Effect of *Saccharomyces cerevisiae* and *Schizosaccharomyces pombe* strains on chemical composition and sensory quality of ciders made from Finnish apple cultivars

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Abstract

Composition of volatile compounds and concentrations of sugars and organic acids were studied in apple ciders produced with *Saccharomyces cerevisiae* and *Schizosaccharomyces pombe* yeasts using eleven different Finnish apple cultivars. Moreover, sensory quality of selected ciders was studied using check-all-that-apply test with untrained panelists. Seventy-seven volatile compounds were detected in the samples using HS-SPME-GC-MS. In general, the ciders had higher concentrations of higher alcohols, aldehydes and acetals whereas the juices contained higher C6-alcohols. Simultaneously, fermentation using *S. pombe* resulted in lower concentrations of malic acid, ethyl pentanoate, ethyl hexanoate, and volatile acids and higher concentrations of residual sugars compared to *S. cerevisiae*. Ciders made using *S. cerevisiae* were characterized as 'alcoholic' and 'yeasty' while *S. pombe* ciders were more frequently described as 'sweet', 'honey-like', and less rated as sour. Besides the strong effect by the yeasts, apple cultivars had significant effects on the compositional and sensorial properties of apple ciders.

Keywords: Apple cultivar; Cider; *Schizosaccharomyces pombe*; Yeast; Volatile compounds; Sensory quality.

1. Introduction

Apple (*Malus domestica* Borkh.) is the second highest consumed and the third most produced fruit in the world with an annual production of 86.2 million tons in 2018 reported by the Food and Agriculture Organization Corporate Statistical Database (FAOSTAT, 2018). While the majority (over 60%) of apple production are sold and consumed fresh, around 20% of them are processed into value-added products, such as apple juice, jam, puree, cider, vinegar, and dehydrated apple product (Shalini and Gupta, 2010). As a fermented alcoholic beverage, cider possesses a complex aroma profile and its alcohol content ranges from 1.2% to 8.5% *(v/v)* (Waston, 2013). Apple cider is one of the fastest growing beverages, the annual growth rate is predicted to rise to 15% by 2021 in the alcoholic beverage markets, and its production gained higher popularity in European countries, mainly in the United Kingdom, France, and Northern European countries (Jamir, Stelick & Dando, 2020; Miles, Alexander, Peck, Galinato, Gottschalk & Nocker, 2020). According to the European Cider and Fruit Wine Association, around 7.6% of the overall apple crops in 2018 were used for cider production and 48.5% of ciders were made from cider apples. Currently, there is increasing interest among cider producers in Northern European countries, especially in Finland, to develop the local cultivars as cider apples. However, there are no breeding programs for speciality cider apples in Finland, and no available data concerning on the potential of Finnish apples in cider production.

Flavor is one of the most important factors for assessing the olfactometric profile and quality of an alcoholic beverage (Symoneaux, Chollet, Patron, Bauduin, Le Quéré & Baron, 2015). The flavor of apple ciders is derived from complex mixtures of non-volatile compounds, like sugars, acids, phenolics, and volatile compounds, including esters, higher alcohols, fatty acids, aldehydes, ketones, terpenoids, and volatile phenols (Antón, Suárez Valles, García Hevia & Picinelli Lobo, 2014). Investigation of the volatile compounds in the final cider products is crucial, as the volatile compounds highly contribute to the sensory identities and flavor properties. The content and profile of various sensory-active volatile compounds in ciders are influenced by several factors, including apple varieties, growing conditions, ripeness, and yeast strains involved in the fermentation process (Alberti et al., 2016; Braga et al., 2013; Rosend, Kuldjärv, Rosenvald & Paalme, 2019). For example, ciders produced from dessert apple cultivars may possess more desirable flavors and mouth-feel whereas cider apple cultivars contain more phenolic compounds and are perceived more sour (Merwin, Valois & Padilla-Zakour, 2008). In addition to the cultivars, the ripeness of apples affects the composition of volatiles. Ciders made from overripe apples contained more volatile compounds, such as higher alcohols and acetate esters, than ciders made from less ripe apples (Braga et al., 2013; Rosend et al., 2019). Moreover, the addition of yeast assimilable nitrogen also enhanced the aromatic complexity of cider, including ethyl and acetate ester concentrations, which has been previously reported by Karl et al (2020).

Many of the volatile compounds in cider are derived from yeast metabolism during the fermentation whereas some compounds originate from the apples (Pietrowski, Dos Santos, Sauer, Wosiacki & Nogueria, 2012). Numerous studies have reported that yeast species has an important role in the volatile compounds of ciders (Albergaria and Arneborg, 2016; Benito, 2019; Luan, Zhang, Duan & Yan, 2018; Wei et al., 2020). *Saccharomyces cerevisiae* is considered as the conventional commercial yeast species used for cider production due to its strong fermentative power, high tolerance to harsh environment and low production of off-flavor compounds (Albergaria et al., 2016). Besides *S. cerevisiae*, the roles of other yeast in *Saccharomyces* genus and various non-*Saccharomyces* yeasts (*Schizosaccharomyces pombe*, *Hanseniaspora opuntiae*, *Pichia kluyveri*, and *Pichia kudroavzevii*) have been assessed in affecting the volatile compositions and enhancing the aroma complexity of ciders. *S. pombe* has been suggested to be a potential alternative to *Saccharomyces* yeasts in fruit wine making due to its equal fermentation capacity to the latter. This species also has been reported to reduce malic acid content and improve aroma complexity of alcoholic beverages compared to *S. cerevisiae* (Mylona et al., 2016). *S. pombe* has been used in apple wine studies (Satora, Semik-Szczurak, Tarko & Buldys, 2018), however, the available data regarding the influence of this yeast on the volatile compounds of apple ciders is still scarce.

The main aim of the present study was to characterize the effects of *S. cerevisiae* and *S. pombe* strains on the chemical compositions of apple cider products. These compositional analyses included investigations of volatile compounds via headspace solid-phase microextraction coupled with gas chromatography mass spectrometry (HS-SPME-GC-MS) and sugars and acids using a GC coupled with flame ionization detector (GC-FID). Moreover, the sensory properties of the selected cider samples were investigated with an untrained consumer panel. Special focus was on the contribution of eleven Finnish apple cultivars (four summer cultivars, five autumn cultivars, one winter cultivar, and one decorative cultivar) to the compositional profiles of ciders. In Finland, early ripening apple crops are traditionally important due to its short growth season, while late ripening apple cultivars contain more optimal conditions for developing chemical and sensory qualities (Seppä, 2014). However, the Finnish apple cultivars have not yet been characterized concerning their potential in cider production. Most of the apple samples used in this study for cider fermentation belonged to old and traditional Finnish cultivars without current significant commercial utilization as this current study aimed to screen cultivars with fermentation potential.

2. Materials and Methods

2.1 Chemicals and strains

The culture of *Saccharomyces cerevisiae* Lalvin V1116 (V1116) was purchased from Lallemand Inc. (Montreal, Canada) and the culture of *Schizosaccharomyce pombe* 3796

(SP3796) was provided by DSMZ Institute (Braunschweig, Germany). The volatile standards of ethyl acetate, ethyl butanoate, methyl butanoate, 2-methylbutan-1-ol, 3-methylbutan-1-ol, 4-methylpentan-2-ol, 1-hexanol, 6-methylhept-5-en-2-one, hexanal, and hexane were purchased from Sigma (St. Louis, MO), Aldrich (Gillingham, U.K.), and VWR (Darmstad, Germany). For sugars and acids analysis, the standards of sucrose, glucose, fructose, sorbitol, malic acid, quinic acid, succinic acid, and ascorbic acid were obtained from Extrasynthese (Genay, France). An alkane mixture (C5-C30) was obtained from Sigma-Aldrich (St. Louis, MO). All the other solvents are of analytical grade.

2.2 Apples

From the total of 97 Finnish seed born local apple cultivars (*Malus* x *domestica* Borkh.) accepted to the Finnish national apple germplasm collection (Heinonen and Bitz, 2019), nine apple cultivars, including 'Alasen Punainen' (AP), 'Kersti' (Kr), 'Lepaan Meloni' (LM), 'Lohjan Kirkas' (LK), 'Aino' (An), 'Gustavs Bästa' (GB), 'Luotsi' (Lt), 'Pieksämäki' (Pk), and 'Turso' (Tr), were selected to the cider fermentation. In addition to the seed born local apple cultivars, the Finnish cultivar 'Juuso' (Ju) from the Finnish breeding program was included in the study. In the set selection of ten cultivated apples for this study, the criteria were selected to obtain a variety of tastes, i.e. levels of sweetness, acidity, and bitterness (Supplementary Table 1). The one decorative apple cultivar (*Malus* 'Hyvingiensis', Hg) of Finnish origin being in professional production was selected to get information about its suitability for cider production. Furthermore, the selected cultivars are in a nursery production thus currently not in wider professional apple production in Finland.

The selected apples growing in the Finnish national apple germplasm collection in Piikkiö (60°25′N, 22°31′E) in southwestern Finland were randomly harvested in the same orchard in the Natural Resources Institute Finland (Luke). Subsequently, the over-ripeness program of apples was carried out at 4 °C in darkness for one month. The completion of over-ripeness was determined by the iodine starch test (Supplementary Table 1). Eight ciders (four cultivars and two yeasts) made from three apple cultivars ‘Gustavs Bästa’, ‘Turso’, and ‘Juuso’ and one decorative apple cultivar ‘Hyvingiensis’ were included in the sensory analysis.

2.3 Cider preparation

Apples were washed with cold tap water and subsequently drained. Thereafter, the samples without obvious external damage were cut into small pieces and squeezed into juice with a centrifugal juice press (Vita Pro-Active JE810, Kenwood). The appearance or size of apples was not used as criteria in the sample selection. The apple juices were first pooled and divided into 50 mL glass tubes and then pasteurized in a hot water bath (95 °C) for 5 min and then cooled down to the room temperature in a cold-water bath.

The cider samples used for chemical analysis were produced by fermentations carried out in 100 mL Duran bottles with aliquots of 80 mL pasteurized apple juice. Prior to inoculation, the strains *S. cerevisiae* 1116 and *S. pombe* 3796 were proliferated in yeast extract-peptone-dextrose (YPD) liquid medium (1% yeast extract, 2% peptone, 2% dextrose) at 25 ℃ for 48 h with shaking at a speed of 150 rpm. The colony populations of *S. cerevisiae* 1116 and *S. pombe* 3796 were determined by spread plate technique after 48 h of propagation, respectively. Afterwards, yeast cells were collected from the broth and centrifuged at 4500 × *g* for 10 min. The pellets were washed using sterile solution of sodium chloride (0.9%) and centrifuged at 4500 × *g* for 10 min, subsequently. The washing process was carried out twice successively. After that, the yeast strains were resuspended in apple must for fermentation. All the cultures were inoculated at the yeast cell amounts of 10^7 CFU/mL. No optimization of fermentation conditions was carried out in the current study. Fermentations were carried out in duplicates at a controlled temperature of 25 ℃ in darkness in an incubator (Memmert GmbH, Schwabach, Germany) and were considered to be completed when °Brix values reached constant levels and no CO_2 production from yeast growth during four consecutive days. The CO_2 production from yeast growth was monitored every two days by calculating the weight loss of bottles. The °Brix value was measured by a °Brix meter from Atago Co. Ltd. (Tokyo, Japan). The unfermented apple juices were set as the controls incubated under same conditions as the samples inoculated with yeast strains. After fermentation, the precipitates and/or yeast cells were removed from both juices and ciders by centrifugation at 3000 × *g* for 10 min, and the obtained supernatants were stored at –80 °C. However, the ciders used for sensory evolution were produced by fermentations conducted in 500 mL Duran bottles using aliquots of 400 mL pasteurized apple juice and stored at –20 °C. All the processes were conducted in food-grade conditions and incubation of yeasts were carried out in aerobic conditions.

2.4 Measurements of pH, ethanol, and concentrations of sugars and organic acids during fermentation

The pH value was measured by a pH meter from WTW (Weilheim, Germany). Ethanol concentration in the fermented apple ciders was determined by Shimadzu GC-2010plus gas chromatograph (Shimadzu, Japan) coupled with flame ionization detector (FID) according to a previous published method (Liu, Laaksonen, Marsol-Vall, Zhu & Yang, 2020). Quantification of ethanol was carried out by using calibration curve of ethanol of different concentrations (R^2= 0.9997).

The determination of individual sugars and organic acids was carried out according to the GC-FID method described in a previous study with slight modifications (Liu, Laaksonen, Kortesniemi, Kalpio & Yang, 2018). In brief, individual sugars (sucrose, fructose, glucose, xylose, and sorbitol) as well as organic acids (malic acid, quinic acid, succinic acid, and ascorbic acid) were identified by comparing the retention times of individual compounds to those of their corresponding authentic standards. While these compounds were quantified using calibration curves established by analysis of series of reference compounds of varying concentrations. The total sugar and organic acid contents were calculated as the concentration sum of concentrations of all individual sugars (sucrose, fructose, glucose, xylose, and sorbitol) and organic acids (malic acid, quinic acid, succinic acid, and ascorbic acid), respectively.

2.5 Analysis of volatile compounds

The determination of volatiles in apple products was carried out using HS-SPME-GC-MS according to a previous published method (Liu et al., 2020). Briefly, 2 mL of apple juice or cider, 0.2 g of sodium chloride, and 10 μL of internal standard (4-methylpentan-2-ol, 802 μg/mL in methanol) were mixed, placed in a 20 mL glass vial, and stored at 4 °C prior to use. The extraction of volatile compounds from headspace was performed using a 2 cm SPME fiber coated with a DVB/CAR/PDMS layer (50/30 μm, Supelco, Bellefonte, PA), and temperature was kept at 45 °C for 30 min with agitation. The SPME fiber was set at 250 °C for 60 min before the extraction process. The extracted compounds in the SPME fiber coating were desorbed into a Trace 1310 (Thermo Scientific) gas chromatograph with a TSQ 8000 EVO mass spectrometer (Thermo Scientific) in splitless mode at 240 °C for 3 min. The separation of volatile compounds was carried out using a DB-WAX (J&W Scientific, Folsom, CA) column (60 m × 0.25 mm × 0.25 μm). A SPB-624 column (30 m × 0.25 mm × 0.25 μm) from Agilent (Santa Clara, CA) was also used to assist the identification of volatiles. Helium was chosen as the carrier gas and its flow rate was set at 1.6 mL/min. The oven temperature was set as 50 °C for 3 min followed by an increase to 200 °C at a rate of 5 °C/min and held at 200 °C for 8 min. Mass spectra of analytes was recorded in electron impact (EI) ionization mode at 70 eV with a scan range from *m/z* 30 to *m/z* 300. The MS transfer line was set at 200 °C while the ionization source temperature was at 220 °C. The identification of volatile compounds were achieved by 1) comparing retention times and mass spectra between analytes and their corresponding authentic standards, when available; 2) matching the obtained mass spectra of analytes with those of the library (NIST 17) and comparing their retention indices (RIs) to the data reported in the NIST Database (2017). Co-injection of a series of C5-C30 alkane mixture under the same chromatographic conditions to that of apple samples was carried out to determine the RI values of analytes. All the individual compounds identified by the DB-WAX column were semi-quantified (relative concentrations) by comparing their base peak areas to that of the internal standard, by using the following equation: $C\ (mg/L) = A_C * C_{I.S.}\ (mg/L)/A_{I.S.}$ (C: relative concentration of analyte; $C_{I.S.}$: final concentration of internal standard in samples; A_C: peak area of analyte; $A_{I.S.}$: peak area of internal standard).

2.6 Sensory evaluation

Voluntary untrained participants (n = 34, 26 females and 8 males, 20–65 years old) were asked to evaluate the samples based on the check-all-that-apply (CATA) method, and the hedonic scale on appearance, odor (orthonasal), and flavor (including retronasal odor, taste, and mouthfeel) as well as the intensities of color and taste by 9-point scales (Supplementary Table 3). CATA method was used to evaluate the characteristics of eight apple ciders (Varela and Ares, 2012). A list of selected sensory attributes (n = 26, Supplementary Table 4) for apple ciders were provided to the participants, and they were instructed to select all suitable descriptors from the list or generate new attributes to describe the cider samples. The samples were served in balanced randomized order (Williams design) at room temperature à 10 mL in 50 mL transparent plastic cups covered with glass lids. Data was collected using Compusense Cloud software (Compusense Inc., Guelph, Canada). The sensory evaluation was carried out in a controlled sensory laboratory.

2.7 Statistical analysis

Variance analysis (ANOVA) and Tukey’s (HSD) test were performed to evaluate the compositional differences among the different apple juices and ciders produced by two different yeast species using IBM SPSS Statistics 25.0 (SPSS Inc., Chicago, IL). Principal components analysis (PCA) and Partial least squares regression discrimination analysis (PLS-DA) were carried out to explore the differences among ciders produced from apples of different cultivars and among processing methods (juice, fermentation with *S. cerevisiae* 1116 and *S. pombe* 3796). Full cross validation was carried out in order to estimate a statistically reliable model. Multivariate method was carried out using Unscrambler X (Version 10.3, CAMO software, Oslo, Norway).

3. Results and discussion

3.1 General fermentation parameters

The general fermentation characteristics, i.e. the total production of CO_2, ethanol contents, pH, organic acids, and residual sugars, of apple juices and their corresponding cider samples are presented in Table 1. The fermentation kinetics varied depending on the different general fermentation parameters (Belda, Navascués, Marquina, Santos, Calderon & Benito, 2015). The fermentation carried out with the *S. cerevisiae* strain was completed after 16 days, while the fermentation with *S. pombe* strain took 18–20 days. During fermentation, CO_2 was released in a range from 3.33 to 6.51 g in the V1116 samples and 4.06 to 5.97 g of CO_2 in SP3796 samples. The average alcohol content in V1116 ciders was 6.67% *(v/v)* whereas in SP3796 ciders was 6.45% *(v/v)*. Ethanol yield was slightly influenced by the yeast strains, and the difference was more dependent on the apple cultivars. For example, ciders made from 'Aino' had the lowest ethanol contents among the cider samples (5.50% for V1116 cider and 5.19% for SP3796 cider). The low ethanol yield of fresh apple juice without additional sugars and acids has been also reported in the previous studies (Pando Bedriñana et al., 2017; Rumpunen, Ekholm, & Nybom, 2017).

Similar to the CO_2 and ethanol productions, pH values were significantly influenced by apple cultivars in both apple juices and ciders (Table 1). Organic acid composition in apple juice is also highly cultivar dependent. The highest amount of malic acid, the major organic acid in apples (Lee and Wrolstad, 1988), was detected in cultivar ‘Aino’ (18.94 g/L), followed by cultivars ‘Juuso’ (11.31 g/L) and ‘Turso’ (9.58 g/L). The ‘Aino’ ciders had the lowest pH among the cultivars, and the ‘Pieksämäki’ ciders contained the highest pH values. The pH values were significantly higher in the ciders produced by *S. pombe* compared to the corresponding juices prepared from apples of the same cultivars. However, there was no significant change in pH values before and after fermentation with *S. cerevisiae*. The differences could be explained by high malic acid consumption of *S. pombe* (Benito, 2019; Liu et al., 2018), as 47–89% of malic acid was consumed in the fermentations with *S. pombe*. In contrast, the corresponding decrease was only 6–18% resulting from fermentation with *S. cerevisiae* as shown in Table 1. The difference between the two yeast strains is also shown along the second PC in the PCA model (Supplementary Figure 1). The PC2 also separated the cultivar ‘Aino’ (An) from the others. After fermentation, the content of quinic acid decreased slightly, whereas ascorbic acid and succinic acid, which were absent in apple juices, became detectable in ciders. The reduction of organic acids with the ciders produced from *S. pombe*, especially malic acid, and therefore the increase of pH values may mitigate the flavor of harsh green apple sourness, acidity, and puckering astringency (Laaksonen, Mäkilä, Tahvonen, Kallio & Yang, 2013).

With regard to sugars, fructose was the main sugar presented in apple juices, followed by sucrose, glucose, and sorbitol (Table 1). These results are in accordance with those reported by Pires et al (2018). Apple cultivars significantly influenced the contents of sugars, the highest amounts of fructose and glucose were detected in cultivar ‘Pieksämäki’ (108.10 g/L) and ‘Hyvingiensis’ (52.85 g/L), respectively. The concentration of sugars decreased dramatically after fermentation with more than 90% of sugars consumed. Fermentations with *S. pombe* 3796 consumed less sugar in comparison to those with the *S. cerevisiae* V1116. The difference in consumption of sugars between those two yeasts could be ascribed to the metabolic characteristics of the yeasts (Liu et al., 2018). The differences in sugars were also presented in the PCA model (Supplementary Figure 1), which showed a clear difference between the initial juice samples and fermented samples.

3.2 Volatile compounds in apple juices and ciders

A total of 77 volatiles were identified in apple juices and their corresponding fermented samples by the DB-WAX Column including 34 esters, 5 aldehydes, 20 higher alcohols, 4 ketones, 1 terpene, 3 acetals, 1 hydrocarbon, 1 oxide, 2 benzenes, and 6 acids (Table 2). Their concentrations in apple juices and completely fermented apple ciders are listed in Supplementary Table 2, whereas the total contents of each volatile compound class are summarized in Table 3. Twenty-nine compounds, mainly ethyl esters and higher alcohols, were detected only in cider samples, while 20 compounds, mainly acetate esters and other esters present in the juices, became undetectable after fermentation.

Esters dominated in numbers among all classes of volatile compounds in the ciders, including ethyl esters, acetate esters, and other esters (Table 3). Although some esters originally existed in the apple juices, most of them were produced during fermentation due to the esterification of alcohols (Peng, Li, Cui & Guo, 2015). Ethyl acetate was the major ester in ciders (Supplementary Table 2). It was reported to contribute to *pineapple*, *sweet*, or *pungent* order (Li, Zhao, Zuo, Zhang, Zhang & Chen, 2020). Fermentation with *S. cerevisiae* yeasts produced more ethyl acetate than that with *S. pombe* yeasts. This is in line with report in wine production (Peinado, Moreno, Maestre, Ortega, Medina & Mauricio, 2004). Among the other minor esters, ethyl butanoate, ethyl decanoate, 3-methylbutyl acetate, phenethyl acetate, and hexyl acetate were the quantitatively predominant fractions of volatile compounds of apple ciders, the results are in agreement with a previous study (Ye, Yue & Yuan, 2014).

Alcohols were the most abundant principal volatile group in the apple ciders in terms of contents (Table 3). Higher alcohols are regarded as one of the most important precursors of esters, but they may have adverse effects on the quality of final products at excessive levels (Satora, Cioch, Tarko & Wołkowicz, 2016). Most of the higher alcohols were produced during yeast fermentation, the contents of higher alcohols in ciders were 7–25 times higher than those in the initial juices. Apple ciders fermented by *S. cerevisiae* strain were more abundant with higher alcohols than those fermented by *S. pombe* yeasts. 2-Methylpropan-1-ol, butan-1-ol, 3-methylbutan-1-ol, pentan-1-ol, 1-hexanol, 6-methyl-5-hepten-2-ol, 2-ethylhexan-1-ol, and pentadecane-8-ol were found in all the apple cider samples. 3-Methylbutan-1-ol is the most predominant higher alcohols according to Supplementary Table 2, similar results have also been reported in Chinese, French, and Danish apple ciders (Fan, Xu & Han, 2011, Qin, Petersen & Bredie, 2018, Villière, Arvisenet, Lethuaut, Prost & Sérot, 2012). 2-Methylbutan-1-ol was identified in initial apple juices, but it showed a significant decrease during yeast fermentation. Butan-1-ol and pentadecane-8-ol showed relatively high concentrations in all cider samples compared to the corresponding apple juices (Supplementary Table 2), and their concentrations were dependent on both cultivar and yeast. Although C6-alcohols have been reported to be very important alcohols in apple juices, they may have a negative effect on apple cider at excessive levels (Qin et al., 2018). Among C6-alcohols identified in the current work, 1-hexanol existed in original apple juices, and its concentrations decreased during fermentations. (*E*)-2-Hexen-1-ol was only present in 'Gustavs Bästa' (GB), 'Luotsi' (Lt), and 'Pieksämäki' (Pk) juices, and was not detected in cider samples (Supplementary Table 2).

Five aldehydes and four ketones were identified in the cider samples and their corresponding juices (Table 2). Acetaldehyde was the most abundant aldehyde in initial juices and fermented samples (Supplementary Table 2). This compound has been reported as a contributor of *fruity* and *nutty* ordors, however, a high concentration of acetaldehyde (> 110 mg/L) may contribute to *pungent* and *ether* aroma (Li et al., 2020, Luan, Zhang, Duan & Yan, 2018). Notably high levels of acetaldehyde were detected in the ciders made from cultivar 'Lepaan Meloni' (LM), 'Lohjan Kirkas' (LK), and 'Gustavs Bästa' (GB), indicating that the accumulation of acetaldehyde in ciders is apple cultivar dependent. Butanal, hexanal, and (*E*)-hex-2-enal were detected in apple juices, and they disappeared after fermentations. Higher levels of 3-hydroxybutan-2-one (acetoin) were detected in the ciders produced from cultivar 'Juuso' (Ju). The other three ketones, 4-methylpentan-2-one, 6-methylhept-5-en-2-one, and 2,6,8-trimethylnonan-4-one, were found in low concentrations from both apple juices and ciders.

Six volatile acids (acetic acid, 2-methylpropanoic acid, butanoic acid, 3-methylbutanoic acid, pentanoic acid, and hexanoic acid) were identified in apple ciders. Volatile acids are important for aromatic complexity in apple ciders and they can contribute to *vinegar-like*, *sweat*, and *rancid* notes of apple ciders (Qin et al., 2018). Acetic acid was found at high contents in all the cider samples in this work. Acetic acid is formed from oxidation of acetaldehyde during alcoholic fermentation potentially contributing to *sour* and *vinegar-like* odors (Niu, Wang, Xiao, Zhu, Sun & Wang, 2019). The highest content of acetic acid was found in the samples fermented with V1116 (Supplementary Table 2). This result is in accordance with a report concerning apple ciders fermented with *Saccharomyces* and non-*Saccharomyces* yeasts (Madrera, Lobo & Alonso, 2010).

The difference between the apple juices and their corresponding cider samples (Y-data, n=3) in the volatile composition (X-data, n = 77) was analyzed using PLS-DA (Figure 1A). In the PLS model with five validated factors (R^2 = 0.959; validated R^2 = 0.913), the apple juices can be separated clearly from the cider samples already on the first factor. Apple juices are located on the right side of factor-1 with strong positive correlation with 2-methylbutan-1-ol (HA_3), hexyl butanoate (OE_6), hexyl 2-methylbutanoate (OE_7), hexanal (Ad_4), 4-methylpentan-2-one (K_1), and 1-hexanol (HA_9). After fermentation, the total concentrations of each group of volatile compounds elevated significantly. The separation of the cider samples fermented with V1116 from those with SP3796 were shown in another PLS-DA model with three validated factors (Figure 1B; $R^2 = 0.972$; validated $R^2 = 0.937$). High production of several ethyl esters, such as ethyl pentanoate (E_6) and ethyl hexanoate (E_7), and volatile acids, such as 2-methylpropanoic (Ai_2), 3-methylbutanoic (Ai_4), pentanoic (Ai_5), and hexanoic (Ai_6) acids, separated V1116 samples clearly from SP3796 samples on the first two factors. At the same time, clear differences were detected among the cultivars along the factor-1, as the cultivars ‘Lohjan Kirkas’ (LK) and ‘Gustavs Bästa’ (GB) characterized by higher concentration of acetals, such as 1-ethpxy-1-methoxyethane (AC_1), 1,1-diethoxythane (AC_2), and 1-(1-ethoxyethoxy) pentane (AC_3), acetate esters, such as 3-methylbutyl acetate (AE_5) and phenethyl acetate (AE_9), higher alcohols, such as 3-methylpentan-1-ol (HA_8), 2-ethylhexan-1-ol (HA_16), and pentadecan-8-ol (HA_20), acetic acid (Ai_1), and acetaldehyde (Ad_1). Although the apple cultivars influenced the volatile compositions, the major difference came from the yeast strains according to the PLS-DA classification. A total of 51 volatile compounds were detected in the ciders fermented with *S. cerevisiae* while 54 volatile compounds were detected in the cider samples fermented with *S. pombe*. Thus, compared to the commercial *S. cerevisiae* yeast, non-*Saccharomyces* yeasts can produce different sets of volatile compounds. However, fermentation with SP3796 produced less ethyl esters, higher alcohols, and volatile acids compared to that with V1116 according to Table 3. The results are in accordance with the findings in bilberry and grape wines (Liu et al., 2020; Peinado et al., 2004).

3.3 Effect of apple cultivars on the volatile composition of apple ciders

Principal component analysis (PCA) models were applied to visualize the relationships between volatile compound profiles and apple cultivars within the three sample types. As shown in Figure 2A with only juice samples, the first PC separated apple juices according to the apple cultivars. Juices made from cultivar ‘Juuso’ (number 10) located on the left side whereas the others on the right of PC1. This cultivar correlated with certain acetate esters (AE_2, propyl acetate; AE_4, butyl acetate; AE_7, hexyl acetate; AE_8, octyl acetate), other esters (OE_1, methyl butanoate; OE_11, diethyl benzene-1, 2-dicarboxylate), and higher alcohols (HA_12, 1-octen-3-ol; HA_14, heptan-1-ol; HA_18, octan-1-ol). The second PC also discriminated some of the juice samples on the basis of their cultivars as the summer cultivars (‘Alasen Punainen’, ‘Kersti’, ‘Lepaan Meloni’, and ‘Lohjan Kirkas’) were located on the negative side of PC2, and the others on the positive side. On the PC2, variables ethyl 2-methylpropanoate (E_3) and 2-methylbutanoate (E_5), hexyl 2-methylpropanoate (OE_3) and 2-methylbutan-1-ol (HA_3) correlated with the summer apple cultivars, while variables butyl and hexyl butanoate (OE_2 and OE_6, respectively), (*E*)-2-hexen-1-ol (HA_11), and 4-methylpentan-2-one (K_1) were linked to the juices of the autumn apple cultivars.

In Figures 2B and 2C with the cider samples fermented with *S. cerevisiae* and *S. pombe*, the first PCs separated the ciders made from cultivars ‘Lepaan Meloni’ (LM), ‘Lohjan Kirkas’ (LK), and ‘Gustavs Bästa’ (GB) from those made from apples of other cultivars due to the difference in concentration of acetate esters and higher alcohols. The second PC in the model for *S. cerevisiae* samples (Figure 2B), separated the cultivars ‘Lohjan Kirkas’ (LK) and ‘Gustavs Bästa’ (GB), but they were not separated in the model based on the ciders fermented with the *S. pombe* samples (Figure 2C). The PC2 in Figure 2C separated also cultivars ‘Aino’ (An) and ‘Luotsi’ (Lt) from the others; ciders of both cultivars correlated positively with 2-methylpropan-1-ol (HA_1) and negatively with methyl acetate (AE_1). Similar separation was not detected with the cider samples fermented with V1116 (Figure 2B). The volatile compound profiles were more influenced by the fermentation process in comparison to the cultivar differences. Moreover, the PCA results for apple ciders (Figure 2A-C) shared similar patterns with juices among apple cultivars were observed. This might be resulted from the different compositional difference in primary volatile compounds among the cultivars indicating the cultivar difference (cultivar X) as a potential reason for variation in this study, which has been investigated also in previous apple cider studies (Alberti et al, 2016; Braga et al., 2013; Rosend et al., 2019).

3.4 Sensory quality of cider samples

Sensory quality of selected eight cider samples, four fermented from each of the two yeast strains, were characterized using the rated sensory attributes and CATA descriptors to highlight the potential differences between the yeasts. As shown in the PCA model in Figure 3A, a clear differentiation based on the yeast strain was observed on the PC1 among the ciders produced from cultivar 'Turso' (Tr), 'Juuso' (Ju), and 'Hyvingiensis' (Hg). The ciders produced by V1116 were rated higher in appearance liking and the intensities of sourness, puckering astringency, and mouth-drying astringency. These results were in line with the higher consumption of malic acids by SP3796 yeast strain than V1116. However, the average ratings were similar between the yeasts (Supplementary Table 3) as only clear differences were observed in sourness and puckering astringency. Interestingly, the perceived bitterness of the ciders was similar between the yeast strains (Supplementary Table 3). This attribute is typically linked to the non-volatile phenolic compounds, which were not investigated in this study. Potentially, the reduction of acidity using *S. pombe* strains may result in higher intensities of other attributes, e.g. bitterness. Moreover, the ciders produced from 'Gustavs Bästa' (GB) behaved differently in comparison to the other cultivars. They were rated as less sour and astringent compared to others. This effect can be explained by the lower organic acid contents and higher sugar contents in this cultivar (Table 1).

The most often selected CATA descriptors were ‘fruity’, ‘cider-like’, ‘fermented’, ‘sweet’, and ‘floral’ (Supplementary Table 4), which were similar with a previous study of commercial apple ciders (Qin et al., 2018). Among the list of 26 descriptors, only eight attributes resulted in significant differences between the samples based on Cochran’s Q-test ($p < 0.05$). In a PCA model using the frequencies of the CATA descriptors (Figure 3B), the samples made with different yeasts were clearly separated along the PC1 based on the CATA attribute variables. In the loadings plot, the samples fermented with V1116 on the right, can be described as ‘sharp’, ‘dry apple’, ‘alcoholic’, ‘cider-like’, ‘yeasty’, ‘earthy’, ‘fermented’, ‘acidic’, and ‘cooked apple’. Ciders fermented with SP3796 located on the left side and were mainly characterized as ‘floral’, ‘fruity’, ‘tropical fruity’, ‘honey’, ‘sweet’, and ‘diverse’. The improvement on ‘fruity’ odor and mouth-feeling from inoculation with non-Saccharomyces yeasts has also been detected in apple cider and fruit wine productions (Magalhães et al., 2017; Varela, 2016). Additionally, the second PC separated the cultivar ‘Gustavs Bästa’ (GB) from the others, being characterized as more ‘spicy’, ‘cooked apple’, and ‘diverse’.

4. Conclusion

In conclusion, the effect of two different yeast strains (*S. cerevisiae* and *S. pombe*) on the chemical composition of ciders was studied using 11 Finnish domestic apple cultivars. Both fermentation processes resulted in sharp increases in the contents of volatile compounds, especially esters, higher alcohols, aldehydes, acetals, and acids. The major differences between cider samples originated from fermentation with these two yeast species, although apple cultivars had significant impact on the final chemical composition. Certain apple cultivars, including ‘Lepaan Meloni’ (LM), ‘Lohjan Kirkas’ (LK), and ‘Gustavs Bästa’ (GB), were clearly separated from the others using multivariate models based on their volatile compositions or non-volatile acid and sugar profiles. Fermentations with different yeast strains also affected sensory properties of the ciders. Use of *S. pombe* in ciders generally decreased the amounts of malic acid and lead to a decrease of sourness in the cider product. However, this effect may also result in the higher intensities of other attributes, such as bitterness. Furthermore, more studies are needed to find out the impact of fermentation with *S. pombe* strains on the phenolic composition of ciders and thus their contribution to the 'bitterness' and 'astringent' properties. At the same time, these ciders were described as more 'floral', 'fruit', and 'sweet' in comparison to the *S. cerevisiae* ciders, which were typically more 'cider-like', and 'alcoholic'. This study demonstrates the potential of using *S. pombe* strains in cider processing. Furthermore, the study promotes the exploitation of old, local, traditional apple cultivars, which are not currently utilized commercially, in cider processing.

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Figure Captions

Figure 1. PLS-DA models of volatiles as X-data (n = 77) to illustrate the differences between apple juices and apple ciders (A) or between the ciders (B) produced by fermentation with two different yeast strains. *S. cerevisiae* 1116 red circles (V, n = 44), *S. pombe* 3796 blue rectangles (SP, n = 44), juices green triangle (J, n = 22). Abbreviations refer to apple cultivars in Supplementary Table 1 and variables refer to Table 2.

Figure 2. PCA plots of volatile compositions in apple juices (**A**: Juice, 44 volatiles, 22 samples) and apple ciders (**B**: *S. cerevisiae* 1116, 51 volatiles, 44 samples; **C**: *S. pombe* 3796, 54 volatiles,

44 samples) produced with different apple cultivars. Abbreviations refer to apple cultivars in Supplementary Table 1 and variables refer to Table 2.

Figure 3. PCA models for sensory attributes of eight apple cider samples. **A**. rated pleasantness and sensory attributes, n = 11 (Supplementary Table 3), **B**. check-all-that-apply attributes, n = 26.

Supporting Information Description:

Supplementary Table 1. Description of the apple cultivars used in this study

Supplementary Table 2. Semi-quantification of volatiles (mg/L) in the apple ciders fermented with S. *cerevisiae* 1116 and S. *pombe* 3796 and their corresponding juices

Supplementary Table 3. Mean and standard deviations of liking and sensory attributes rated on scales 1-9.

Supplementary Table 4. Sensory descriptors used in the CATA test and their frequencies (n) presented in the order of most often selected attributes.

Supplementary Figure 1. PCA models for sugar and acid compounds in juice and cider samples (n = 110; two analytical replicates from 55 samples). Juices blue rectangles (n = 22), *S. cerevisiae* 1116 green triangles (n = 44), *S. pombe* 3796 red circles (n = 44). Abbreviations in the loading plot refer to apple cultivars in Supplementary Table 1.

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Table 1. Chemical composition of ciders fermented with two yeast strains (S. *cerevisiae* 1116 and S. *pombe* 3796) and corresponding apple juices.

Sample	Malic acid (g/L)	Quinic acid (g/L)	Ascorbic acid (g/L)	Succinic acid (g/L)	Total acids (g/L)	Fructose (g/L)	Glucose (g/L)	Sorbitol (g/L)	Sucrose (g/L)	Xylose (g/L)	Total sugars (g/L)	pH	Brix	Ethanol content (*v/v*, %)	Total CO_2 production (g)
Juices															
AP	8.26 ± 0.22 cd	1.10 ± 0.09 a	ND	ND	9.36 ± 0.31 d	93.02 ± 3.43 d	18.56 ± 0.13 a	3.76 ± 0.24 a	47.17 ± 0.72 d	0.32 ± 0.02 a	162.83 ± 4.54 b	3.24 ± 0.04 b	-	-	-
Kr	2.85 ± 0.22 a	0.93 ± 0.16 a	ND	ND	3.78 ± 0.38 a	89.86 ± 15.82 cd	18.22 ± 0.16 a	5.39 ± 0.22 b	57.54 ± 1.21 e	0.33 ± 0.07 a	171.34 ± 17.88 bc	4.17 ± 0.08 d	-	-	–
LM	4.09 ± 0.17 b	1.22 ± 0.05 a	ND	ND	5.31 ± 0.22 b	95.30 ± 0.80 d	21.51 ± 0.23 a	9.14 ± 0.05 c	34.51 ± 1.10 c	0.22 ± 0.09 a	160.68 ± 2.49 b	3.65 ± 0.01 c	-	-	–
LK	6.41 ± 0.05 c	1.37 ± 0.06 a	ND	ND	7.78 ± 0.11 c	85.67 ± 6.93 c	21.82 ± 0.54 a	5.74 ± 0.07 b	39.29 ± 0.51 c	0.51 ± 0.01 b	153.03 ± 8.06 b	3.07 ± 0.01 b	-	-	–
An	18.94 ± 2.06 f	10.28 ± 2.30 b	ND	ND	29.22 ± 4.36 g	63.70 ± 2.56 a	17.57 ± 2.31 a	9.68 ± 1.53 c	20.39 ± 4.32 ab	0.34 ± 0.05 a	111.68 ± 10.77 a	2.68 ± 0.02 a	-	-	–
GB	3.25 ± 0.24 a	1.02 ± 0.04 a	ND	ND	4.27 ± 0.28 a	91.55 ± 2.11 d	18.61 ± 0.41 a	2.48 ± 0.10 a	60.04 ± 0.46 e	0.21 ± 0.01 a	172.89 ± 3.09 c	3.54 ± 0.03 c	-	-	–
Lt	8.09 ± 1.08 cd	1.20 ± 0.17 a	ND	ND	9.29 ± 1.25 cd	63.75 ± 1.07 a	22.96 ± 1.76 ab	2.23 ± 0.40 a	33.40 ± 3.03 c	0.17 ± 0.03 a	122.51 ± 6.29 a	3.11 ± 0.02 b	-	-	–
Pk	3.43 ± 0.11 a	0.98 ± 0.01 a	ND	ND	4.41 ± 0.12 a	108.10 ± 1.02 e	23.62 ± 0.10 b	4.29 ± 0.02 b	21.06 ± 0.09 b	0.48 ± 0.02 b	157.55 ± 1.25 b	4.09 ± 0.02 d	-	-	–
Tr	9.58 ± 0.38 d	0.89 ± 0.03 a	ND	ND	10.47 ± 0.41 e	78.77 ± 1.90 b	19.27 ± 0.97 a	4.92 ± 0.29 b	50.57 ± 1.90 d	0.13 ± 0.01 a	153.66 ± 5.07 b	3.11 ± 0.02 b	-	-	–
Ju	11.31 ± 0.34 e	0.70 ± 0.02 a	ND	ND	12.01 ± 0.36 f	91.72 ± 2.53 d	20.69 ± 1.23 a	4.69 ± 0.36 b	51.35 ± 4.53 d	0.15 ± 0.03 a	168.60 ± 8.68 bc	3.11 ± 0.01 b	-	-	–
Hg	7.74 ± 0.31 c	0.74 ± 0.02 a	ND	ND	8.48 ± 0.33 c	84.88 ± 1.87 c	52.85 ± 0.64 c	6.54 ± 0.87 b	15.58 ± 0.11 a	0.33 ± 0.02 a	160.18 ± 3.51 b	3.41 ± 0.02 c	-	-	–
mean	7.63 B	1.87 B	ND	ND	9.48 B	85.95 B	23.22 B	5.23 A	39.13 C	0.29 A	153.82 B	3.38 A			
S. cereviaise 1116 ciders															
AP	6.74 ± 0.11 b	0.69 ± 0.09 a	0.40 ± 0.23 ab	1.29 ± 0.12 b	9.12 ± 0.43 b	ND	0.32 ± 0.09 b	3.22 ± 0.37 ab	0.14 ± 0.03 a	0.24 ± 0.01 b	3.92 ± 0.50 ab	3.29 ± 0.01 b	4.25 ± 0.07 a	6.82 ± 0.46 ab	5.20 ± 0.04 c
Kr	2.62 ± 0.12 a	0.51 ± 0.06 a	0.29 ± 0.07 a	1.05 ± 0.05 a	4.47 ± 0.25 a	ND	0.18 ± 0.05 a	3.83 ± 0.45 b	ND	0.50 ± 0.02 d	4.51 ± 0.52 b	3.74 ± 0.02 d	4.20 ± 0.00 a	7.42 ± 0.16 b	5.70 ± 0.09 d
LM	3.22 ± 0.11 a	0.69 ± 0.07 a	0.59 ± 0.33 ab	1.25 ± 0.05 b	5.75 ± 0.51 a	0.11 ± 0.01 a	0.39 ± 0.08 b	8.38 ± 0.67 d	ND	0.35 ± 0.01 c	9.23 ± 0.77 d	3.76 ± 0.07 d	4.45 ± 0.07 ab	6.67 ± 0.42 ab	4.78 ± 0.26 bc

LK	6.07 ± 0.05 b	0.92 ± 0.13 a	0.54 ± 0.03 b	1.37 ± 0.15 bc	8.90 ± 0.21 b	ND	0.24 ± 0.05 a	5.80 ± 0.71 c	ND	0.44 ± 0.03 d	6.48 ± 0.79 c	3.24 ± 0.02 b	4.80 ± 0.00 b	7.25 ± 0.50 b	6.51 ± 0.26 e
An	17.73 ± 0.71 e	6.33 ± 0.40 b	0.52 ± 0.06 b	1.33 ± 0.11 bc	25.91 ± 1.17 d	ND	0.19 ± 0.06 a	4.23 ± 0.28 bc	ND	0.21 ± 0.01 b	4.63 ± 0.35 b	2.72 ± 0.01 a	6.00 ± 0.00 c	5.50 ± 0.50 a	3.77 ± 0.07 a
GB	3.06 ± 0.12 a	0.75 ± 0.12 a	0.32 ± 0.04 a	1.58 ± 0.13 c	5.71 ± 0.28 a	ND	0.23 ± 0.12 ab	2.45 ± 0.36 a	ND	0.16 ± 0.04 ab	2.84 ± 0.52 a	3.67 ± 0.04 d	4.05 ± 0.07 a	6.18 ± 0.24 a	4.33 ± 0.11 b
Lt	7.13 ± 0.26 b	0.74 ± 0.21 a	0.45 ± 0.06 a	1.41 ± 0.05 c	9.73 ± 0.56 b	ND	0.35 ± 0.11 b	2.04 ± 0.28 a	ND	0.13 ± 0.01 a	2.52 ± 0.40 a	3.29 ± 0.03 b	4.30 ± 0.00 a	5.97 ± 0.34 a	4.89 ± 0.06 c
Pk	3.16 ± 0.12 a	0.62 ± 0.04 a	0.73 ± 0.05 c	1.27 ± 0.06 b	5.78 ± 0.21 a	0.23 ± 0.05 a	0.52 ± 0.09 c	3.93 ± 0.09 b	ND	0.82 ± 0.02 e	5.27 ± 0.20 bc	3.85 ± 0.02 d	4.30 ± 0.00 a	6.51 ± 0.21 ab	4.68 ± 0.05 bc
Tr	8.79 ± 0.31 c	0.74 ± 0.03 a	0.43 ± 0.11 ab	1.63 ± 0.08 c	11.59 ± 0.45 c	ND	0.18 ± 0.02 a	5.11 ± 0.22 c	ND	0.12 ± 0.01 a	5.41 ± 0.25 bc	3.20 ± 0.03 b	4.60 ± 0.14 b	7.04 ± 0.19 b	5.04 ± 0.08 c
Ju	10.49 ± 0.47 d	0.44 ± 0.07 a	0.60 ± 0.04 b	1.59 ± 0.13 c	13.12 ± 0.58 c	ND	0.11 ± 0.01 a	4.46 ± 0.59 bc	0.19 ± 0.01 a	0.13 ± 0.01 a	4.89 ± 0.62 b	3.27 ± 0.01 b	4.55 ± 0.07 b	6.72 ± 0.18 ab	6.06 ± 0.09 e
Hg	6.65 ± 0.47 b	0.43 ± 0.06 a	0.59 ± 0.09 b	1.88 ± 0.08 d	9.55 ± 0.62 b	ND	0.57 ± 0.08 c	6.08 ± 0.93 c	ND	0.27 ± 0.03 b	6.92 ± 1.05 c	3.52 ± 0.02 c	4.60 ± 0.14 b	7.37 ± 0.24 b	5.14 ± 0.15 c
mean	6.88 B	1.16 A	0.51 A	1.42 A	9.95 B	0.03 A	0.31 A	4.51 A	0.03 A	0.31 A	5.18 A	3.41 A	4.55 A	6.67 A	5.10 A
S. pombe 3796 ciders															
AP	0.95 ± 0.06 a	0.78 ± 0.09 a	0.53 ± 0.02 b	2.14 ± 0.22 c	4.40 ± 0.17 a	0.75 ± 0.06 b	2.80 ± 0.40 b	3.61 ± 0.44 ab	0.89 ± 0.28 b	0.27 ± 0.01 b	8.32 ± 1.82 bc	4.43 ± 0.11 bc	4.15 ± 0.07 a	6.08 ± 0.23 b	4.62 ± 0.06 b
Kr	0.48 ± 0.03 a	0.68 ± 0.02 a	0.13 ± 0.01 a	1.81 ± 0.04 b	3.10 ± 0.06 a	0.49 ± 0.08 a	1.66 ± 0.32 a	4.62 ± 0.28 b	0.23 ± 0.09 a	1.08 ± 0.03 d	8.08 ± 0.80 bc	4.62 ± 0.18 c	4.20 ± 0.00 a	6.66 ± 0.25 bc	5.97 ± 0.14 d
LM	0.97 ± 0.15 a	0.85 ± 0.06 a	0.19 ± 0.08 a	1.55 ± 0.08 a	3.56 ± 0.59 a	0.91 ± 0.21 b	2.12 ± 0.52 ab	9.85 ± 0.67 d	0.18 ± 0.03 a	0.35 ± 0.01 bc	13.41 ± 1.44 d	4.61 ± 0.07 c	4.50 ± 0.00 b	6.55 ± 0.07 bc	4.31 ± 0.25 ab
LK	1.97 ± 0.21 bc	0.91 ± 0.08 a	0.18 ± 0.01 a	1.96 ± 0.24 bc	5.02 ± 0.30 b	0.38 ± 0.02 a	1.98 ± 0.11 ab	6.02 ± 0.14 c	0.24 ± 0.08 a	0.41 ± 0.01 c	9.03 ± 0.36 c	4.39 ± 0.35 bc	4.65 ± 0.07 b	6.80 ± 0.44 cd	5.13 ± 0.01 c
An	12.23 ± 0.33 d	6.16 ± 0.46 b	0.24 ± 0.13 a	1.61 ± 0.05 a	20.24 ± 0.92 d	0.27 ± 0.02 a	1.71 ± 0.19 a	4.13 ± 0.27 b	0.36 ± 0.07 a	0.22 ± 0.01 a	6.69 ± 0.56 ab	2.87 ± 0.03 a	5.75 ± 0.07 c	5.19 ± 0.20 a	4.16 ± 0.03 a
GB	0.85 ± 0.16 a	0.79 ± 0.05 a	0.17 ± 0.05 a	1.86 ± 0.13 b	3.67 ± 0.32 a	0.65 ± 0.07 b	1.63 ± 0.50 a	2.44 ± 0.23 a	0.09 ± 0.01 a	0.17 ± 0.01 a	4.98 ± 0.82 a	4.25 ± 0.10 bc	4.00 ± 0.00 a	6.25 ± 0.05 b	4.06 ± 0.13 a
Lt	3.12 ± 0.52 c	1.05 ± 0.61 a	0.40 ± 0.16 ab	1.55 ± 0.12 a	6.12 ± 1.29 c	0.21 ± 0.08 a	2.99 ± 0.45 b	2.77 ± 0.26 a	0.21 ± 0.03 a	0.14 ± 0.03 a	6.32 ± 0.85 ab	4.71 ± 0.10 c	3.95 ± 0.07 a	5.93 ± 0.45 b	4.72 ± 0.23 b
Pk	1.42 ± 0.09 b	0.57 ± 0.09 a	0.72 ± 0.11 b	1.72 ± 0.06 ab	4.43 ± 0.29 ab	1.08 ± 0.24 b	3.56 ± 0.63 b	3.72 ± 0.94 ab	0.31 ± 0.09 a	0.48 ± 0.11 c	9.15 ± 1.11 c	5.05 ± 0.05 c	4.40 ± 0.00 ab	6.52 ± 0.30 bc	4.65 ± 0.04 b
Tr	0.77 ± 0.14 a	0.72 ± 0.18 a	0.28 ± 0.02 a	1.95 ± 0.12 bc	3.72 ± 0.34 a	0.68 ± 0.16 ab	1.86 ± 0.32 a	4.83 ± 0.82 bc	0.22 ± 0.07 a	0.12 ± 0.01 a	7.71 ± 1.38 bc	4.59 ± 0.04 bc	4.30 ± 0.00 a	6.91 ± 0.16 c	5.33 ± 0.22 c
Ju	1.89 ± 0.25 b	0.48 ± 0.02 a	0.32 ± 0.09 ab	2.19 ± 0.15 c	4.88 ± 0.36 ab	0.89 ± 0.11 b	1.38 ± 0.11 a	4.73 ± 0.16 b	0.09 ± 0.01 a	0.15 ± 0.01 a	7.24 ± 0.40 b	3.80 ± 0.15 b	4.40 ± 0.28 ab	7.22 ± 0.28 d	4.87 ± 0.15 b

Hg	2.42 ± 0.51 bc	0.48 ± 0.05 a	0.86 ± 0.06 b	1.88 ± 0.17 bc	5.64 ± 0.62 b	0.95 ± 0.23 b	3.23 ± 0.39 b	6.33 ± 1.00 c	1.02 ± 0.19 b	0.29 ± 0.01 b	11.82 ± 1.82 d	4.89 ± 0.10 c	4.50 ± 0.00 b	6.84 ± 0.07 c	5.49 ± 0.05 c
mean	2.51 A	1.24 A	0.35 A	1.79 B	5.88 A	0.67 A	2.56 A	4.87 A	0.37 B	0.78 B	9.24 A	4.38 B	4.43 A	6.45 A	4.85 A

Results represent the mean ± standard deviation. Apple juices in duplicate and apple ciders in four replicates. ND: not detected.

Statistically significant differences between cultivars within each sample type (juice, *S. cerevisiae* or *S. pombe*) are shown with lower case letters a-g and for the mean values are shown with upper case letters A-C (ANOVA with Tukey’s test; p<0.05).

Abbreviations of cultivar numbers refer to Supplementary Table 1.

Table 2. Identification of volatiles by HS-SPME-GC-MS in unfermented apple juices and ciders fermented with *S. cerevisiae* strain 1116 and *S. pombe* strain 3796.

Peak number[a]	Compounds	RI[b]		BP[c]	Formula	Identification[d]	Odor descriptor[e]	Abbreviations
		DB-WAX	SPB-624					
Ethyl esters								
1	ethyl acetate	894	1203	43	$C_4H_8O_2$	MS, LRI, STD	pineapple, sweet, pungent[1]	E_1
2	ethyl propanoate	957		57	$C_5H_{10}O_2$	MS, LRI	fruity[1]	E_2
3	ethyl 2-methylpropanoate	965	1342	43	$C_6H_{12}O_2$	MS, LRI	sweet, tropical fruit, rubber[2]	E_3
4	ethyl butanoate	1037	1483	71	$C_6H_{12}O_2$	MS, LRI, STD	fruity[3]	E_4
5	ethyl 2-methylbutanoate	1053		57	$C_7H_{14}O_2$	MS, LRI	fruity[1]	E_5
6	ethyl pentanoate	1134	1643	88	$C_7H_{14}O_2$	MS, LRI	apple, dry fish, yeast[3]	E_6
7	ethyl hexanoate	1235	1802	88	$C_8H_{16}O_2$	MS, LRI	green apple, brandy, fruity[4]	E_7
8	ethyl octanoate	1440		88	$C_{10}H_{20}O_2$	MS, LRI	fruity, brandy[3]	E_8
9	ethyl 3-hydroxybutanoate	1527		43	$C_6H_{12}O_3$	MS, LRI	grape, roasted nut[5]	E_9
10	ethyl nonanoate	1545		88	$C_4H_{10}O_2$	MS, LRI	fruity[5]	E_10
11	ethyl decanoate	1647		88	$C_{12}H_{24}O_2$	MS, LRI	brandy, burnt, fruity[4,6]	E_11
12	ethyl benzoate	1670		105	$C_9H_{10}O_2$	MS, LRI	fruity, fat, flowery[5]	E_12
13	ethyl dodecanoate	1850		88	$C_{14}H_{28}O_2$	MS, LRI	floral, fruity, green apple[7]	E_13
14	ethyl 3-hydroxydodecanoate	1945		117	$C_{14}H_{28}O_3$	MS, LRI	apple brandy[4]	E_14
Acetate esters								
15	methyl acetate	828		43	$C_3H_6O_2$	MS, LRI	ester, green, sweet[5]	AE_1
16	propyl acetate	977		43	$C_5H_{10}O_2$	MS, LRI	celery, floral, pear[4,6]	AE_2
17	2-methylpropyl acetate	1014		43	$C_6H_{12}O_2$	MS, LRI	apple, banana, floral[4]	AE_3
18	butyl acetate	1072	1506	43	$C_6H_{12}O_2$	MS, LRI	apple, fruit, pungent[6]	AE_4
19	3-methylbutyl acetate	1121	1607	43	$C_7H_{14}O_2$	MS, LRI	apple, fruit, sweet[7]	AE_5
20	pentyl acetate	1175		43	$C_7H_{14}O_2$	MS, LRI	banana, fruit, sweet[8]	AE_6
21	hexyl acetate	1274	1825	43	$C_8H_{16}O_2$	MS, LRI	fruity[4]	AE_7
22	octyl acetate	1481		43	$C_{10}H_{20}O_2$	MS, LRI	citrus, fat, wood[5]	AE_8
23	phenethyl acetate	1831	2123	104	$C_{10}H_{12}O_2$	MS, LRI	floral, fruit, honey[8]	AE_9

Other esters								
24	methyl butanoate	986	1362	43	$C_5H_{10}O_2$	MS, LRI, STD	fruit, ester, floral[7]	OE_1
25	butyl butanoate	1220	1794	71	$C_8H_{16}O_2$	MS, LRI	floral[4]	OE_2
26	hexyl 2-methylpropanoate	1347		43	$C_{10}H_{20}O_2$	MS, LRI	fruity, apple, beer[6]	OE_3
27	methyl octanoate	1394		74	$C_9H_{18}O_2$	MS, LRI	fruity, orange, sweet, wine[6]	OE_4
28	butyl hexanoate	1416		56	$C_{10}H_{20}O_2$	MS, LRI	fruity, grass, green[7]	OE_5
29	hexyl butanoate	1420	2014	43	$C_{10}H_{20}O_2$	MS, LRI	fruity, apple, fresh[4]	OE_6
30	hexyl 2-methylbutanoate	1432	2054	57	$C_{11}H_{22}O_2$	MS, LRI	strawberry[6]	OE_7
31	methyl decanoate	1604		74	$C_{11}H_{22}O_2$	MS, LRI	fresh, wine[6]	OE_8
32	hexyl hexanoate	1618		43	$C_{12}H_{24}O_2$	MS, LRI	apple, fruity[8]	OE_9
33	butyl 3-hydroxybutanoate	1716		45	$C_8H_{16}O_3$	MS, LRI	fruity, brandy[7]	OE_10
34	diethyl benzene-1,2-dicarboxylate	2041		149	$C_{12}H_{14}O_4$	MS, LRI		OE_11
Aldehydes								
35	acetaldehyde	705	924	44	C_2H_4O	MS, LRI	pungent, ripe apple[1,4]	Ad_1
36	butanal	876	1185	44	C_4H_8O	MS, LRI	banana, pungent[6]	Ad_2
37	3-methylbutanal	919	1278	44	$C_5H_{10}O$	MS, LRI	malt, pungent[7]	Ad_3
38	hexanal	1088	1510	44	$C_6H_{12}O$	MS, LRI, STD	grassy, green apple[8]	Ad_4
39	(*E*)-hex-2-enal	1221		41	$C_6H_{10}O$	MS, LRI	green, pungent[1,5]	Ad_5
Higher alcohols								
40	2-methylpropan-1-ol	1095	1255	43	$C_4H_{10}O$	MS, LRI	apple, fusel, malt[6]	HA_1
41	butan-1-ol	1146	1308	56	$C_4H_{10}O$	MS, LRI	medicine, fruit[4,5]	HA_2
42	2-methylbutan-1-ol	1207	1425	57	$C_5H_{12}O$	MS, LRI, STD	banana, fusel, green, malt[3,4,5]	HA_3
43	3-methylbutan-1-ol	1211	1421	55	$C_5H_{12}O$	MS, LRI, STD	alcohol, nail polish[3]	HA_4
44	pentan-1-ol	1252	1470	42	$C_5H_{12}O$	MS, LRI	balsamic, fruity[5]	HA_5
45	4-methylpentan-1-ol	1317		56	$C_6H_{14}O$	MS, LRI	almond, toasted[3]	HA_6
46	2-heptanol	1321		45	$C_7H_{16}O$	MS, LRI	mushroom[4]	HA_7
47	3-methylpentan-1-ol	1330		56	$C_6H_{14}O$	MS, LRI	green, pungent, wine[4,6]	HA_8
48	1-hexanol	1356	1632	56	$C_6H_{14}O$	MS, LRI, STD	green, herbaceous[5]	HA_9
49	3-octanol	1400		59	$C_8H_{18}O$	MS, LRI	citrus, nut, oily[3,5]	HA_10
50	(*E*)-2-hexen-1-ol	1409		57	$C_6H_{12}O$	MS, LRI	grass[6]	HA_11
51	1-octen-3-ol	1452		57	$C_8H_{16}O$	MS, LRI	thyme[5]	HA_12

52	(+)-(*3R,4R*)-3,4-epoxyhexan-1-ol	1456		85	$C_6H_{12}O_2$	MS, LRI		HA_13
53	heptan-1-ol	1460		70	$C_7H_{16}O$	MS, LRI	oily[4,5]	HA_14
54	6-methyl-5-hepten-2-ol	1467		95	$C_8H_{16}O$	MS, LRI	rose[5]	HA_15
55	2-ethylhexan-1-ol	1495		57	$C_8H_{18}O$	MS, LRI	citrus, green, rose[3,5]	HA_16
56	2,4,6-trimethylheptan-4-ol	1509		69	$C_{10}H_{22}O$	MS, LRI		HA_17
57	octan-1-ol	1563		56	$C_8H_{18}O$	MS, LRI	chemical, metal, burnt[4]	HA_18
58	butane-2.3-diol	1582		45	$C_4H_{10}O_2$	MS, LRI	fruity[7]	HA_19
59	pentadecan-8-ol	1559		83	$C_{15}H_{32}O$	MS, LRI		HA_20
Ketones								
60	4-methylpentan-2-one	1025		43	$C_6H_{12}O$	MS, LRI	sulfur[6]	K_1
61	3-hydroxybutan-2-one	1291		45	$C_4H_8O_2$	MS, LRI	buttery, fatty[6]	K_2
62	6-methylhept-5-en-2-one	1341		43	$C_8H_{14}O$	MS, LRI, STD	pungent[6]	K_3
63	2,6,8-trimethylnonan-4-one	1405		69	$C_{12}H_{24}O$	MS, LRI		K_4
Terpenes								
64	α-farnesene	1755		41	$C_{15}H_{24}$	MS, LRI		T_1
Acetals								
65	1-ethoxy-1-methoxyethane	845		59	$C_5H_{12}O_2$	MS, LRI	fruity[3]	Ac_1
66	1,1-diethoxyethane	897	1352	45	$C_6H_{14}O_2$	MS, LRI	fruity, cream[6]	Ac_2
67	1-(1-ethoxyethoxy)pentane	1108	1735	73	$C_9H_{20}O_2$	MS, LRI	fruity, alcoholic[8]	Ac_3
Hydrocarbons								
68	hexane	600		57	C_6H_{14}	MS, LRI, STD	apple processed[5]	H_1
Oxides								
69	2,4,5-trimethyl-1,3-dioxolane	946	1359	43	$C_6H_{12}O_2$	MS, LRI	fruity, wine[7]	O_1
Benzenes								
70	1-ethyl-3-methylbenzene	1248		105	C_9H_{12}	MS, LRI		B_1
71	benzaldehyde	1555		105	C_7H_6O	MS, LRI	almond, cherry[7]	B_2
Volatile acids								
72	acetic acid	1466	1267	43	$C_2H_4O_2$	MS, LRI	sour, vinegar-like[6]	Ai_1
73	2-methylpropanoic acid	1588		43	$C_4H_8O_2$	MS, LRI		Ai_2
74	butanoic acid	1652		60	$C_4H_8O_2$	MS, LRI	rancid[7]	Ai_3
75	3-methylbutanoic acid	1694		60	$C_5H_{10}O_2$	MS, LRI		Ai_4

76	pentanoic acid	1703		60	$C_5H_{10}O_2$	MS, LRI		Ai_5
77	hexanoic acid	1873	1842	60	$C_6H_{12}O_2$	MS, LRI	sweat[8]	Ai_6

[a] Number of volatiles investigated by DB-WAX

[b] Retention indices of volatiles investigated by DB-WAX and SPB-624

[c] BP: base peak of mass spectrum

[d] Identification, MS: mass spectrum; LRI: literature retention index; STD: standard.

[e] Odor descriptors based on literature. [1] Li et al., 2020, [2] Alberti et al., 2016, [3] Qin et al., 2018, [4] Luan et al., 2018, [5] http://www.vcf-online.nl/VcfCompounds.cfm, [6] Varela, 2016, [7] Zió Tufariello, Pati, D'Amico, Bleve, Losito & Grieco, 2019, [8] Niu et al., 2019

Table 3. Average concentrations of volatiles (mg/L) in ciders fermented with two yeast strains (S. *cerevisiae* 1116 and S. *pombe* 3796) and corresponding apple juices.

Sample	Ethyl esters	Acetate esters	Other esters	Total esters	Aldehydes	Higher alcohols	Ketones	Terpenes	Acetals	Hydrocarbon	Oxides	Benzenes	Volatile acids
Juices													
AP	263.46 ± 9.19 f	0.31 ± 0.04 a	6.13 ± 1.02 b	269.91 ± 10.25 g	36.11 ± 1.91 e	181.23 ± 1.73 e	1.32 ± 0.07 c	10.82 ± 0.10 e	ND	ND	0.42 ± 0.02 a	1.14 ± 0.02 bc	ND
Kr	33.02 ± 0.38 c	22.75 ± 0.96 b	2.06 ± 0.16 a	57.83 ± 1.50 b	17.81 ± 0.75 c	147.35 ± 7.30 d	0.86 ± 0.05 ab	0.34 ± 0.09 a	ND	ND	0.87 ± 0.01 b	1.64 ± 0.11 c	ND
LM	93.56 ± 2.10 e	72.75 ± 1.83 c	7.49 ± 0.75 b	173.79 ± 4.69 f	32.78 ± 0.99 e	130.61 ± 0.76 c	1.27 ± 0.09 c	0.34 ± 0.07 a	ND	ND	0.40 ± 0.01 a	1.08 ± 0.09 bc	0.52 ± 0.05 a
LK	87.29 ± 1.29 e	1.61 ± 0.12 a	3.49 ± 0.31 a	92.40 ± 1.65 c	38.41 ± 0.61 e	163.76 ± 3.21 de	0.59 ± 0.03 a	ND	ND	ND	3.01 ± 0.06 c	0.99 ± 0.03 b	ND
An	46.82 ± 2.33 cd	ND	0.33 ± 0.00 a	47.15 ± 1.23 ab	1.52 ± 0.12 a	88.19 ± 2.11 a	1.31 ± 0.11 c	0.98 ±0.03 b	ND	ND	ND	0.54 ± 0.08 a	ND
GB	9.57 ± 1.21 b	66.85 ± 9.23 c	23.72 ± 2.54 c	100.14 ± 12.97 cd	6.58 ± 0.60 b	139.95 ± 3.86 cd	0.84 ± 0.08 ab	1.27 ± 0.02 c	ND	ND	ND	0.78 ± 0.02 ab	0.36 ± 0.06 a
Lt	12.90 ± 1.20 b	65.31 ± 6.59 c	31.86 ± 2.80 d	110.07 ± 10.60 d	8.70 ± 0.73 b	116.86 ± 5.99 b	3.56 ± 0.35 e	0.76 ± 0.08 b	ND	ND	ND	0.99 ± 0.09 b	ND
Pk	13.04 ± 0.54 b	3.16 ± 0.11 a	23.22 ± 1.07 c	39.43 ± 1.72 a	22.38 ± 0.96 d	227.67 ± 2.52 f	0.99 ± 0.05 b	2.58 ± 0.51 d	ND	ND	ND	1.07 ± 0.12 bc	1.08 ± 0.03 b
Tr	2.56 ± 0.08 a	110.30 ± 2.16 d	20.87 ± 1.13 c	133.74 ± 3.38 e	6.65 ± 0.11 b	127.28 ± 4.91 c	1.14 ± 0.09 bc	ND	ND	ND	ND	1.12 ± 0.02 bc	ND
Ju	58.27 ± 2.87 d	490.40 ± 18.04 e	30.19 ± 3.62 d	578.87 ± 24.53 h	26.68 ± 0.87 d	218.47 ± 15.19 f	2.71 ± 0.35 d	ND	ND	ND	0.21 ± 0.03 a	1.61 ± 0.04 c	1.12 ± 0.20 b
Hg	53.05 ± 1.13 d	4.88 ± 0.07 a	1.69 ± 0.13 a	59.62 ± 1.33 b	7.22 ± 0.54 b	98.51 ± 2.23 a	0.62 ± 0.03 a	1.01 ± 0.08 b	ND	ND	ND	1.00 ± 0.01 b	ND
mean	61.23 A	76.21 A	13.73 B	151.18 A	18.62 A	149.08 A	1.38 A	1.65 B	ND	ND	0.45 A	1.09 A	0.28 A
S. cerevisiae 1116 ciders													
AP	95.08 ± 8.75 bc	25.65 ± 2.19 a	12.99 ± 0.42 d	133.72 ± 11.36 b	39.71 ± 5.18 b	2543.95 ± 50.09 d	0.94 ± 0.09 ab	0.95 ± 0.10 a	11.48 ± 0.83 ab	0.85 ± 0.09 a	8.35 ± 0.85 a	2.45 ± 0.17 b	41.23 ± 2.86 bc
Kr	107.71 ± 8.98 c	27.95 ± 2.72 a	0.84 ± 0.49 a	136.49 ± 12.68 b	60.58 ± 2.00 c	1279.22 ± 11.90 a	0.44 ± 0.03 a	ND	19.93 ± 1.06 b	1.48 ± 0.53 ab	22.95 ± 4.25 c	1.69 ± 0.20 a	28.22 ± 1.44 a
LM	109.60 ± 6.02 c	86.33 ± 4.18 cd	1.22 ± 0.16 a	197.14 ± 10.28 c	366.41 ± 13.92 e	2086.84 ± 33.69 c	4.00 ± 0.30 c	0.52 ± 0.06 a	134.58 ± 10.18 cd	1.05 ± 0.07 a	77.78 ± 5.84 d	2.50 ± 0.22 b	36.06 ± 2.55 b

LK	155.12 ± 12.42 e	48.94 ± 4.56 b	1.85 ± 0.63 ab	206.01 ± 17.61 c	395.70 ± 6.93 f	3983.63 ± 115.40 g	4.12 ± 0.49 c	ND	129.69 ± 11.70 c	1.15 ± 0.30 ab	200.57 ± 5.94 e	3.20 ± 0.12 c	64.92 ± 3.82 e
An	76.17 ± 4.09 a	25.24 ± 1.58 a	0.94 ± 0.05 a	102.35 ± 5.72 a	42.34 ± 5.31 b	2683.71 ± 50.70 de	0.88 ± 0.09 a	ND	6.15 ± 0.65 a	1.27 ± 0.34 ab	14.97 ± 0.79 b	1.86 ± 0.16 a	56.36 ± 2.09 d
GB	137.05 ± 8.40 d	80.90 ± 4.05 c	0.68 ± 0.03 a	218.63 ± 12.48 c	309.57 ± 29.89 d	2133.04 ± 53.65 c	5.08 ± 0.20 d	2.01 ± 0.59 b	152.22 ± 9.91 d	1.27 ± 0.35 ab	27.94 ± 2.95 c	2.48 ± 0.18 b	46.57 ± 2.75 c
Lt	90.59 ± 7.34 b	82.07 ± 3.57 c	2.05 ± 0.13 b	174.71 ± 11.03 bc	62.24 ± 3.27 c	2719.40 ± 75.34 e	1.32 ± 0.11 b	1.84 ± 0.38 b	12.29 ± 1.11 ab	1.88 ± 0.39 b	4.95 ± 0.71 a	2.24 ± 0.20 b	57.57 ± 2.58 d
Pk	98.93 ± 4.97 b	35.09 ± 2.13 ab	1.03 ± 0.21 a	135.04 ± 7.31 b	23.18 ± 1.11 a	1929.20 ± 44.35 b	0.42 ± 0.07 a	0.46 ± 0.04 a	7.25 ± 0.29 a	1.60 ± 0.29 b	3.57 ± 0.15 a	1.71 ± 0.14 a	29.56 ± 2.32 a
Tr	102.10 ± 5.38 bc	92.97 ± 4.21 d	2.37 ± 0.40 b	197.44 ± 9.99 c	25.31 ± 0.80 a	3037.98 ± 49.66 f	0.53 ± 0.04 a	ND	8.00 ± 0.15 a	1.39 ± 0.11 ab	5.39 ± 0.08 a	2.45 ± 0.11 b	42.84 ± 4.53 bc
Ju	113.14 ± 2.90 c	181.69 ± 12.15 e	1.24 ± 0.21 a	296.07 ± 15.26 d	32.25 ± 2.78 ab	2468.52 ± 31.74 d	0.52 ± 0.09 a	ND	8.44 ± 0.41 a	1.48 ± 0.21 ab	9.00 ± 0.89 ab	2.85 ± 0.19 bc	56.17 ± 3.27 d
Hg	94.09 ± 2.21 b	48.93 ± 4.91 b	7.89 ± 0.19 c	150.90 ± 7.30 b	34.58 ± 4.31 ab	3224.57 ± 115.91 f	0.34 ± 0.05 a	ND	8.67 ± 1.76 a	1.44 ± 0.05 ab	6.59 ± 0.92 a	1.78 ± 0.08 a	40.51 ± 2.52 bc
mean	107.24 C	66.87 A	3.00 A	177.14 B	126.53 C	2553.64 C	1.69 A	0.53 A	45.34 A	1.35 A	34.73 C	2.29 B	45.46 C
S. pombe 3796 ciders													
AP	66.23 ± 3.66 b	11.13 ± 0.75 a	1.31 ± 0.08 ab	78.67 ± 4.48 a	27.40 ± 2.49 a	1611.71 ± 50.38 b	0.38 ± 0.07 a	0.37 ± 0.05 a	8.18 ± 0.40 a	1.01 ± 0.15 a	8.67 ± 0.65 ab	2.05 ± 0.17 ab	16.46 ± 1.20 b
Kr	78.11 ± 2.23 c	25.67 ± 1.97 bc	0.59 ± 0.06 a	104.38 ± 4.26 b	34.95 ± 2.63 a	1252.22 ± 10.89 a	0.40 ± 0.09 a	ND	13.91 ± 2.04 a	1.79 ± 0.14 a	14.74 ± 0.97 bc	1.95 ± 0.12 ab	14.28 ± 1.35 b
LM	88.29 ± 6.15 d	72.33 ± 1.84 e	1.53 ± 0.22 ab	162.14 ± 8.21 d	242.49 ± 6.65 b	1722.54 ± 14.01 bc	3.79 ± 0.36 c	ND	85.94 ± 7.07 b	1.00 ± 0.15 a	34.22 ± 1.55 e	2.24 ± 0.23 ab	20.71 ± 1.52 c
LK	125.66 ± 6.53 e	30.86 ± 2.36 c	4.75 ± 0.34 d	161.28 ± 9.23 d	290.21 ± 15.39 c	2963.64 ± 50.97 e	5.87 ± 0.19 d	ND	110.90 ± 11.95 c	1.50 ± 0.47 a	37.45 ± 5.03 e	2.55 ± 0.24 b	59.21 ± 2.03 f
An	69.57 ± 3.97 b	25.61 ± 0.72 bc	2.71 ± 0.13 b	97.89 ± 4.81 b	42.39 ± 7.58 a	2986.76 ± 90.09 e	0.91 ± 0.07 b	ND	8.39 ± 0.59 a	1.08 ± 0.67 a	19.92 ± 1.62 c	2.39 ± 0.21 ab	33.86 ± 1.97 e
GB	68.24 ± 4.20 b	62.59 ± 4.40 d	10.37 ± 0.47 e	141.20 ± 9.06 cd	260.27 ± 22.48 bc	2249.04 ± 75.39 d	4.18 ± 0.32 c	1.17 ± 0.12 b	125.98 ± 11.95 c	1.28 ± 0.15 a	25.26 ± 0.76 d	2.31 ± 0.30 ab	34.81 ± 2.54 e
Lt	73.04 ± 3.93 bc	75.75 ± 4.55 e	3.45 ± 0.27 c	152.24 ± 8.75 d	29.62 ± 4.70 a	2175.40 ± 45.09 d	1.13 ± 0.12 b	0.59 ± 0.10 a	10.14 ± 0.59 a	1.20 ± 0.49 a	3.66 ± 0.77 a	2.00 ± 0.29 ab	26.52 ± 1.89 d
Pk	74.35 ± 7.03 bc	21.88 ± 2.40 bc	9.51 ± 0.28 e	105.75 ± 9.71 bc	29.54 ± 6.79 a	1801.25 ± 38.83 c	0.43 ± 0.05 a	ND	11.41 ± 1.11 a	0.84 ± 0.15 a	2.89 ± 0.76 a	2.47 ± 0.56 b	17.05 ± 0.79 b
Tr	52.12 ± 2.89 a	70.60 ± 5.56 e	1.49 ± 0.29 ab	124.21 ± 8.75 c	32.93 ± 6.99 a	1852.65 ± 72.30 c	0.38 ± 0.06 a	ND	20.22 ± 1.49 a	1.30 ± 0.21 a	6.64 ± 0.72 a	2.52 ± 0.16 b	11.93 ± 0.90 a
Ju	48.15 ± 2.05 a	166.36 ± 6.54 f	0.89 ± 0.19 a	215.41 ± 8.79 e	30.66 ± 3.05 a	1369.92 ± 26.55 a	12.47 ± 0.33 e	ND	12.64 ± 1.40 a	1.51 ± 0.19 a	14.01 ± 1.93 bc	1.52 ± 0.08 a	10.90 ± 0.71 a

Hg	96.69 ± 5.32 d	18.13 ± 0.89 a	2.44 ± 0.29 b	117.26 ± 6.51 c	28.45 ± 3.15 a	2101.43 ± 39.11 d	0.37 ± 0.08 a	ND	10.27 ± 0.40 a	1.57 ± 0.51 a	2.35 ± 0.19 a	1.79 ± 0.11 a	14.44 ± 0.83 b
mean	76.40 B	52.81 A	3.55 A	132.77 A	95.36 B	2007.87 B	2.75 B	0.19 A	38.00 A	1.28 A	15.44 B	2.16 B	23.65 B

Results represent the mean ± standard deviation. Apple juices in duplicate and apple ciders in four replicates. ND: not detected.

Statistically significant differences between cultivars within each sample type (juice, ciders fermented with *S. cerevisiae* 1116 or *S. pombe* 3796) are shown with lower case letters a-h and for the mean values are shown with upper case letters A-C. (ANOVA with Tukey’s test; $p<0.05$)

Abbreviations of samples refer to Supplementary Table 1.

Figure 1

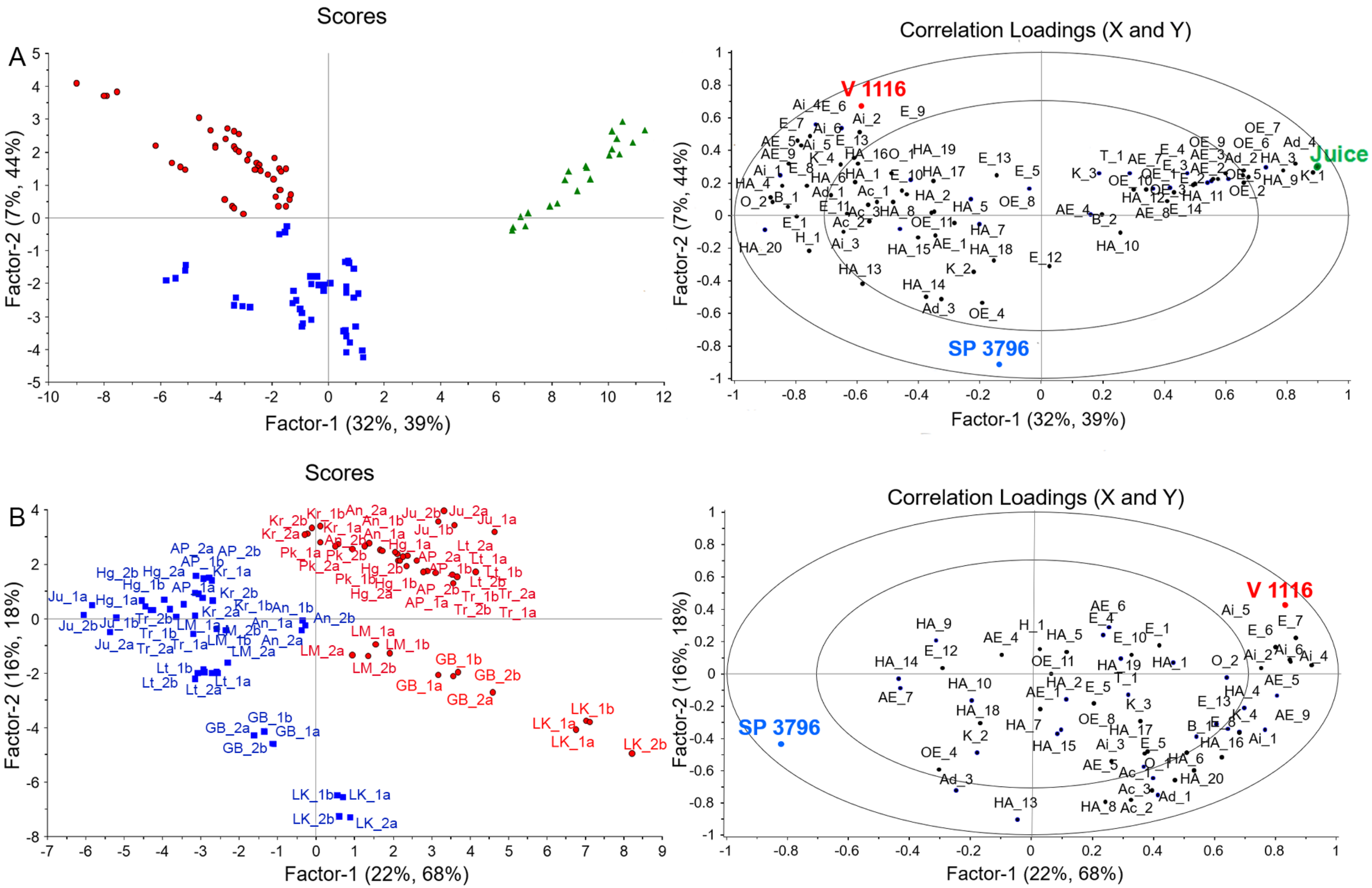

A
Scores
Factor-2 (7%, 44%)
Factor-1 (32%, 39%)
5
4
3
2
1
0
-1
-2
-3
-4
-5
-10
-8
-6
-4
-2
0
2
4
6
8
10
12
Correlation Loadings (X and Y)
V 1116
Juice
SP 3796
Factor-2 (7%, 44%)
Factor-1 (32%, 39%)
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
B
Scores
Factor-2 (16%, 18%)
Factor-1 (22%, 68%)
4
2
0
-2
-4
-6
-8
-7
-6
-5
-4
-3
-2
-1
0
1
2
3
4
5
6
7
8
9
Correlation Loadings (X and Y)
V 1116
SP 3796
Factor-2 (16%, 18%)
Factor-1 (22%, 68%)

Figure 2

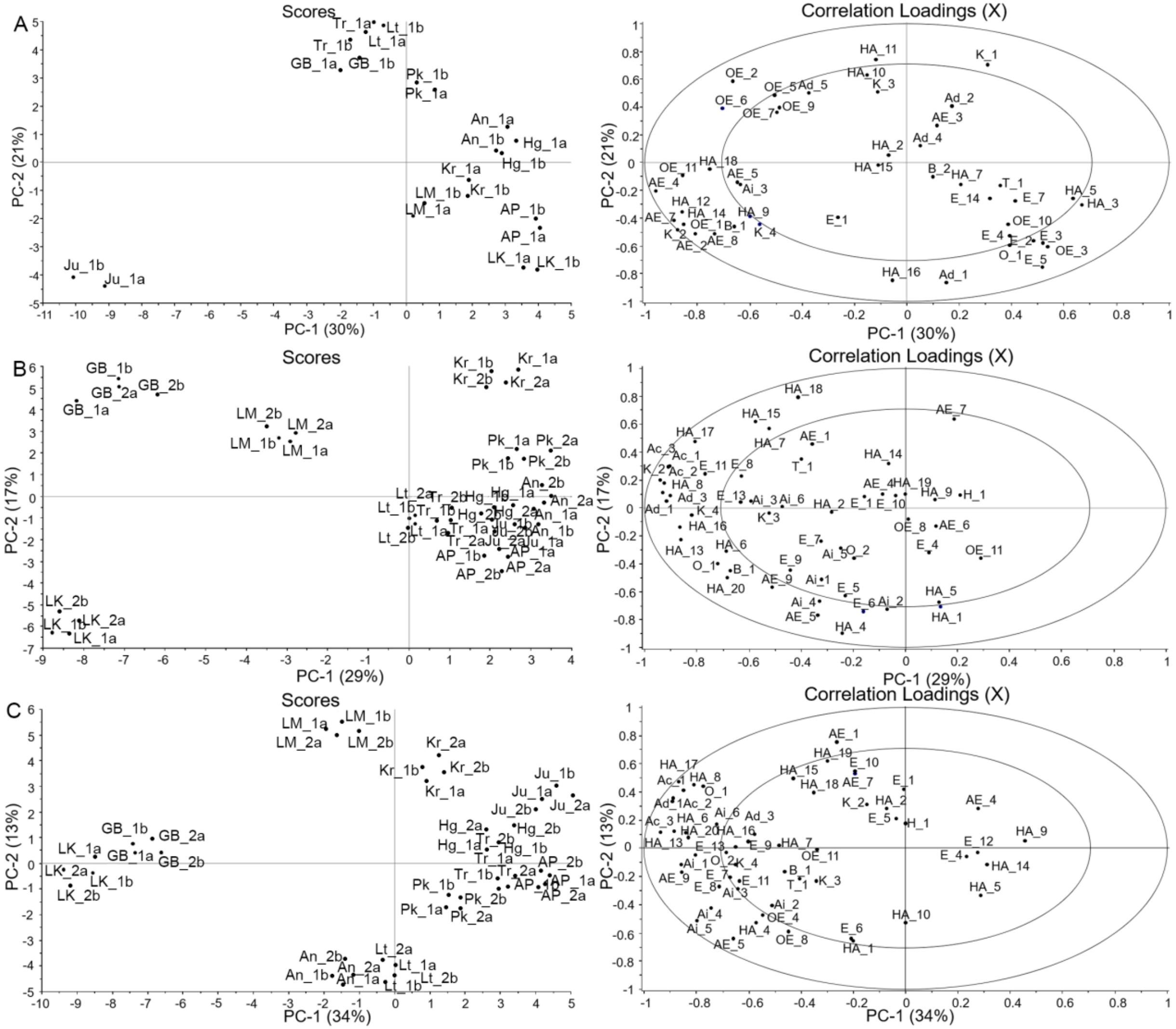
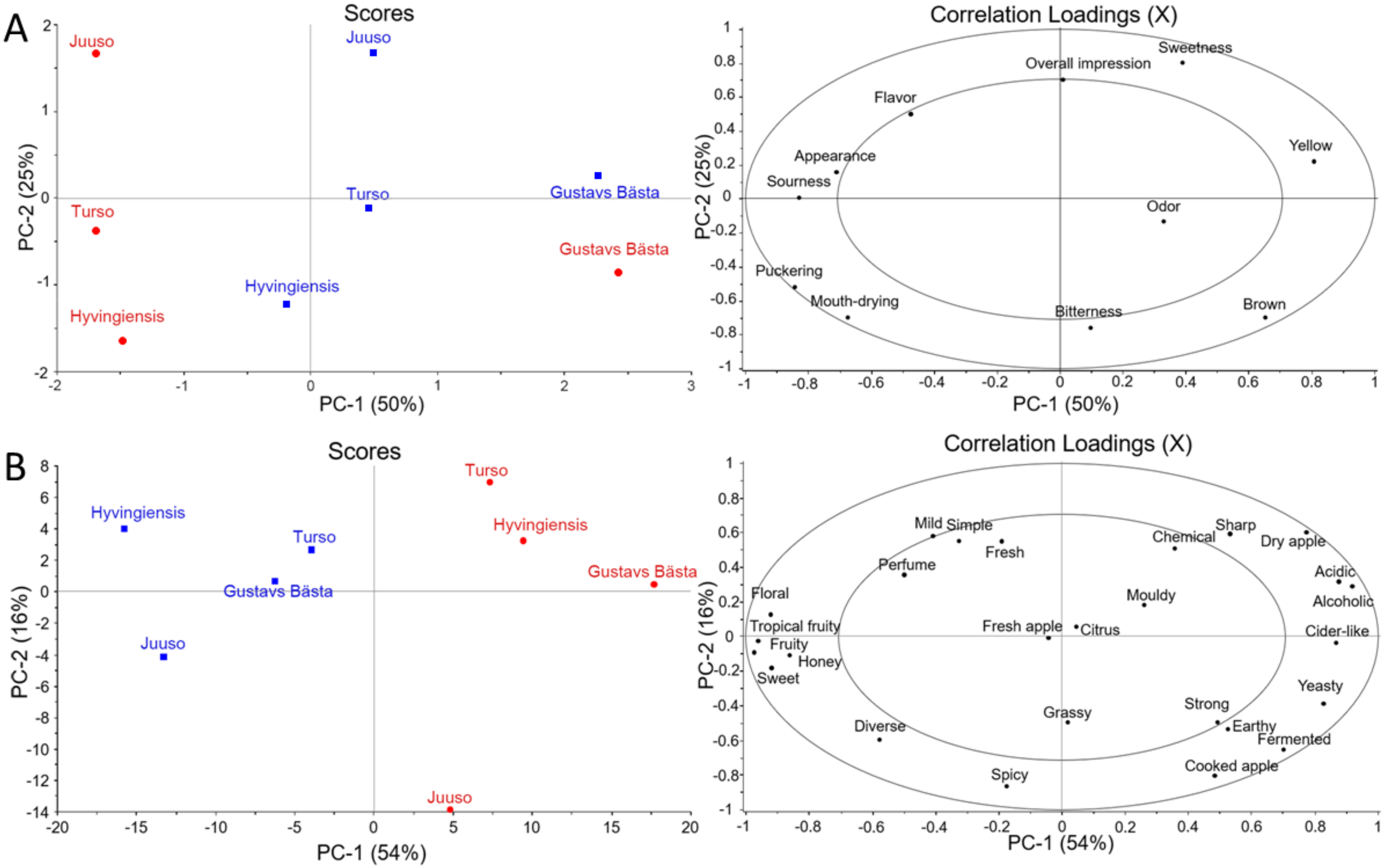

A
Scores
Tr_1a
Lt_1b
Tr_1b
Lt_1a
GB_1a
GB_1b
Pk_1b
Pk_1a
An_1a
An_1b
Hg_1a
Hg_1b
Kr_1a
Kr_1b
LM_1b
LM_1a
AP_1b
AP_1a
LK_1a
LK_1b
Ju_1b
Ju_1a
PC-1 (30%)
PC-2 (21%)
Correlation Loadings (X)
HA_11
K_1
HA_10
OE_2
OE_5
Ad_5
K_3
OE_6
OE_7
OE_9
Ad_2
AE_3
Ad_4
HA_2
OE_11
HA_18
AE_5
HA_15
B_2
HA_7
T_1
AE_4
Ai_3
E_14
E_7
HA_5
HA_3
HA_12
HA_14
HA_9
E_1
AE_7
OE_1
B_1
K_4
OE_10
K_2
AE_8
E_4
E_3
AE_2
E_2
OE_3
O_1
E_5
HA_16
Ad_1
PC-1 (30%)
PC-2 (21%)
B
Scores
GB_1b
GB_2a
GB_2b
GB_1a
LM_2b
LM_2a
LM_1b
LM_1a
Kr_1b
Kr_1a
Kr_2b
Kr_2a
Pk_1a
Pk_2a
Pk_1b
Pk_2b
An_2b
An_2a
An_1a
An_1b
Hg_1a
Hg_1b
Hg_2b
Hg_2a
Lt_2a
Tr_2b
Lt_1b
Tr_1b
Lt_1a
Tr_1a
Lt_2b
Tr_2a
Ju_2a
Ju_1a
Ju_2b
Ju_1b
AP_1b
AP_1a
AP_2b
AP_2a
LK_2b
LK_1b
LK_2a
LK_1a
PC-1 (29%)
PC-2 (17%)
Correlation Loadings (X)
HA_18
AE_7
HA_15
HA_17
HA_7
AE_1
Ac_3
Ac_1
HA_14
K_2
Ac_2
E_11
E_8
T_1
HA_8
AE_4
HA_19
HA_9
H_1
Ad_3
E_13
Ai_3
Ai_6
HA_2
E_1
E_10
Ad_1
K_4
K_3
OE_8
AE_6
HA_16
E_7
HA_13
HA_6
Ai_5
O_2
E_4
OE_11
E_9
O_1
B_1
AE_9
Ai_1
HA_20
E_5
Ai_4
E_6
Ai_2
HA_5
AE_5
HA_4
HA_1
PC-1 (29%)
PC-2 (17%)
C
Scores
LM_1b
LM_1a
LM_2a
LM_2b
Kr_2a
Kr_1b
Kr_2b
Kr_1a
Ju_1b
Ju_1a
Ju_2a
Ju_2b
GB_1b
GB_2a
GB_1a
GB_2b
LK_1a
LK_2a
LK_1b
LK_2b
Hg_2a
Hg_2b
Hg_1a
Tr_2b
Hg_1b
Tr_1a
AP_2b
Tr_1b
Tr_2a
AP_1a
AP_1b
AP_2a
Pk_1b
Pk_2b
Pk_1a
Pk_2a
An_2b
Lt_2a
An_2a
Lt_1a
An_1b
An_1a
Lt_2b
Lt_1b
PC-1 (34%)
PC-2 (13%)
Correlation Loadings (X)
AE_1
HA_19
HA_17
E_10
HA_15
HA_8
Ac_1
AE_7
E_1
HA_18
O_1
Ad_1
Ac_2
K_2
HA_2
AE_4
Ai_6
Ad_3
E_5
H_1
Ac_3
HA_6
HA_20
HA_16
HA_9
HA_13
E_13
E_9
HA_7
E_12
OE_11
E_4
Ai_1
O_2
K_4
HA_14
B_1
AE_9
E_7
E_11
T_1
K_3
HA_5
E_8
Ai_3
Ai_2
HA_10
Ai_4
OE_4
Ai_5
HA_4
E_6
OE_8
AE_5
HA_1
PC-1 (34%)
PC-2 (13%)

Figure 3


A
Scores
Juuso
Juuso
Turso
Turso
Gustavs Bästa
Gustavs Bästa
Hyvingiensis
Hyvingiensis
PC-2 (25%)
PC-1 (50%)
-2
-1
0
1
2
3
Correlation Loadings (X)
Sweetness
Overall impression
Flavor
Yellow
Appearance
Sourness
Odor
Puckering
Mouth-drying
Bitterness
Brown
PC-2 (25%)
PC-1 (50%)
-1
-0.8
-0.6
-0.4
-0.2
0
0.2
0.4
0.6
0.8
1
B
Scores
Turso
Hyvingiensis
Hyvingiensis
Turso
Gustavs Bästa
Gustavs Bästa
Juuso
Juuso
PC-2 (16%)
PC-1 (54%)
8
6
4
2
0
-2
-4
-6
-8
-10
-12
-14
-20
-15
-10
-5
0
5
10
15
20
Correlation Loadings (X)
Mild
Simple
Fresh
Chemical
Sharp
Dry apple
Perfume
Acidic
Alcoholic
Floral
Mouldy
Tropical fruity
Fresh apple
Citrus
Cider-like
Fruity
Honey
Sweet
Yeasty
Grassy
Strong
Earthy
Fermented
Diverse
Spicy
Cooked apple
PC-2 (16%)
PC-1 (54%)
-1
-0.8
-0.6
-0.4
-0.2
0
0.2
0.4
0.6
0.8
1