency and increases sweet floral layers	Lorenzini et al. (2019)
<i>Hanseniaspora uvarum</i>	Apple cider	Pure	Hexyl acetate↑, isoamyl acetate↑	Intensify typical banana and pear sweet aromas	Lorenzini et al. (2019)
	Apple wine	Pure	Acetic acid↑, VOCs↓	Carry high spoilage risk with potential vinegar taint	Wei et al. (2019)
<i>Kluyveromyces marxianus</i>	Apple cider	Pure	Ethanol↓, ethyl acetate↑	Develop low-alcohol products with enhanced fruity esters	Gschaedler, 2017; Reina-Posso and Gonzales-Zubiate, 2025
<i>Lachancea thermotolerans</i>	Apple cider	Pure	Ethanol↓, higher alcohols↓	Produce clean, light-style beverages with low fusel oil	Fejzullahu et al. (2021)
	Apple cider	SimF SC	Higher alcohols↓, esters↑	Optimize ester-to-alcohol ratio for better balance	Fejzullahu et al. (2021)
	Apple cider	SimF TD&SC	Ethanol↓, acetaldehyde↑, higher alcohols↓	Achieve bioacidification and mitigate climate-driven low acidity	Fejzullahu et al. (2021)
<i>Metschnikowia pulcherrima</i>	Pear wine	SeqF SC	VOCs↑, esters↑, fatty acids↓	Enrich floral notes and provide bio-protection	Yang et al. (2022)
	Apple-pear blended wine	SeqF SC	VOCs↑, ethyl esters↑, higher alcohol↑	Maximize aromatic complexity in blended products	Yang et al. (2022)
<i>Pichia kluyveri</i>	Apple wine	Pure	Ethanol↓, VOCs↑, acetate esters↑	Reinforce tropical fruit character without alcohol burden	Wei et al. (2019)
	Apple cider	Pure	Hexyl acetate↑, low ethanol↓, ethyl acetate↑	Provide bright green-fruit traits like pear skin	Gschaedler (2017)
	Apple cider	SimF HU	Ethanol↓, acetic acid↑, VOCs↑, acetate esters↑	Strengthen tropical traits and balances low-alcohol feel, requiring strict volatile acid control	Wei et al. (2020)
<i>Pichia membranaefaciens</i>	Apple cider	Pure	Ethanol↓, VOCs↑	Suitable for niche low-alcohol craft cider markets	Gschaedler (2017)
<i>Schizosaccharomyces pombe</i>	Apple cider	Pure	Ethyl esters↓, higher alcohols↓, volatile acids↓	Facilitate complete biological deacidification for high-acid musts	He et al. (2021)
	Apple wine	Pure	Esters↑, acetic acid↑	Enhance body thickness via polysaccharide release, but pose high vinegar spoilage	Satora et al. (2018)
	Apple wine	SimF SC	Ethanol↑, methanol↑, volatile esters↑, volatile acids↑	Increase aroma concentration while ensuring high alcohol content, monitoring methanol safety	Satora et al., 2018; Ferreiri Leali et al., 2024
<i>Starmerella bacillaris</i>	Apple cider	Pure	Ethanol↓, volatile acids↓, acetate esters↓, benzyl alcohol↑	Soften acidity and boosts sweet almond-like floral note	Lorenzini et al. (2019)
<i>Torulaspora delbrueckii</i>	Pear cider	SeqF SC	Ethyl acetate↓, 1-butanol↑	Improve mouthfeel and aromatic purity	Guerrini et al. (2023)
	Apple cider	Pure	Ethanol↓, acetaldehyde↑, higher alcohols↓	Use low acetic acid yield traits to improve high-end cider fermentation purity	Fejzullahu et al. (2021)
	Apple cider	Pure	Sorbitol↑, ethanol↓, benzyl alcohol↑	Increase perceived sweetness and mouthfeel viscosity	Lorenzini et al., 2019; Klimczak et al., 2024
	Apple cider	SimF SC	Volatile acidity↓, ethanol↓, higher alcohols↓, esters↑	Balance fermentation intensity and aroma synthesis, reducing harshness from acetic acid accumulation	Fejzullahu et al. (2021)
	Pear wine	Pure	Ethyl hexanoate↑, ethyl decanoate↑, ethyl 9-decenoate↑	Strengthen "ripe fruit" and "intense fruitiness" traits, upgrading pear wine quality	Liu et al. (2022)
	Pear wine	Pure	Ethanol↑	Demonstrate excellent sugar tolerance and conversion for high-gravity systems	Wei et al., 2019; Martínez et al., 2024
	Pear wine	SeqF SC	VOCs↑, esters↑	Enhance complexity and aftertaste through extracellular enzyme-mediated precursor release	Yang et al. (2022)
	Apple-blended	SeqF SC	VOCs↑, esters↑	Improve overall harmony of blends with full floral and fruity aromatic layers	Yang et al. (2022)
<i>Torulaspora quercuum</i>	Apple cider	Pure	Ethanol↑	Provide solid alcohol framework for high-typicality traditional dry ciders	Wei et al. (2019)
<i>Zygosaccharomyces bailii</i>	Apple cider	Pure	Ethanol↓, volatile acids↓, acetate esters↓, benzyl alcohol↑	Impart unique herbal or sweet traits and enhances bio-stability	Lorenzini et al. (2019)
	Pear cider	Pure	Alcohol↑, Aldehydes↓, acetic esters↓	Produce smooth-tasting pear wine with low off-flavor risk	Zhang et al. (2024)
<i>Zygosaccharomyces rouxii</i>	Apple cider	Pure	Ethanol↓, ethyl acetate↑	Suitable for low-alcohol beverages with stable aroma	Gschaedler, 2017; Ren et al., 2025
	Pear cider	Pure	Isobutanol↑, isoamylol↑, 2-methylbutan-1-ol↑, hexanol↑, phenethyl alcohol↑, volatile acids↑	Strengthen body thickness	Zhang et al. (2024)

<sup>a</sup> SimF SC: simultaneous fermentation with *Saccharomyces cerevisiae*, SimF HU: simultaneous fermentation with *Hanseniaspora uvarum*, SimF TD & SC: simultaneous fermentation with *Saccharomyces cerevisiae* and *Torulaspora delbrueckii*, SeqF SC: sequential fermentation with *Saccharomyces cerevisiae*.

<sup>b</sup> Compared to unfermented: ↑ increase; ↓ decrease; VOCs: volatile organic compounds.

**Table 3**  
Effects of yeast strains on the volatile organic compounds (VOCs) of AFBs.

Products	Yeast species	Fermentation type <sup>a</sup>	Main effects on the volatile organic compounds (VOCs) <sup>b</sup>	Practical Implication	References
Stone fruits					
Cherry wine	<i>Saccharomyces cerevisiae</i>	Pure	Acetic acid↑, 3-methylbutanol↑	Support a robust fermented aroma skeleton	Qi et al., 2026; Sun et al., 2011
Lychee wine	<i>Saccharomyces boulardii</i>	Pure	Ethanol↑	Enable the development of functional probiotic fruit beverages with enhanced health benefits	Terhaag et al. (2025)
	<i>Saccharomyces cerevisiae</i>	Pure	Ethyl octanoate↑, ethyl decanoate↑, ethyl acetate↑, ethyl hexanoate↑, isoamyl acetate↑	Precisely target typical tropical lychee aromas to ensure product varietal identity	Chen & Liu, 2014; Chen, Zhu, et al., 2025
Plum wine	<i>Saccharomyces cerevisiae</i>	SimF MLF	Ethyl lactate↑	Soften sharp acidity for a creamy, smooth finish	Chen and Liu (2016)
	<i>Saccharomyces cerevisiae</i>	SimF MP	Phenethyl alcohol↑, 5-methyl-hexanol↓, terpenes↑, phenylacetaldehyde↓	Significantly enhance elegant rose-like floral notes	Zhang et al. (2022)
<b>Citrus Fruits</b>					
Citrus wine	<i>Saccharomyces cerevisiae</i>	SimF TD	Higher alcohol↑, acetate↑, terpene↑, volatile fatty acids↓	Intensify citrus brightness while removing cheesy off-odors	Hu et al. (2020)
<b>Kiwifruit Fruits</b>					
Kiwifruit wine	<i>Pichia kudriavzevii</i>	SeqF SC	Ethyl octanoate↑, ethyl decanoate↑, ethyl 9-decanoate↑	Enhance tropical kiwi and passion fruit character, strengthening sensory identity	Sun et al. (2024)
<b>Tropical/Exotic Fruits</b>					
Pineapple wine	<i>Brettanomyces bruxellensis</i>	Pure	Ethyl butyrate↑	Reinforce characteristic fresh pineapple pulp aroma	Almeida dos Anjos et al. (2024)
	<i>Brettanomyces lambicus</i>	Pure	Hydroxyphenylethanol↑	Add phenolic complexity and enhance mouthfeel thickness	Almeida dos Anjos et al. (2024)
	<i>Saccharomyces cerevisiae</i>	Pure	Isoamyl acetate↑, ethyl butyrate↑	Produce typical candy-like flavors for high drink ability	Almeida dos Anjos et al. (2024)
Sweet melon wine	<i>Saccharomyces cerevisiae</i>	Pure	Esters↑, alcohols↑, aldehydes↓	Upcycle melon into high-value fruity dry wine	Salas-Millán et al. (2022)

<sup>a</sup> SeqF SC: sequential fermentation with *Saccharomyces cerevisiae*, SimF TD: simultaneous fermentation with *Torulaspora delbrueckii*, SimF MLF: simultaneous fermentation with *Oenococcus oeni*, SimF MP: simultaneous fermentation with *Metschnikowia pulcherrima*.

<sup>b</sup> Compared to unfermented: ↑ increase; ↓ decrease; VOCs: volatile organic compounds.

production when compared with *S. cerevisiae*. Notably, the fermentation of *C. zemplinina* showed relatively weak ethanol generation ability and showed high levels of acetic acid, glycerol, and volatile compounds production. The utilization of this non-*Saccharomyces* yeast was demonstrated to be more involved in the flavor formation and diversity establishment (esters and higher alcohols) during the natural wine fermentation processes rather than enhancing the alcohol contents (Magyar & Tóth, 2011). In this case, *C. zemplinina* is increasingly recognized as a key microbial resource in the modern enology, particularly for crafting AFBs with distinctive aromatic complexity and moderate alcohol contents. Hong et al. (2021) found that the ice wines made from co-fermentation with *C. zemplinina* and *S. cerevisiae* showed high levels of glycerol and ethyl esters when compared with the single yeast inoculation of *S. cerevisiae*.

The *Hanseniaspora* spp., originating from the mature grape surfaces, are particularly important during the early fermentation stages, and it could be also found in the orchard soil, wine cellars, and harvesting machinery. Owing to the abundant secretion of enzymes and aroma compounds, *H. spp.* are widely utilized in the winemaking for their roles in boosting the aromatic complexity and enhancing the wine structure. For example, *H. guiliermondii* and *H. vineae* are particularly notable for producing large amounts of  $\beta$ -phenylethyl acetate esters, contributing fruity and floral notes in AFBs. The utilization of *H. uvarum* and *H. guiliermondii* also contributes in the production of sulfur-containing aromatic compounds during the fermentation of AFBs. The metabolic success of *H. spp.* in enhancing aromatic complexity is driven by a robust extracellular enzymatic profile and unique genetic features, such as the *EatH* (ethanol acetyltransferase from *H. uvarum*) gene, which encodes an alcohol acetyltransferase involved in the efficient synthesis of acetate esters (Ni et al., 2025). The co-fermentation of *S. cerevisiae* and *H. spp.* could enhance the flavor complexity and sensory acceptability according to the previous reports (Martin et al., 2018). Other yeast species belongs to the *H. spp.*, such as *H. osmophila* and *H. uvarum*, have been reported to increase the ethyl acetate contents and improve the overall quality of AFBs by single inoculation or co-inoculation with other yeast

species (Delgado et al., 2021; Liu et al., 2020).

Compared with the traditional wine brewing yeasts, *K. marxianus* was reported to possess a series of unique physiological and metabolic characteristics that confer significant potential for the application of industrial biotechnology. Most of the *K. marxianus* strains exhibit Crabtree negativity and prefer aerobic respiration over anaerobic ethanol fermentation, which helps in reducing the formation of byproduct ethanol and thereby enhancing the yield of target metabolites. The application of *K. marxianus* exhibits high tolerance to high temperatures (>40 °C), rapid growth speed, and contains large ability to utilize diverse carbon sources, like lactose and inulin, has been widely used in the pharmaceutical, food, and feed sectors, serving as a significant supplement and alternative to traditional *Saccharomyces* yeasts (Karim et al., 2020). However, its metabolic and aroma related performance varies considerably among strains and is strongly influenced by fermentation conditions, as differences in oxygen availability, temperature, and carbon source can shift the balance between respiratory and fermentative metabolism, leading to different ethanol and volatile compound profiles among studies (Lane & Morrissey, 2010).

*L. thermotolerans* has attracted significant attention in the recent years for its unique metabolic abilities in wine making, especially for its pH lowering and acidity enhancement ability (Vicente et al., 2025). *L. thermotolerans* is commonly separated from the fruit peels such as grapes and typically appeared during the early stages of fermentation period. The inoculation of *L. thermotolerans* helps in producing high levels of lactic acid (1–9 g/L), which imparts a fresh palate to the AFBs and slightly reduce (approximately 0.5–1 %vol) the alcoholic contents in the final alcoholic beverages (Vilela, 2018). Among the commercial yeasts, *L. thermotolerans* has been regarded as the most promising bio-acidifying yeast species in wine brewing, particularly for its ethanol reduction capacity, glutathione and polysaccharide production, color enhancement and aroma enhancement capacity. These findings provide a foundation for breeding strains with comprehensively enhanced performance, facilitating the development of commercial strains capable of independently completing medium-alcohol fermentation and adapting

to diverse winemaking objectives. The co-fermentation of *L. thermotolerans* and other non-*Saccharomyces* yeasts and lactic acid bacteria could significantly reduce the fermentation period and improving the acetic acid control, color stability, and flavor expression (Vicente, Navascués, et al., 2021). *M. plucherrima* exhibits remarkable versatility, capable of co-fermenting with other yeast strains to regulate the synthesis of secondary metabolite and enhance flavor profiles, as well as exhibits strong enzymatic activity and significant bio-control potential (Morata et al., 2019). However, the single inoculation of *M. plucherrima* would lead to excessive production of ethyl acetate and negative sensory effects, and the co-inoculation of *M. pulcherrima* and *S. uvarum* reduced the ethyl acetate and increased the formation of 2-phenylethanol and 2-phenylethyl acetate. The high enzymatic activities, like  $\beta$ -D-glucosidase and cysteine  $\beta$ -lyase, could help in promoting the release of aromatic precursors and producing higher amounts of esters and higher alcohols during alcoholic fermentation (Puyo et al., 2023). Testa et al. (2024) has demonstrated that the inoculation of *M. pulcherrima* could suppress the harmful microorganisms in grape juices and reduce the utilization of sulfur dioxide, and its promotion of multiple enzymatic activities, like polygalacturonase,  $\beta$ -glucosidase,  $\beta$ -endosidase, and protease, which helps in production of higher amounts of wine aroma and clarity (Bene et al., 2025).

The *Pichia* genus is a group of non-*Saccharomyces* yeasts that has been widely applied to improve VOCs during AFBs fermentation (Wang et al., 2024). For example, *P. kluyveri* is widely recognized as a non-*Saccharomyces* yeast species with significant aromatic potential, capable of producing abundant amounts of flavor components, such as esters, aldehydes, and thiols, which significantly enhanced the fruitiness and flavor complexity of AFBs (Méndez-Zamora et al., 2021). *P. kluyveri* demonstrated good potential for enhancing the wine flavor quality by increasing the thiols, fruity esters, and terpenes, as well as decreasing the hexanol contents (Mazzucco et al., 2025). Whereas *P. membranaefaciens* has been demonstrated to have the potential to enhance the varietal aroma and polysaccharide accumulation at approximately 140 % higher than the controlled *S. cerevisiae* fermentation, it could also reduce the ethanol contents and increase the acetic acid levels (Vicente, Navascués, et al., 2021).

The *Schizo.* spp. has been reported to ferment and produce high ethanol concentrations at approximately 15 %vol, and the content is mainly dependent on the yeast strain. Additionally, with supplemental magnesium nutrients, the alcoholic contents of AFBs can be high at 20 % vol. Moreover, the inoculation of *Schizo.* spp. is able to ferment the malic acid from 50 % to 100 % (Benito, 2020). The physiological success of these species of high-acid fruits is mainly driven by the active malate transport system together with a cytosolic malic enzyme that enables the efficient malo-alcoholic fermentation. More co-fermentation strategies with *Schizo.* spp. and other yeasts are always needed to solve the excessive acetic acid production in AFBs (Lyu et al., 2024; Zhang et al., 2025). Among the *Schizo.* spp., *Schizo. pombe* exhibit multiple promising enological characteristics during the fermentation of alcoholic beverages, by promoting the synthesis of glucosamine, releasing cell wall polysaccharides, which helps shorten the fermentation time, improve the mouthfeel and color stability. The fermentation rate of *Schizo. pombe* is relatively slow and may introduce certain typical aroma compounds. However, the impact of *Schizo. pombe* on volatile compound formation, particularly ester and higher alcohol profiles, often shows variability across studies, which can be largely attributed to differences in strain selection and fermentation regimes, including nutrient availability, inoculation strategy, and microbial interactions (Paramithiotis et al., 2025). It should also be noted that the undesirable byproducts can be effectively mitigated through the immobilization techniques and sequential fermentation strategies. Thus, the application of *Schizo. pombe* can be used in replacing malolactic fermentation and enhancing the structures of pigments and polyphenols (Loira et al., 2018).

*Starm. bacillaris* has garnered significant attention in the recent years for its unique brewing potential, which exhibits strong fruity affinity and

cold tolerance. Lemos Junior et al., 2019 has investigated that *Starm. bacillaris* yielded low ethanol, high glycerol, and moderate volatile acid. Metabolically, the low ethanol yield of *Starm. bacillaris* is driven by the high carbon flux toward the glycerol pathway, facilitated by the tandem duplication of the GPP1 gene and the absence of regulatory kinases (Ypk1p/Ypk2p) that normally inhibit GPD activity. In addition, its Crabtree-negative respiratory metabolism allows substantial sugar dissipation under early aeration conditions, further limiting ethanol accumulation (Canonico et al., 2025; Lemos Junior et al., 2018). Previous study has demonstrated that the sequential fermentation of *Starm. bacillaris* and *S. cerevisiae* could significantly enhanced the aroma complexity and sensory properties, which amplified sensory attributes like floral, fruity, and caramel notes (Li et al., 2023). Englezos et al. (2017) indicated that the sequential fermentation of *Starm. bacillaris* and *S. cerevisiae* could significantly reduce the ethanol contents by 0.5–0.9 % vol and increase the glycerol and titratable acidity levels. The co-inoculation of *Starm. bacillaris* could reduce the undesirable byproducts and enhance the wine sensory quality (Listur et al., 2025).

*T. delbrueckii* has been reported to show unique advantages in reducing ethanol contents, increasing glycerol levels, and enhancing flavor complexity, which is particularly suitable for addressing the high alcohol risk associated with high-sugar fruits. The sequential fermentation of *T. delbrueckii* and *S. cerevisiae* has been reported to slightly reduce the ethanol contents, typically by 0.15–0.50 %vol. This is mainly due to the fermentation limitation of *T. delbrueckii*, and larger reductions of alcoholic contents are always associated with the incomplete fermentation of the residual sugars. The sequential fermentation treatment of *T. delbrueckii* and *S. cerevisiae* was also correlated with the increase of ethyl esters, like ethyl propionate, ethyl isobutyrate, and ethyl dihydrocinnamate (Benito, 2018). Additionally, this co-inoculation treatment was able to significantly improve the floral notes, freshness, wine structure as well as imparting distinctive sensory characteristics. However, it should be noted that *T. delbrueckii* strains exhibit pronounced intraspecific variability in volatile compound production and fermentative behavior, as well as the differences in genotype and fermentation conditions such as nutrient availability and temperature can result in markedly different ester, higher alcohol, and organic acid profiles across studies (Silva-Sousa et al., 2024). *T. delbrueckii* exhibits lower tolerance to high-ethanol environments, and this yeast strain always dominated in the early fermentation stages and required synergistic usage with more resilient yeast strains during the later stages until complete fermentation. Such strain-dependent behavior has also been observed under varying nitrogen levels and environmental stresses, highlighting that fermentation conditions strongly modulate volatile compound production and aroma profiles in *T. delbrueckii* (Mecca et al., 2020). This yeast species has been demonstrated to have promising applications in beer, mezcals, and cider, where it can significantly enhance the production of various aromatic compounds, such as esters and terpenes, to intensify the fruitiness and aroma complexity. The promising application of *T. delbrueckii* as important yeast strains in the production of diverse alcoholic beverages has been widely studied (Fernandes et al., 2021).

*Z. spp.* are always regarded as spoilage yeast in the AFBs due to their potential to lead to secondary fermentation and produce carbon dioxide during fermentation. However, the robust survival capabilities under extreme conditions like high ethanol, low oxygen, and high osmotic pressure also provide advantages for the potential of producing sparkling wines (Escott et al., 2018). From a metabolic and physiological perspective, the success or failure of specific yeast–fruit fermentation often reflect the intrinsic traits of the yeasts and their capacity to adapt to the unique stressors of the fruit matrix. *Z. spp.* exhibit exceptional tolerance to high ethanol concentrations, osmotic pressure, and weak acids, allowing them to persist and actively metabolize sugars in challenging fruit fermentation environments (Alcalá-Jiménez et al., 2025). The most famous *Z. spp.* are *Z. bailii* and *Z. rouxii*. Compared with *S. cerevisiae*, *Z. bailii* exhibits superior acid tolerance and is capable of

growing under relatively low pH conditions, thus, *Z. bailii* is always regarded as an ideal yeast for lactic acid production during AFBs fermentation. For example, the engineered *Z. bailii* can accumulate up to 35 g/L of lactic acid without ethanol production. *Z. rouxii* exhibits good ability of malic acid synthesis, and it could produce abundant amounts of organic acid under aerobic conditions (Solieri, 2021). Furthermore, previous studies indicated that the co-inoculation of *Z. rouxii* with *S. cerevisiae* fermentation showed minimal impact on the growth of *S. cerevisiae*, which could induce the upregulation of glycolytic genes and lead to the accumulation of stress-related polysaccharides like trehalose and glycogen. These metabolic responses indicated that *Z. bailii* showed good potential of alcohol reduction as well as enhance wine structure and flavor expression (Capece et al., 2022). The co-fermentation of *Z. bailii* and *H. opuntiae* showed stronger acetate generation ability when compared with the conventional *S. cerevisiae* in the pear wine fermentation, which significantly enhanced the sensory complexity of the final fermented pear beverages.

## 5. Challenges and future prospects

Unavoidably, the traditional AFBs market has faced with several problems like the annual material and product losses, which can be resulted from the excessive fruit production, reduced sale growth in fruit wines, and the imbalance of fruit wine supply chain (Merlino et al., 2021). Nowadays, the competition existed in the AFBs market has shifted from the simple price competition into flavor, quality and brand competition, which is highly complex and unavoidable. Thus, how to produce best-selling AFBs is essential for alcoholic beverage producers and acquired them to deeply integrate the advanced fermentation technology, precise market positioning, as well as the modern quality management systems. For researchers, it is essential to select yeast strains with specific metabolic characteristics based on differential fruit bases and produce AFBs with desired flavor profiles. Nowadays, the researches based on the yeast strains and their mechanisms when inoculated in the AFBs remained insufficient. The overreliance on the single yeast strain has been demonstrated to provide a monotonous flavor profile, excessive acidity, and elevated ethanol contents in AFBs. The application of non-*Saccharomyces* yeasts has arisen increasingly interests in the beverage companies due to their advantageous flavor attributions, their limited fermentation capacity, low alcohol tolerance, and poor stability still constrain their application in the industrial production (He et al., 2024). However, there exists limitations like the high cost of these yeasts and the increased need for sulfur dioxide addition. Concurrently, the selection and application of suitable indigenous strains for AFBs contains high challenges to the industrialization and standardization process. Additionally, the complex and uncontrollable composition of fermented microbial communities in the AFBs fermentation system is relatively difficult to control, which resulted in the insufficient flavor stability, elevated levels of ethanol, off-flavor, and harmful metabolites (Fazio et al., 2023). Furthermore, more chemical additives could be added during the fermentation process, leading to the excessive contents of chemical additives in the final AFBs. For example, the fermentation process of plum wine relies excessively on the empirical knowledge, which lacks the systematic and standardized control of the process parameters (Chen, Zhu, et al., 2025). Thus, this fundamental constraints ultimately the consistent output of standardized products with uniform flavor profiles and reliable quality (Yuan et al., 2024). The unique metabolism pathway of *Saccharomyces non-cerevisiae* and non-*Saccharomyces* yeasts may lead to the reduced ethanol contents of final AFBs. Thus, there is a need for systematic and in-depth studies to evaluate the influences of these largely under-explored yeasts and their effects on the chemical and sensory quality of final AFBs.

More research needs to prioritize the precise regulation of yeast co-culture systems, especially by optimizing inoculation ratios and fermentation time to achieve the directional control of metabolic fluxes. Parallel testing of different strain combinations, inoculation ratios, and

fermentation times on the growth and metabolite production of VOCs (esters, higher alcohols, aldehydes, ketones, and volatile acids) could quickly screen an optimal strategy that can be used in industrial levels. For example, the sequential inoculation of *K. pastoris* and *S. cerevisiae* at 48 h intervals could significantly increase the aroma diversity and antioxidant capacity (Zhang et al., 2025). Additionally, the construction of artificial microbial consortia with clearly defined roles is also a good option beyond inoculations of natural yeast strains. For example, one engineered yeast strain could be used to secrete pectinase for pectin degradation, the second yeast strain could be used to handle the main alcoholic beverage fermentation, and the third yeast for production of certain ester flavors. Meanwhile, the application of systematic biology tools, such as genome-scale metabolic model and dynamic flux balance analysis, could be used to predict the volatile synthesis and their responses to environmental factors at molecular levels (Lu et al., 2019; Scott et al., 2023). The multi-omics approach combining metagenomics and flavoromics is also important for revealing microbial interaction mechanisms and ensuring the quality stability of complex AFB systems (Li et al., 2025). The collection of multi-omics data could be carried out based on the historical fermentations, process parameters, and sensory evaluations to train the machine learning models, like random forests and neural networks. These models could be used to predict the linkage between raw material and their components to the final flavor profiles of AFBs, which could help in the standardize process of AFBs.

The prospects for developing fruit-based wines are highly promising and directly driven by the growing consumer demand for innovative alcoholic beverages and increased awareness of health benefits. The quality improvement of AFBs could be approached by the following steps, including the optimization of materials and pre-treatment, selection of yeast strains and control of fermentation process, and enhancement of aging and post-treatment. Appropriate utilization of enzymatic hydrolysis could be effective to modify the clarity of fruit juices, and thus improve viscosity and filterability of the fruit juice (Espejo, 2021). Furthermore, the selection of fruit types and maturity levels both influenced the quality and flavor profiles of AFBs, as well as the fermentation ability during fermentation process (Rosend et al., 2019). During the fermentation process, the proper utilization (pure or mixed) of *Saccharomyces* and non-*Saccharomyces* yeasts could markedly enhance the diversity and complexity of VOCs. Control of fermentation temperatures, pH, and nitrogen supplements is crucial for the formation of VOCs (García-Ríos et al., 2024; Seguinot et al., 2020). The ageing and post-fermentation treatments also strongly influence the quality of AFBs. For example, the utilization of ultra-high treated oak chips could notably enhance the acidity, aromatic complexity, and phenolic compositions as soon as possible, thereby achieving the quality of AFBs comparable to the traditional aging wines within a considerably shorter period (Yan et al., 2024).

## 6. Conclusion

In conclusion, the AFBs are produced by specialty fruit cultivars with optimal sugar levels and ripeness, excluding grapes, and the fermentation process of AFBs is mostly similar to that of grape wines. Generally, *S. cerevisiae* is considered to be the most commonly utilized yeast strains in the wine fermentation, and the selection of yeast strains is of high economic importance in the industry. Traditionally, *Saccharomyces non-cerevisiae* and non-*Saccharomyces* yeasts are considered to be spoilage yeasts, but nowadays, these yeasts are also considered to be a recent and growing trend in the wine beverage industry as they can create more versatile flavor profiles. For example, the inoculation of *S. bayanus*, *S. paradoxus*, *S. uvarum*, *L. thermotolerans*, *Starm. bacillaris*, *S. pombe* significantly reduce the acetic acid contents in the final AFBs. The AFBs produced by *S. paradoxus*, *Starm. bacillaris*, *T. delbrueckii* significantly reduce ethanol yield, whereas *S. bayanus*, *Schizo. pombe* and *Zygosaccharomyces spp.* enhance ethanol contents in the final AFBs. Moreover, the co-inoculation of different non-*Saccharomyces* yeast strains are

also utilized to enhance the aroma complexity in the AFBs. For example, the sequential fermentation of *S. cerevisiae* and *T. delbrueckii* significantly enhance the ester and higher alcohol contents while reduce the volatile fatty acids. These previous findings highlight the potential of other *Saccharomyces* and non-*Saccharomyces* yeasts in AFBs.

A better understanding of the contributions of diverse yeast species to flavor regulation and industrial production of AFBs is essential and equally important. For example, the application of non-*Saccharomyces* yeasts, including *H. uvarum*, *P. kluyveri*, and *L. thermotolerans*, have been proved to enhance the aroma and sensory complexity of AFBs. Furthermore, the sequential or simultaneous fermentation process could help in balancing the ethanol and other volatile acids. Developing commercial starter cultures with specific non-*Saccharomyces* yeasts and *S. cerevisiae* could provide alcoholic beverage producers with tools to create differentiated products with targeted aroma profiles, higher freshness, and desirable ethanol content. Future studies should focus on strain-specific metabolic pathways, fermentation kinetics at commercial scale, and large-scale sensory evaluation to translate laboratory findings into practical winemaking applications.

#### CRedit authorship contribution statement

**Wenjia He:** Writing – review & editing, Writing – original draft. **Tiantian Dong:** Writing – original draft. **Yiwei Zhang:** Writing – original draft. **Maaria Kortessniemi:** Writing – review & editing. **Shuxun Liu:** Writing – review & editing. **Yuting Ding:** Writing – review & editing. **Xuxia Zhou:** Writing – review & editing. **Oskar Laaksonen:** Writing – review & editing. **Baoru Yang:** Writing – review & editing.

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

During the preparation of this work the authors used Microsoft 365 Copilot Chat with GPT-5 in order to improve readability and language. After using this service, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

#### Declaration of competing interest

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

#### Acknowledgements

We acknowledge the financial supports from First Division Alar City Financial Science and Technology Plan Project (No. 2024SP01) and National Natural Science Foundation of China (No. 32402151).

#### Data availability

Data will be made available on request.

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