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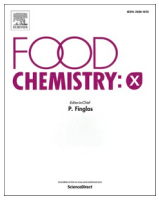

Exploring the potentials of indigenous *Saccharomyces cerevisiae* and *Pichia kudriavzevii* for enhancing flavour and aromatic characteristics in apricot wines

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ABSTRACT

In this study, we investigated the oenological performance of key yeast populations previously identified from apricot wine fermentation, aiming to obtain indigenous starters suitable for apricot wine production. Twenty-one isolates were characterized physiologically, and two isolates each of *Saccharomyces cerevisiae* and *Pichia kudriavzevii* were selected for laboratory-scale fermentations. Results showed that *S. cerevisiae* S9 exhibited significantly higher sugar consumption than S2 and CECA strains, with the former demonstrating a fructophilic character. Mixed fermentations of *P. kudriavzevii* N11 and N12 resulted in lower citric acid content (decreasing by 12–25 %) and higher glycerol levels (increasing by 12–47 %) compared to pure fermentation. In the mixed fermentation, indigenous *S. cerevisiae* species supported the survival of *P. kudriavzevii*, effectively enhancing the fruity esters and terpenes content of apricot wine. This study provides technical support for screening specialized starters for apricot wine production.

1. Introduction

Apricot (*Prunus armeniaca* L.), a member of the Rosaceae Li subfamily, is primarily cultivated in the Xinjiang, Shaanxi, and Shandong provinces of China (Zhao et al., 2022). The fruit is highly favored by consumers due to its rich nutritional components, involving vitamins, minerals, and amino acids, alongside abundant sugars and acids (Ella Missang et al., 2012). The Hongmei apricot is a prominent agricultural product of Xianyang County in Shaanxi Province, located in the northwest region of China. However, apricot fruits have an accelerated senescence rate at the room temperature, typically lasting only 3–5 days (C. Liang et al., 2023; Zhao et al., 2022). During this inevitable and irreversible process, the quality of apricot fruits deteriorates in terms of color, sugar and acid content, taste, flavour, and nutrient value (Hua et al., 2022), which further impacts their edible values and economic returns. Currently, numerous studies focus on delaying the postharvest senescence of apricot fruits, but few scholars have explored the exploitation of their related by-products postharvest (Chen et al., 2022). Exploring these by-products could enhance the added value and meet consumer demands.

Fruit wines represent a typical alcoholic beverage with a unique taste and diverse flavour, derived from fruits through fermentation facilitated by various microorganisms, involving complex biochemical reactions (Elhalis et al., 2023; W. Liu et al., 2023).Yeast populations are generally categorized as *Saccharomyces cerevisiae* and non-*Saccharomyces cerevisiae* based on their fermentative performance, playing a crucial role in fruit wine production (Wang et al., 2024). *S. cerevisiae* is widely recognized as the ideal starter for alcoholic beverage production because of its high ethanol production, efficient sugar consumption, and strong environmental stress tolerance (Chen et al., 2022). Additionally, this specie is known for its robust production capacity of aromatic compounds, e.g., higher alcohols, fruity esters, and terpenes (Guzzon et al., 2021; López-Enríquez et al., 2022). Despite the importance of *S. cerevisiae* to fermented food manufacturers, commercially available *Saccharomyces* strains are limited due to the current inability to use genetically modified technology in the beverage industry (Jolly et al., 2014; López-

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Enríquez et al., 2022). On the other hand, owing to the enormous biodiversity of non-*Saccharomyces* yeasts, their oenological potentials have been observed, especially in positive sensory characteristics. These populations were ignored and even identified as contaminants for a past long time (Jolly et al., 2014; Lai et al., 2022). For instance, populations of *Lachancea thermotolerans* with high lactic acid production have been commercially utilized to increase acidity and maintain the balance of wine body (Y. Su et al., 2024). *Pichia barkeri* and *Torulaspora delbrueckii* have been successfully used to decrease acetic acid and increase glycerol production (Guo et al., 2024; Tronchoni et al., 2017). *Metschnikowia pulcherrima* has been identified as a potential starter for reducing low ethanol production in wines (Hranilovic et al., 2020). Moreover, due to their impressive aroma characteristics, these non-*Saccharomyces* yeasts, which have higher enzymatic activities than *S. cerevisiae*, can enhance varietal and fermentative volatiles, such as ethyl caprylate (apple), ethyl hexanoate (pear), isoamyl acetate (banana), and various terpenes (floral, fruity) (C. Kong et al., 2024; Z. Liang et al., 2021). Despite the positive effects observed, most non-*Saccharomyces* yeasts cannot complete alcoholic fermentation, attributing to their weak ethanol tolerance in winemaking conditions (approximately 5 % vol) (Chen et al., 2023; Jolly et al., 2014). Co-fermentations with *S. cerevisiae* populations, including simultaneous and sequential inoculations, are an effective method to enhance the flavour and quality of fruit wines. Considering the strong interaction between species (Barber et al., 2022), the positive or negative impact of this mixed fermentation mode on the final product cannot be ignored and warrants further exploration.

In recent years, there has been some characterization of the flavour and quality of apricot fruit, but research on apricot-related by-products has been limited. Zhao et al. (2022) and C. Su et al. (2020) identified over 60 volatiles in variant apricot cultivars in Xinjiang of China, revealing distinct volatile biomarkers among variant cultivars. Among these, linalool and (E)-2-hexenal were defined into the characteristic aroma components in small white apricots. Pu et al. (2023) used a commercial CEC01 (originating from grape must in Ningxia region of China) to produce apricot wines, but the final product had a poor taste. Although spontaneous fermentation practices helped showcase regional characteristics of this geographical fruit in a previous study (Chen et al., 2023), the long fermentation period has limited the commercial potential of apricot wine. Therefore, utilizing indigenous starters throughout the fermentation process is highly recommended in the field, as it allows for greater control over both the final product and the fermentation process. This work aimed to comprehensively inspect, for the first time, the oenological performances of all isolated *S. cerevisiae* populations and essential non-*Saccharomyces* yeasts in apricot wine fermentation. This fills the gap of a lack of a special starter for apricot wine and provids technical support for the rejuvenation of China's indigenous starter for the apricot industry.

2. Materials and methods

2.1. Cultivation and growth of yeast species

All tested strains (Table S1), which were isolated from two regions of Shaanxi during apricot wine fermentation (Chen et al., 2023), were kindly stored at −40 °C in the laboratory. The tested *S. cerevisiae* strains originated from nine previous genotypes, while the analyzed non-*S. cerevisiae* species were derived from the genera of *Pichia* with representative morphotypes (Chen et al., 2023). The involved medium of the autoclaved reserve refers to Yeast Extract Peptone Dextrose (YPD, 20 g/L of glucose, 10 g/L yeast extract and 20 g/L peptone) medium and Wallerstein Laboratory Nutrient Agar medium (WLN, Hope Biotechnology Co., LTD, Qingdao, China), which were sterilized at 121 °C for 15 min. The stored cultures were inoculated on the WLN medium at 28 °C for 48 h, then a single colony was activated in 50 mL YPD medium (170 rpm and 30 °C for 36 h in a shaker) to obtain the seeds.

2.2. Further screening indigenous strains based on physiological property experiments

Physiological property experiments were conducted by analyzing growth characteristics, tolerances (ethanol, sugar, pH, SO_2), and flocculability. Specifically, 100 μL of seed culture was inoculated into 100 mL of YPD medium contained in a 250-mL Erlenmeyer flask and incubated at 30 °C with shaking at 170 rpm. Growth curves were drafted by monitoring the optical density (OD) of each flask at 600 nm for each 4 h until the OD values plateaued. For ethanol tolerance, 100 μL of seed culture was added into 100 mL of YPD medium adjusted to different ethanol concentrations [6 %, 8 %, 10 %, and 12 % (*v*/v)], and OD_{600nm} values were determined after 48 h of incubation at 30 °C with shaking at 170 rpm. Flocculability were assessed using the method described by Bony et al. (1998). Briefly, yeast cells were washed twice with buffer (50 mM sodium citrate, 5 mM EDTA, pH adjusted to 3.0 with hydrochloric acid), resuspended in fresh buffer to a concentration of 1×10^8 cells/mL, and 5 mL of cell suspension was transferred to a 10 mL test tube. Flocculation was induced by adding calcium chloride to a final concentration of 20 mM, followed by stirring at 50 shakes per minute for 5 min and then allowing the suspension to stand vertically for 3 min. A 0.6 mL aliquot of the suspension was mixed with 0.6 mL of 0.25 M EDTA, and the OD at 600 nm was measured. Flocculation was expressed as the difference in OD between the completely dispersed cell suspension (measured in 0.25 M EDTA) and the sample. Additionally, an orthogonal experiment was designed with three factors: sugar, pH, and SO_2, as detailed in Fig. 1A. Each treatment was replicated three times. Ethanol was filtered using a 0.22-μm organic filter to remove impurities.

2.3. Micro-vinification of apricot wines by the selected strains

The Hongmei apricot fruits were collected from each three orchards in the Liquan region (Shaanxi of China) at the harvest-stage in June 2023. The apricot fruits were stored in a room with a constant temperature of 8 °C until they were washed and destemmed. The fresh fruits were quickly pitted and crushed, with potassium metabisulfite and pectinase added at concentrations of 60 mg/L and 0.03 kg/mL. The total sugar and titratable acidity (TA) of apricot juice were determined according to the Chinese national standard GB15038–2006 and are displayed in Table S2. The pH was measured using a BPH-7100 A pH meter (BELL Analytical Instruments Co., Ltd., Dalian, China). Before inoculation, the initial sugar content of apricot juice was regulated to 140 g/L via sucrose (Chen et al., 2023). Nine yeast treatments included three *S. cerevisiae* strains and two non-*S. cerevisiae* species in two inoculation modalities. Commercial *S. cerevisiae* CECA (Angel Yeast Co., Ltd., Yichang, China) was used as the control, while two indigenous *S. cerevisiae* strains were considered the experimental groups under the monoculture modalities. The co-inoculation treatments involved random pairings of two *Pichia* species and three *S. cerevisiae* strains. All treatments were inoculated at total concentrations of 2×10^6 cells/mL in pure and simultaneous inoculations, respectively. Additionally, referred to the previous studies (Li et al., 2022), both *Pichia* and *S. cerevisiae* strains were inoculated at a concentration of 1×10^6 cells/mL in simultaneous inoculations. The inoculated strains were spread out on YPD plates (YPD liquid medium with agar of 2 g/L). After two days of incubation at 28 °C, single colonies were transferred into 50-mL YPD liquid medium. Yeast cells were incubated at the same temperature as before to reach the inoculation concentration, and then washed with sterilized water before inoculations. The dinitrosalicylic acid (DNS) method was used to measure the sugar concentration for monitoring the fermentation process until the end of fermentation (sugar <4.0 g/L) (Teixeira & Santos, 2022). All fermentations were carried out in triplicate.

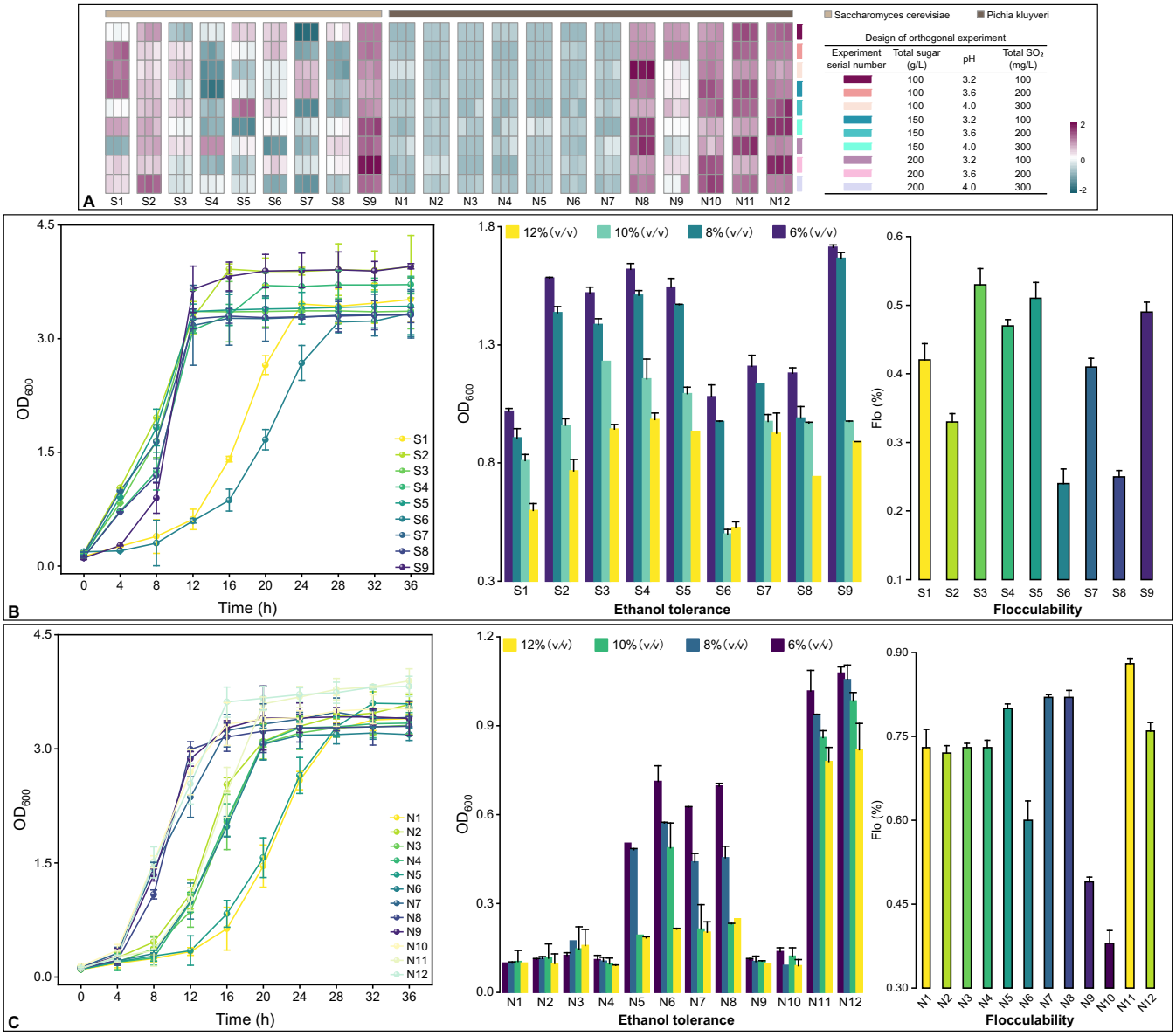

Fig. 1. The physiological results of indigenous yeasts isolates. The characteristics of *S. cerevisiae* (A)and *P. kudriavzevii* (B) populations were present in growth kinetic (the left side), ethanol tolerance (the middle), and flocculability (the right side). The orthogonal experiment was designed according to the tolerances of sugar, pH, and sulfur dioxide (SO_2) with each three single-factor (C). Each row of the heatmap represents each combined condition taken in consideration in this study, and data were normalized for visualization.

2.4. Yeast dynamics of S. cerevisiae and P. Kudriavzevii during fermentation

The dynamics of yeast populations were monitored using the WLN medium for each 24 h, with clear clarification depending on the morphologic method (Chen et al., 2023).

2.5. Determinations of physiochemical parameters and volatile compounds

Considering the sensory attributes of physiochemical parameters (Guo et al., 2024; Pu et al., 2023), concentrations of glucose, fructose, glycerol, ethanol, and organic acids (citric, succinic, malic, lactic, acetic), were evaluated throughout high efficiency liquid chromatography (HPLC) analysis, using an LC-2050C 3D system (Shimadzu, Japan) equipped with an ultraviolet detector set to 210 nm (for organic acids) and a refractive index detector (RID; for hexoses and alcohols). The detailed chromatographic conditions were described in a previous report without any modification (Hranilovic et al., 2020).

The volatile profiles of apricot wines were analyzed using a Trace 1610 gas chromatograph system combined with a TriPlus RSH SMART auto-sampler and an ISQ 7610 mass spectrometer (Thermo Fisher Scientific, USA), as referenced in previous reports (Chen et al., 2022; Li et al., 2022). Each 5-mL wine sample was placed into a 20-mL sealed glass vial, to which 10 μL of internal standard (4-methyl-2-pentanol, 1.0031 g/L) and 1.2 g of NaCl were added. Subsequently, the extraction of volatile compounds involved using a DVB/CAR/PDMS SPME fiber, which was incubated in the headspace for 30 min following a 30-min agitation at 40 °C. The fiber was then thermally desorbed for 8 min at an injector temperature of 250 °C. The analysis of volatiles was conducted using a TG-WAX column (60 m × 0.32 mm × 0.25 μm, Thermo Fisher Scientific, USA). Helium was employed as the carrier gas at a constant flow rate of 1 mL/min. The oven temperature initially set at 50 °C was held for 1 min, then ramped up to 220 °C at a rate of 3 °C/min,

and maintained at this temperature for 5 min. The ion source, quadrupole, and mass selective detector (MSD) transfer line temperatures were held at 230 °C, 150 °C, and 250 °C, respectively. The quantification of volatile compounds was calculated according to the calibration curve established in a model solution containing 8 % vol of ethanol, 3.25 g/L of tartaric acid, 1.5 g/L of citric acid, and pH adjusted to 3.3 with 6 mol/L sodium hydroxide. The odor activity values (OAVs) of the volatiles were calculated using the previous formula, which is commonly aiming to evaluate the aromatic contribution of volatile compounds to alcoholic beverages (Chen et al., 2022).

2.6. Determinations of E-nose and E-tongue

The same electronic nose (E-nose) system (PEN3.0, Airsense Analytics, Schwerin, Germany) was coupled with a metal oxide semiconductor sensor array of 10 different sensors, as detailed in a previous (Chen et al., 2023). The electronic tongue (E-tongue; Insent Co., Ltd., Tokyo, Japan) system utilized in the study was outfitted with six lipid membranes, each assigned to characterize the sweetness, sourness, saltiness, bitterness, astringency, and umami of apricot wine. Prior to the measurement, all sensors were immersed in positive and negative cleaning solutions for 60 s to guarantee result reliability. Four repeated tests were conducted for each sample, with the last three measurements selected for raw data analysis.

2.7. Data analysis and visualization

The Tukey-Kramer's Honest Significant Difference (HSD) test (level of significance 0.05) was used to access the statistical differences among apricot wine samples via one-way analysis of variance (ANOVA), in the software SPSS 26.0 (IBM, USA). All principal component analysis (PCA) and orthogonal projections to latent structures-discriminant analysis (OPLS-DA) were carried out using SIMCA 14.1 software. Variable importance in the projection (VIP) value was used to identify the differently volatile compounds among different treatments. The metabolic network was drafted in Adobe Illustrator 2021 software (Adobe, USA) according to the Kyoto Encyclopedia of Genes and Genomes database (KEGG, https://www.kegg.jp/).

3. Results

The study involved the selection of indigenous yeast strains, which began with a total of 21 isolates obtained from the spontaneous fermentation of apricot wines, previously collected from two regions of Shaanxi in China (Table S1). Among these isolates, there were nine populations of *S. cerevisiae* and twelve species of *P. kudriavzevii* purified from WLN medium. The identification of *S. cerevisiae* (designated as S) and *P. kudriavzevii* (designated as N) colonies with different morphologies were carried out through interdelta fingerprinting and sequencing of the 26S rRNA D1/D2 region, respectively.

3.1. Selection of indigenous strains based on comparative analysis of physiological characteristics

The results of the investigated physiological characteristics are represented in Fig. 1. An orthogonal experiment was designed to assess the ability of 21 indigenous species to grow at different tolerance levels (Fig. 1A). Not all strains were capable of growing and fermenting under all conditions, particularly the *S. cerevisiae* populations. Conversely, only indigenous S2 and S9 isolates could thrive in environments with higher sugar and SO_2 concentrations, along with lower pH values. Besides, the growth curves for all isolates were drafted (on the left side of Fig. 1B and C), with seven S and five N strains showing robust growth activity in the initial 12 h. The growth ability of these species at different concentrations of ethanol (6, 8, 10, and 12 % *v*/v) was analyzed (in the middle of Fig. 1B and C). All most of tested strains showed a strong decrease of their viability at 10 and 12 % (*v*/v) of ethanol. On the other hand, several isolates demonstrated higher resistance to high ethanol concentrations, involving four *S. cerevisiae* strains (S2, S3, S4, S9) and two *P. kudriavzevii* populations (N11 and N12) populations. Regarding the flocculability, most *Pichia* isolates exhibited greater strength than the *S. cerevisiae* populations (on the right side of Fig. 1B and C), except for N9 and N10. Despite the superior fermentation ability of N8, N9, N10, N11, and N12 in the orthogonal experiment, N11 and N12 were further selected to generate the micro-vinification in apricot juice at a pilot scale, owing to their higher ethanol tolerance.

3.2. Physiochemical parameters of apricot wines in different treatments

All isolates were able to finish the alcoholic fermentation, with residual sugar levels dropping to less than 4.0 g/L. Within 6–8 days, the residual sugar was consumed to 2.21 g/L. Indigenous *S. cerevisiae* S2 and commercial CECA took longer for 7 and 8 days respectively (Fig. 2A). The combination of indigenous strains was found to enhance the initial fermentation rate, but this pattern was reversed when simultaneously inoculating indigenous *Pichia* species and commercial CECA. Among the pure inoculation treatments, indigenous *S. cerevisiae* S9 showed the highest fermentation rate. The isolate S9 demonstrated the significantly higher sugar consumption than S2 and CECA strains, with the former displaying a fructophilic character (Fig. 2B, C), which varied among different strains. All treatments exhibited higher sugar consumption in co-fermentation patterns than in pure inoculation, particularly in glucose consumption. This consumption pattern was also reflected in citric acid content (Fig. 2D). Whether using pure or simultaneous inoculations, apricot wines related to *S. cerevisiae* S9 were observed the lowest levels of citric acid. The isolate S2 produced apricot wines with the highest acetic acid values (0.15 g/L), although the acetic acid concentrations in all treatments remained below the Chinese national standard GB/T 18656–2012 (Fig. 2E). Final glycerol concentrations in apricot wines were up to 12 % (S2 + N12) and 47 % (S2 + N11) higher in co-inoculation treatments than in the pure fermentations, respectively (Fig. 2F).

3.3. Yeast dynamic during apricot wine fermentation

The dynamics of different yeast populations were illustrated and characterized using the colony plate counting method during apricot wine fermentation according to the morphologic differences (Fig. 3). In the pure inoculations, the growth patterns of three *S. cerevisiae* populations showed similar trajectories within the first six days of fermentation (Fig. 3A). Noticeable decreases were observed during the inoculated *S. cerevisiae* CECA and S2 fermentation in the last 48 h, with the former showing significance ($p < 0.01$ by one-way ANOVA), from 7.63 ± 0.20 log CFU/mL to 6.23 ± 0.11 log CFU/mL. As pure cultures, indigenous *S. cerevisiae* S2 and S9 species presented a stronger survival than that of commercial CECA, especially in the end of apricot wine fermentation. In the co-fermentation systems, the maximum biomass concentrations of three *S. cerevisiae* populations were 7.60 (CECA in Fig. 3B), 8.29 (S2 in Fig. 3C), and 8.25 (S9 in Fig. 3D) log CFU/mL at the 96th hour of fermentation, respectively. The growth rates of two *P. kudriavzevii* were comparable to the indigenous strains in the first 48 h of co-fermentation from a starting inoculum concentration of 5.00 ± 0.13 log CFU/mL, after which the *Pichia* species slowly decreased in rates. In comparison, these *Pichia* strains were inhibited by the commercial CECA until they were completely eliminated throughout the entire fermentation process.

3.4. Volatile profiles of apricot wines by variant inoculation strategies

3.4.1. The pure inoculations of S. cerevisiae populations

A total of 67 volatile compounds were detected by GC–MS analysis in three apricot wines of pure inoculated fermentation. These volatiles

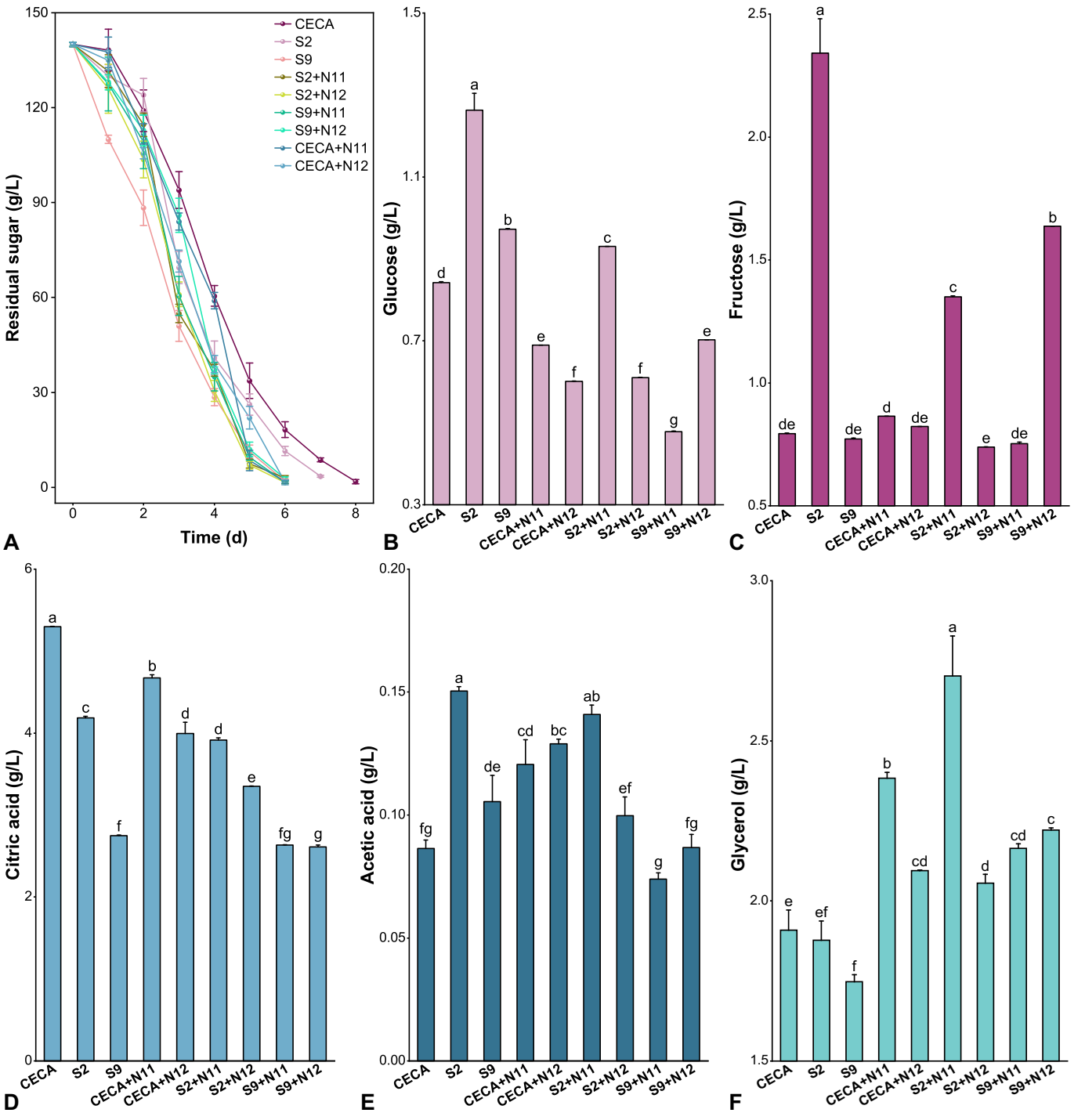

Fig. 2. Kinetic (A) and analytical chemical parameters were produced with different treatments during apricot wine fermentation. Several chemicals were involving glucose (B), fructose (C), citric acid (D), acetic acid (E), and glycerol (F).

were categorized into eight chemical families, namely higher alcohols, C6 alcohols, acetate esters, ethyl esters, other esters, fatty acids, terpenes, and others. Variations in the content levels of some chemical families were observed among different pure inoculation treatments, mainly in higher alcohols, C6 alcohols, and acetate esters (Fig. S1). The indigenous strains (S2 and S9) exhibited lower concentrations of total acetate and ethyl esters, with the highest content levels in higher alcohols (apricot wines by S9) and C6 alcohols (by S2). Differences in volatile composition between apricot wines fermented by species CECA, S2, and S9 were evident when comparing different compounds, as highlighted in PCA plots (Fig. 4A) and hierarchical clustering (Fig. 4B). The first component (PC1) explained 56 % of the total variance between the S2 and S9 apricot wine samples and distinguished them from commercial apricot wines, with around 48 % of the total composition associated with the S9 apricot wines. The second component (PC2) highlighted the 28.7 % of total variance in differences in volatile compositions that varied among strains. Some higher alcohol compounds, including 1-propanol and 1-butanol, were related to the control apricot wines by commercial CECA. S2 apricot wines were positioned in the lower right of the plot, characterized by higher concentrations of farnesol and trans-rose oxide, with 2-ethyl-1-hexanol, 3-methyl-1-pentanol, and isopentyl hexanoate driving the separation along PC2. The S9 apricot wine

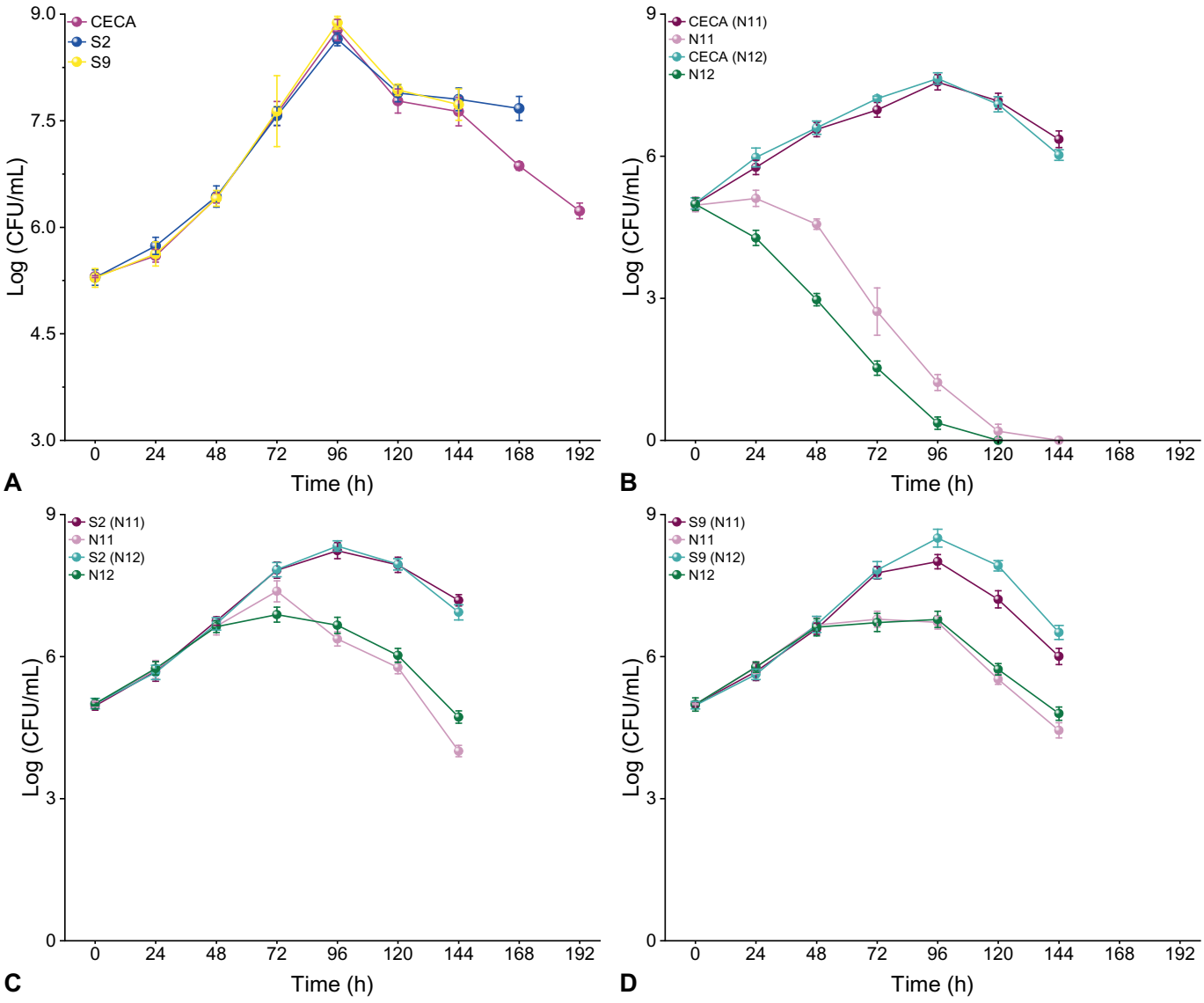

Fig. 3. Microbial dynamic among pure cultivations of *S. cerevisiae* and their co-cultivations with indigenous *P. kudriavzevii* in apricot wine fermentation, in respect to growth as determined by the spread plate method. Error bars represent standard deviation ($n = 3$).

samples were separated from the other two pure inoculation treatments (Fig. 4B), mainly associated with the high content level of several higher alcohols, terpenes, and volatile phenol compounds (4-ethylphenol, 2,4-di-tert-butylphenol, 4-ethyl-2-methoxy-phenol). Owing to the OAV > 1.0, S9 apricot wines were detected more aromatic compounds from these differential volatiles by ANOVA, accounting for more than 50 % of the total volatiles (OAV > 1.0).

3.4.2. *The co-fermentations of indigenous Pichia kudriavzevii with Saccharomyces cerevisiae strains*

Volatile compositions in the co-fermentations were performed in the replicate apricot wines. Nearly all of the volatiles showed statistically significant differences according to the ANOVA ($p < 0.05$). Therefore, the volatiles with OAV > 1.0 were subjected to PCA analysis (Fig. 4). The co-inoculated wines by strains CECA and S2 had higher concentrations of higher alcohols and esters (ethyl and acetate). Especially in the CECA-related apricot wines, the concentrations were 1.16 to 1.63 times higher than the corresponding pure-inoculated fermentations (Fig. 4C). Conversely, a decrease in higher alcohol levels was observed in the S9-related co-fermentations compared to the pure inoculation of *S. cerevisiae* S9. Total fatty acid and terpene compounds were also higher in the apricot wines from the co-fermentation of CECA with *P. kudriavzevii* N11. PCA of volatile profiles of apricot wines in co-fermentation presented the distinct separations among the different combinations. Across all co-inoculated treatments, the first two principal components accounted for 61.6 % of the total variance, with 1-propanol (OAV1), 3-methyl-1-butanol (OAV3), 1-octen-3-ol (OAV4), 1-heptanol (OAV5), ethyl benzoate (OAV15), D-limonene (OAV20), and β-ionone (OAV24) driving the separation along PC1 (40.5 %). Except for the S2-related apricot wine samples, the remaining samples were less distinguished along the first principal component than along the second principal component (PC2: 21.1 %). There was a clear separation of different co-inoculated fermentations, showing the variances of the aromatic compounds with OAV > 1.0 (Fig. 4D). The S2 + N11 apricot wine samples were mainly characterized by the highest concentrations of several terpenes (linalool, (Z)-3,7-dimethyl-2,6-Octadien-1-ol, and geraniol) and ethyl ester compounds (ethyl 3-hydroxybutyrate, ethyl caprylate, ethyl 9-decenoate, ethyl caprate, ethyl hexanoate, ethyl isovalerate, ethyl 2-methylbutanoate). Some higher alcohols (1-heptanol, 3-methyl-1-butanol, 2-methyl-1-propanol, 1-octen-3-ol) with higher content levels were mainly associated with the N11-related apricot wines, while these compounds were observed at the lowest

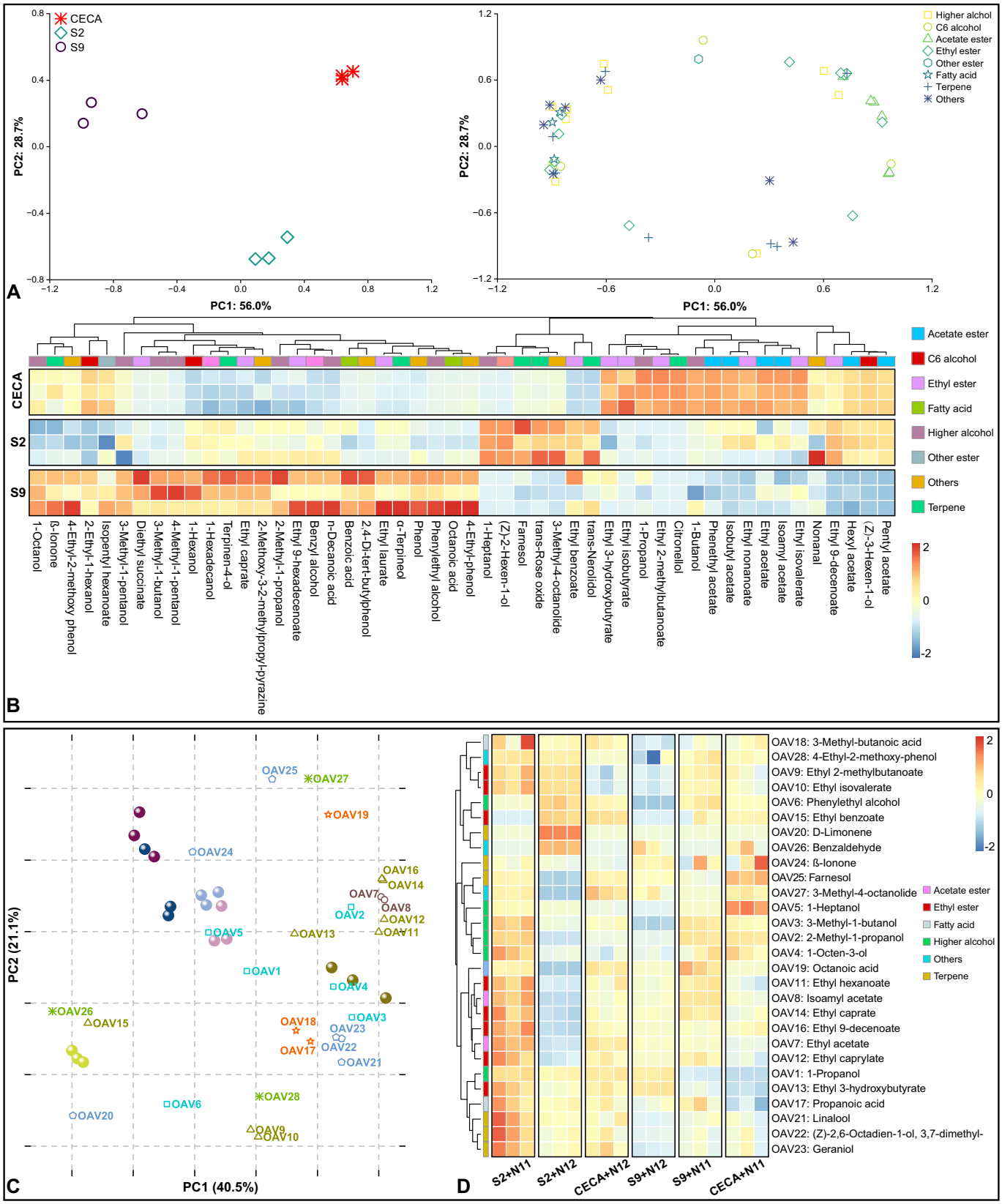

Fig. 4. Volatile profiles of the final apricot wines from pure inoculations (A, B) and co-inoculations (C, D). Principal component analysis of volatile compositions in apricot wines from different treatments: the pure fermentations of *S. cerevisiae* (A) and co-fermentations with *P. kudriavzevii* strains (C). The cluster heatmaps present significantly different volatiles ($p < 0.05$) according to above treatments by one-ANOVA.

concentrations in the S2 + N12 samples.

3.5. Evaluations of sensory attribution in apricot wines based on E-tongue and E-nose

In the study, the E-tongue and E-nose were utilized for the objective assessment of apricot wines in terms of taste and aroma, respectively. The taste properties of the nine apricot wines were displayed and differentiated based on E-tongue profiles, showing distinct characteristics compared to the inoculated treatments (Fig. 5A). The multiple probes of the E-tongue determined the sourness, astringency, aftertaste-A, aftertaste-B, umami, saltiness, sweetness, richness, and bitterness of apricot wines, with only top five indexes showing a significant response. S2 + N12 samples exhibited the highest response values in aftertaste-A and saltiness sensors, while displaying lower response values in sweetness sensors. The *S. cerevisiae* S9 yielded the highest sourness and lowest umami values significantly ($p < 0.05$), while the related S9 apricot wines from co-fermentations showed lower astringency response values. Conversely, apricot wines by S2 strain provided the lowest astringency responses with the highest umami values. Eight e-nose sensors in Fig. 5B showed significant responses to the apricot wine volatiles from different inoculation treatments. Commercial apricot wines exhibited higher signal intensity in W1W, W1S, W2W, and W6S sensors, while the highest response values of W2S, W3S, and W5S sensors were found in S9 + N11 apricot wines (Fig. 5B). By contrast, the S9 + N12 samples demonstrated the lowest signal intensity in these sensors, with the exception of W6S sensors. The principal component analysis (PCA) model distinguished different apricot wines according to the E-tongue and E-nose profiles (Fig. 5C, and D), explaining 76.5 % (for PC1) and 13.7 % (for PC2) of the total explained variance in the first two principal components. As displayed in Fig. 5C, apricot wines with varied inoculation strategies exhibited distinct flavour characteristics in aroma and taste profiles. The control apricot wines from pure inoculation fell in the down-left quadrant, associated with the W1S, W6S, saltiness, and umami sensors (Fig. 5D), while the S9 + N11 samples, correlated to the W2S and W3S sensors, were situated in the up-left quadrant. The two N12-related samples, CECA+N12 and S9 + N12 apricot wines, were located in the right quadrant, potentially contributing to the sweetness, W1C, W3C, and W5C sensors. The remaining samples were relatively clustered in the center of the score plot, driven by the response values of aftertaste-A, aftertaste-B, sourness, W1S, W2W, and W5S sensors.

4. Discussion

Recent trends in seeking the improvement of microorganisms for the flavour of related-fruit products have been observed, as microbial fermentation is an effective means in providing multiple flavour (Nisiotou et al., 2018), extending shelf life (Zhao et al., 2022), and increasing the economic value of agriculture products (D. Liu et al., 2021). In addition to using commercial starters for large-scale production (Wang et al., 2024), there is growing interest in utilizing indigenous microbial sources (Chen et al., 2022). This study extends previous

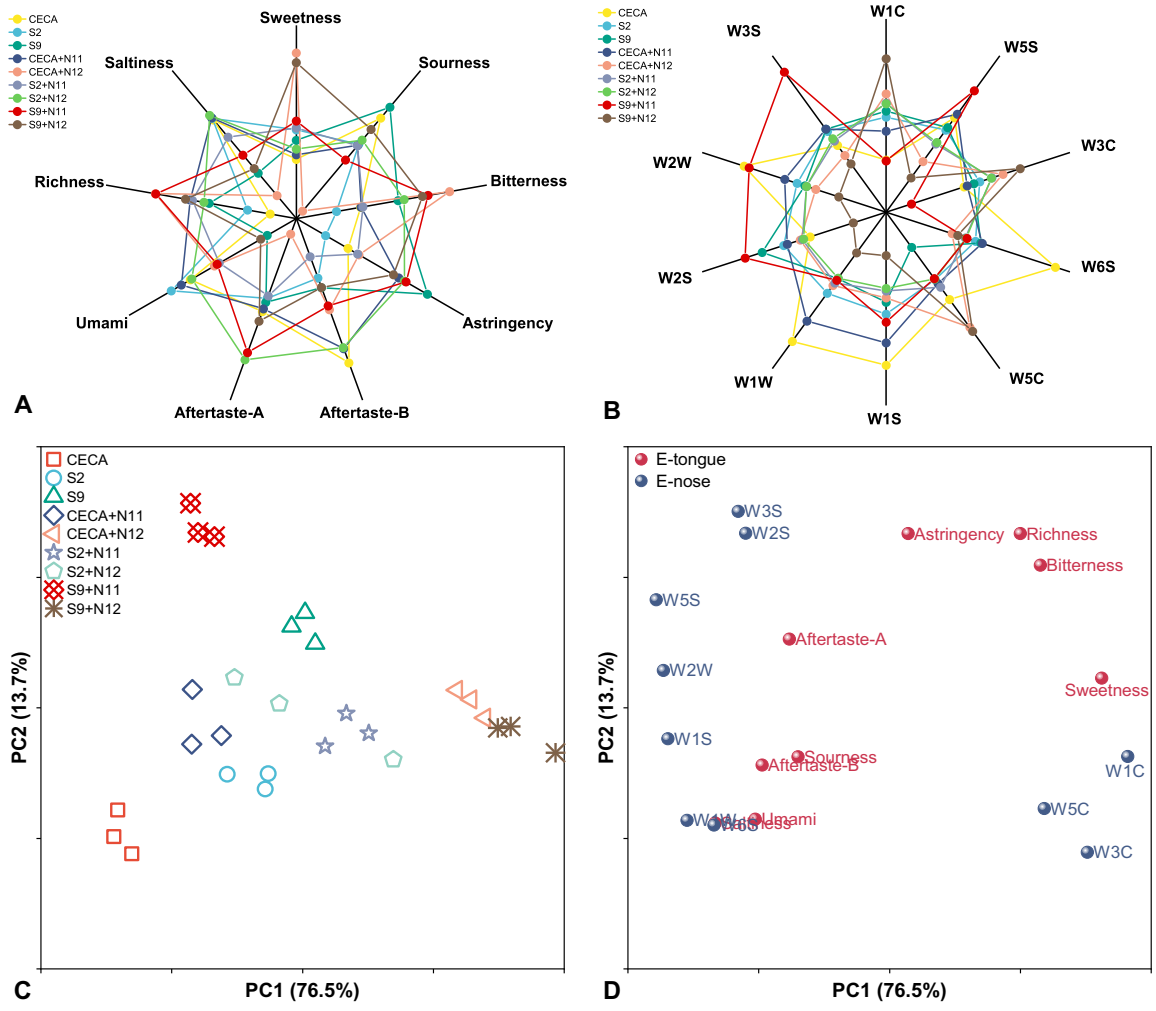

Fig. 5. The results of flavour evaluations based on *E*-tongue and E-nose. Radar chart about the differences of aroma (A) and mouthfeel (B) of apricot wines from different fermentations. Principal component analysis of E-tongue and E-nose profiles in apricot wines: yeast treatments (C) and correlation circle (D).

research on the dynamics of microbial diversity and communities in apricot wine fermentations (Chen et al., 2023). Previous studies have emphasized the significant role of the *Pichia* genus in shaping the flavour profile of apricot wine, resulting in distinct volatile compositions. Furthermore, as a dominant microorganism in alcohol fermentation, the crucial role of *S. cerevisiae* populations and their impact on other microorganisms during apricot wine fermentation cannot be overlooked (D. Liu et al., 2021; López-Enríquez et al., 2022). In the study, we initially assessed the oenological characteristics of indigenous *S. cerevisiae* and non—*S. cerevisiae* populations from previous research (Chen et al., 2023). From these, two populations each was further selected to evaluate the influence of indigenous *S. cerevisiae* and combined inoculations with *P. kudriavzevii* on the flavour quality of apricot wine.

As a first step, differences in fermentative populations along the oenological phenotypes have been investigated, as higher microbial and species diversity were observed during the alcoholic fermentation process (D. Liu et al., 2021). Under the favorable conditions commonly used in microbiology (Elhalis et al., 2023), variations in growth were noted among yeast populations, particularly in growth rate and maximum biomass (Fig. 1). Tolerance experiments were not determined in the sequential cultures, with the study focusing solely on the 48-h growth period (Serafino et al., 2023). Yeasts significant to oenology, such as *S. cerevisiae* S2 and S9, as well as *P. kudriavzevii* N11 and N12, were selected for analysis due to their strong growth rates, high ethanol [12 % (*v*/v)] and SO_2 (300 mg/L) tolerance, alongside broad pH adaptability (3.2–4.0). In oenological settings, *S. cerevisiae* populations, known for their robust fermentation capabilities, were able to achieve ethanol levels of up to 16 % v/v and 43.67 mg/L of free SO_2 (Doughty et al., 2021; Guzzon et al., 2021), while maintaining a pH below 3.0 (Tian et al., 2020). In contrast, most non-*Saccharomyces* yeasts, including *Hanseniaspora* spp., *Pichia* spp., *Kluyveromyces* spp., *Metschnikowia* spp., and *Torulaspora* spp., exhibited lower ethanol and SO_2 tolerances (Lai et al., 2022; Wang et al., 2024; Zhong et al., 2020). However, current findings have shown that *P. kudriavzevii* populations can exhibit tolerance up to 20 % v/v ethanol (Lai et al., 2022). Therefore, screening the starters depending on these physiological characteristics is meaningful, especially considering that properties like ethanol tolerance are largely strain-dependent (Serafino et al., 2023). Our results showed that under high-ethanol conditions, *P. kudriavzevii* N11 and N12 displayed higher growth rates than indigenous *S. cerevisiae* S1 and S6 (Fig. 1).

The internal mechanisms underlying interactions among the strains we used remain partially unknown. Although all treatments were able to ferment to dryness (residual sugar <4.0 g/L), the chemical parameters of final apricot wines and microbial dynamics were inconsistent. Both indigenous *S. cerevisiae* strains exhibited faster fermentative kinetics compared to the commercial CECA strain (Fig. 2A), with the indigenous strains showing higher survival probability than the control at the end of fermentation (Fig. 3A). From the 2nd to 5th days of fermentations, the corresponding co-inoculations of indigenous *P. kudriavzevii* strains enhanced fermentation rates compared to pure inoculations of the three *S. cerevisiae* populations, while *P. kudriavzevii* strains gradually lagged in co-fermentation with commercial CECA. As previously reported, the existence of *P. kudriavzevii* shortened fermentation time and shifted microbial succession (Chagas Junior et al., 2021). This interaction has been identified as a cooperative response for ethanol production under acid stress (Deng et al., 2020). In addition, yeast dynamic profiles also illustrated that the interaction patterns of the two *Pichia* species depended on *S. cerevisiae* sub-population diversity (Fig. 3). In fact, although few studies have reported the internal mechanisms of interactions between *P. kudriavzevii* and *S. cerevisiae*, it is widely known that non-*Saccharomyces* yeasts enhance glycolytic activity of mixed cultures via inducing the expression of *PAU*, *PDC1*, and *ADH1* genes in *S. cerevisiae* (Tronchoni et al., 2017). Here, an alternative interaction was observed in mixed fermentation without the commercial strain, previously described as a coexistence mechanism (Barber et al., 2022). Two *P. kudriavzevii* strains in co-inoculations with indigenous *S. cerevisiae* were still capable of surviving until the end of fermentation as ethanol content gradually increased, which is consistent with previous studies (Chen et al., 2023; Wei et al., 2020) but contradicts others (Miguel et al., 2024; Rodríguez Madrera et al., 2021). Finally, these data provide evidence that important active components synthesized by indigenous *S. cerevisiae* support the enduring survival of *P. kudriavzevii* strains in the apricot winemaking environment.

Pure inoculation trials highlighted the superior oenological characteristics of the isolates designated as S9, which displayed the highest sugar consumption, the lowest citric acid production, and a fructophilic character (Serafino et al., 2023). The ability to degrade citric acid has also been emphasized in *Pichia fermentans* and *Oenococcus oeni*, as previously reported by Zhong et al. (2020), but this trait is rarely observed in *Saccharomyces* populations. Nonetheless, citric acid degradation was observed in the *S. cerevisiae* S9 isolate, warranting further investigation. Beyond these typical oenological parameters, it is fundamental to definite the influences of starter on apricot wines flavour to determine whether the selected strains can match commercial winemaking standards. Non-commercial species can improve the production of aromatic compounds, but their potential negative effects on beverage flavour profiles should not be ignored (Elhalis et al., 2023; Hranilovic et al., 2020). In the current study, apricot wines produced by different yeasts and inoculation methods exhibited significant variations in aromatic volatile concentrations, with the highest levels of diethyl succinate, ethyl caprate, ethyl laurate, phenylethyl alcohol, and α-terpineol found in S9 samples during pure fermentation (Fig. 4). These volatile compounds contribute pleasant and desirable sensory attributes to alcoholic beverages, such as muskmelon (diethyl succinate), coconut (ethyl caprate), rose and honey (phenylethyl alcohol) flavour (Chen et al., 2022; Li et al., 2022; Nisiotou et al., 2018; Welke et al., 2014). The *Pichia* genera is recognized for producing higher concentrations of phenylethyl alcohol during various beverage fermentations (C.-L. Kong et al., 2019; Li et al., 2022; W. Liu et al., 2023). However, in this study, the production of phenylethyl alcohol by *P. kudriavzevii* N12 was influenced by the presence of *S. cerevisiae*, resulting in lower concentrations in S9 + N12 samples.

To further investigate the differences in yeast-derived volatile compounds, OPLS-DA models were conducted to distinguish the different biomarkers between inoculation treatments (Fig. 6). In *S. cerevisiae* modeling, almost all aromatic compounds (VIP > 1.0, and OAV > 1.0), including isoamyl acetate, ethyl acetate, ethyl 3-hydroxybutyrate, and 1-propanol (Fig. 6E), were significantly enriched in the control samples. These key volatiles accounted for 5.97 % (4/67) of the total detected composition, suggesting a similar core carbon metabolism in commercial and indigenous *S. cerevisiae* populations, with partial limitations on the effect on apricot wine flavour for *S. cerevisiae* species. Conversely, most volatiles in the inoculation treatment model, identified as the odor-active components (Chen et al., 2022; Nisiotou et al., 2018; Welke et al., 2014), increased in co-fermentation of *P. kudriavzevii* species (Fig. 6D), highlighting the crucial role of non-*Saccharomyces* species in enhancing aromatic complexity in fermentative beverages (C.-L. Kong et al., 2019; D. Liu et al., 2021). Notably, several volatile esters responsible for fruitiness in alcoholic beverages (C. Kong et al., 2024), involving ethyl acetate (fruity), ethyl caprylate (apple), ethyl 3-hydroxybutyrate (grape), and ethyl 2-methylbutanoate (sweet fruity), were enriched in co-fermentation with *P. kudriavzevii* populations. This aromatic effect is mainly attributed to yeast polysaccharides retarding ester hydrolysis and volatilization through distinct binding forces during storage (C. Kong et al., 2024; Lytra et al., 2013). Although previous studies have only mentioned *Pichia fermentans* and *Pichia kluyveri*, the tested *P. kudriavzevii* populations in our study also presented homologous influences, i.e. improving the production of fruity esters in apricot wines. Terpene compounds are primarily present in the fruit in a bound form and are released into alcoholic beverages by yeast-derived enzymes (Z. Liang et al., 2021; Svedlund et al., 2022). In this study, terpenes were

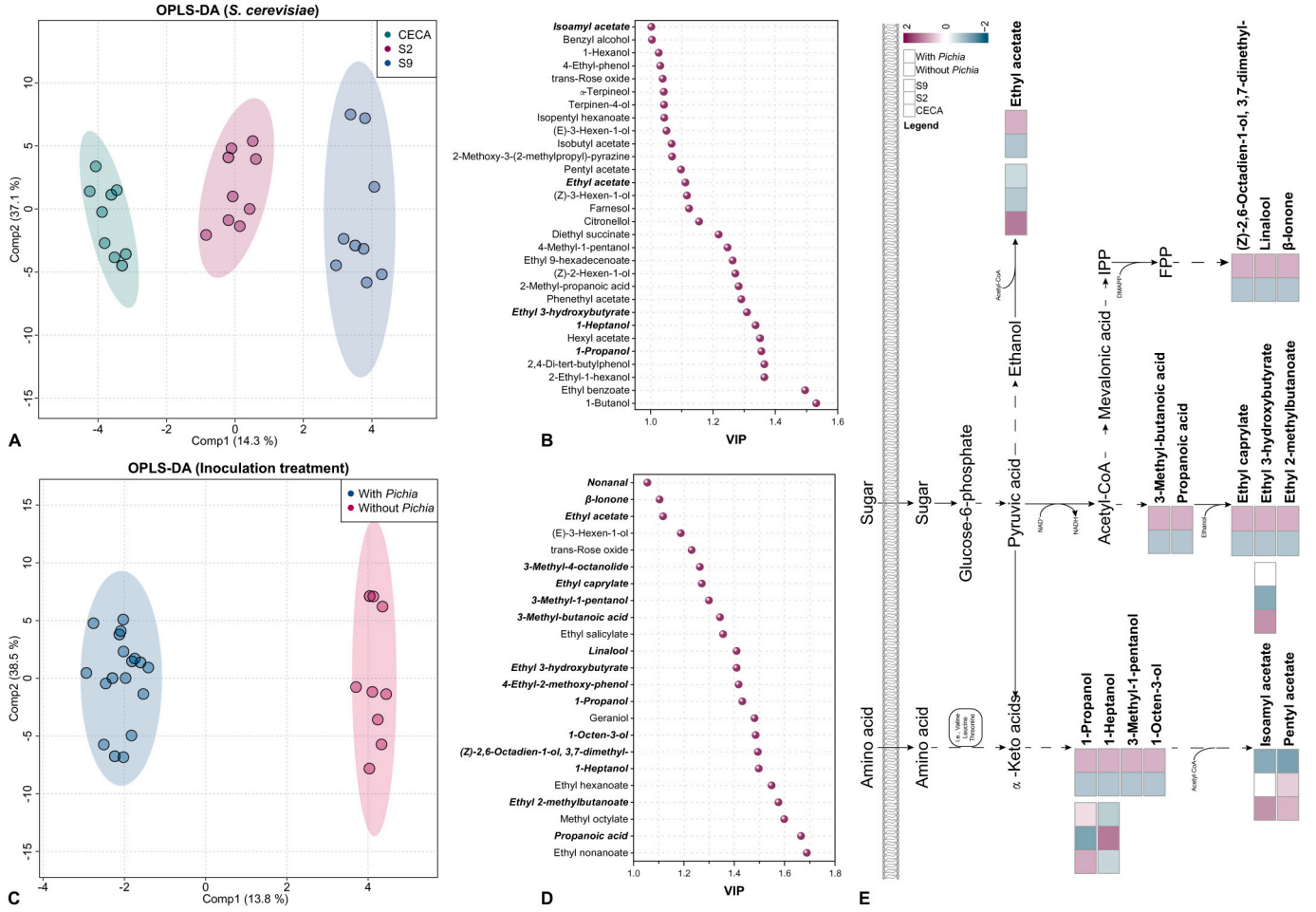

Fig. 6. The identifications of different volatiles (VIP values >1.0) in apricot wines from variant fermentation treatments under the adjustment of *S. cerevisiae* (A, B) and *P. kudriavzevii* (C, D) strains by OPLS-DA. Concentration changes of different volatile metabolites (bold) as determination in heatmaps on metabolic network (E). Arrows in the network indicate a single (real line) or multiple step (broken line) connecting two metabolites. IPP: isopentenyl diphosphate. FPP: farnesyl pyrophosphate. DMAPP: dimethylallyl diphosphate.

significantly affected by the existences of *P. kudriavzevii* and were largely retained in apricot wine, illustrating that *P. kudriavzevii* N11 and N12 can release terpene alcohols with floral and fruity aromas by cleaving glycosidic bonds (Svedlund et al., 2022). Moreover, as increases in 1-propanol and 1-heptanol are not only attributed to *S. cerevisiae* but also to *P. kudriavzevii*, it is worth further exploring whether the differential productions are related to a co-culture response. These high values in aromatic volatiles were found in co-fermentations of indigenous strains compared to related-CECA inoculations are considered of interest, confirming the optimal performance of these indigenous populations.

5. Conclusion

In this study, an in-depth characterization of indigenous yeasts involved in apricot wine production was conducted to enhance the added values of apricot fruit. The findings emphasize the importance of characterizing indigenous yeasts capable of improving apricot wine quality, particularly highlighting the promising role of co-fermenting indigenous *P. kudriavzevii* with indigenous *S. cerevisiae* populations. Although the selected indigenous *S. cerevisiae* strains did not play an admirable role in the fermentation of apricot wine, especially in terms of aromatic properties, the regulation of indigenous *P. kudriavzevii* and their interactions with *S. cerevisiae* improved the overall quality of the apricot wine. This improvement was notably evident in the increase of fruity esters, the release of more terpenes, and the adjustment of acidity. The selection of indigenous starters could help address challenges in the apricot industry, as the demand for apricots with high economic benefits and their by-products with diverse sensory experiences continues to rise.

CRediT authorship contribution statement

Yu Chen: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation. **Xingmeng Lei:** Writing – review & editing, Visualization, Software, Formal analysis. **Luxing Sun:** Methodology, Investigation, Formal analysis, Data curation. **Binghong Gao:** Methodology, Investigation, Formal analysis, Data curation. **Peng An:** Methodology, Formal analysis, Data curation. **Dongqing Ye:** Methodology, Formal analysis, Data curation. **Haibin Mu:** Methodology, Formal analysis, Data curation. **Yi Qin:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Yuyang Song:** Writing – review & editing, Funding acquisition, Formal analysis, Data curation. **Yanlin Liu:** Writing – review & editing, Visualization, Methodology, Funding acquisition, Formal analysis.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fochx.2025.102178.

Data availability

No data was used for the research described in the article.

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