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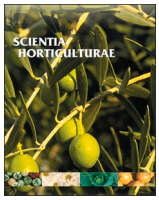

Research Paper

Impact of postponed harvests and withering on the aromas development of Yellow Muscat “fiori d’arancio” berries

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ABSTRACT

The composition of grape berries, and consequently wine characteristics, can be deeply modified by late harvest (LH) or withering (W). Alternatively, a practice called "Poly Double Maturation Reasoned" (PDMR) has been developed, consisting of the cutting of fruit-bearing vines followed by the "reasoned" harvest. PDMR differs from LH or W mainly for what concerns water loss rates and re-programming of berry metabolism. This study aimed to investigate molecular, biochemical, metabolic and sensorial changes in *Vitis vinifera* cv. Yellow Muscat grape berries subjected to LH, W, and PDMR techniques. Analyses pointed out significant differences in both primary and secondary metabolites. According to gene expression, LH, PDMR, and W berries an up-regulation of genes involved in sugar biosynthesis and a down-regulation of those involved in malate catabolism when compared to traditional harvest (TH) was observed. Transcripts involved in monoterpenes biosynthesis were significantly altered in PDMR berries. Analysis of volatiles indicated that PDMR wines showed levels of linalool and linalool oxides similar to TH ones, while their homovanillic alcohol/acid content was more similar to that of W-wines. Our results suggest that PDMR can be either applied to preserve the typicity of yellow Muscat "Fior d’Arancio" or to produce new wine types.

1. Introduction

The degree of grape ripeness at harvest is a main factor affecting the aroma profile of a particular grape variety. This is particularly important because grapes are non-climacteric fruits and do not continue to ripen after being harvested (Galli et al., 2021; Piazzolla et al., 2015). The harvest date is traditionally determined by the sugar content of the juice or by reference to indices considering both sugar content and acidity (Ribereau-Gayon et al., 2006). However, these indices are not always matched by the aromatic maturity of the grape berry evaluated according to its aromatic potential, which impact the wine aroma, a key attribute shaping wine styles (Zhao et al., 2019). In particular, terpenes’ content may decrease once optimal sugar levels are attained, although this may be influenced by temperature and water availability during grape ripening (Buesa et al., 2021; Ribereau-Gayon et al., 2000; 2006). Terpenes are one of the most important groups of volatile compounds contributing to the aroma profile of grapes and wines (Li et al., 2023; Marais, 1983). With climate change, intense heat waves are more frequent, and grapes from varieties particularly rich in terpenes, and characterized by these aroma compounds such as Muscat, need to be harvested earlier in comparison to the other cultivars. This solution can be suitable for maintaining an adequate level of terpenes but, often, cannot ensure satisfactory levels of soluble solids and organic acids. A possible alternative to early harvesting is the “Poly Double Maturation Reasoned” (PDMR). PDMR consists in a sort of on-plant withering obtained through the reasoned cut of the heads to fruit and/or of shoots (Cargnello, 1992; Cargnello et al., 1995). This is a distinctive approach to plant care and holding the potential to impact both the quality and quantity of wine production. Initially proposed by Cargnello et al. (1996), PDMR was later adapted for raisin grape cultivation by Carbonneau and Murisier (2009). Actually, cutting canes produces two cluster populations: the first is located above the cut, where the

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Table 1
Description of the samples along with their respective harvest days concerning TH samples.

Samples	Description	Days relative to TH
TH	Traditional Harvest	0
LH	Late Harvest	21
PDMR1	Poly Double Reasoned Maturation	8
PDMR2	Poly Double Reasoned Maturation	15
PDMR3	Poly Double Reasoned Maturation	21
PDMRW1	Poly Double Reasoned Maturation 3 + Withering 1	17
PDMRW2	Poly Double Reasoned Maturation 3 + Withering 2	36
W1	Withering at 10 % of water loss	17
W2	Withering at 30 % of water loss	36

connection between cluster and vine is still active, whereas the second comprises clusters for which the connection with the plant is interrupted. The metabolite profile of the first cluster population closely resembles that of late harvest (LH) berries. This is because in both cases, the vascular connection is preserved and dehydration events that usually occur during the over-ripening process are not always present. Whereas, in the second cluster population, biochemical changes occur related to water loss (e.g. a strong increase of sugar content) similarly to what already observed in berries subjected to withering (W) (Corso et al., 2013). The adoption of PDMR causes significant changes of both primary (increase in sugar content, reduction of malate decreases) and secondary metabolism (re-equilibrium of polyphenols profile) in the berry, due to the stress caused by the application of PDMR (Bonghi et al., 2012; Jahnke et al., 2023). Therefore, the composition of PDMR berries is significantly modified in comparison to traditional harvest (TH), LH or W berries, these modifications resulting in an improvement of the sensory quality of wines (Corso et al., 2013; Reščič et al., 2016). Yellow Muscat berries are used to produce the "Fior d'Arancio" in the Euganean Hills (Padova, Italy), the only DOCG (Denominazione di Origine Controllata e Garantita) for this area. Fior d'Arancio is generally a light-bodied, making it an approachable and easy-to-drink wine. Its lower alcohol content, typically around 6–7 %, adds to its lightness and makes it a popular choice as dessert wine (https://www.collieuganeidoc.com/en/colli-euganei-fior-darancio-docg-2). As a matter of fact, the demand for "Fior d'Arancio" sparkling type is constantly growing, however a diversification of these wines without altering their typical aromatic bouquet is required by the local wineries to enlarge the market, as the new special wine classified in the "passito" and "dry" wine categories (https://www.collieuganeidoc.com/en/colli-euganei-fior-darancio-docg-dry). In this context, the aim of this research was to investigate the effects of the application of the PDMR technique by comparing it with LH and W at 10 % and 30 % of water loss, as well as with the combination of PDMR and W. The effects of these different techniques on metabolic processes responsible characteristics of grapes and wines have been evaluated by biochemical, molecular and aroma analyses.

2. Material and methods

2.1. Plant material

Trials were conducted on Yellow Muscat berries, grafted onto Kober 5BB rootstock and trained using the arcuate Guyot system. The berries were harvested in 2013 from 9-year-old vines grown in a commercial vineyard owned by Società Agricola Veronese, located in Valnogaredo di Cinto Euganeo, in the Euganean Hills (province of Padova, Italy), at coordinates 45°18′01.94″N and 11°39′13.72″E (Supplementary Fig. S1). The vineyard has rows oriented in a west-east direction and given the short length of the rows and the location, it was assumed that no significant differences in terrain (such as exposure, drainage, soil type, and depth) existed between or within rows. The vineyard is situated on a terrain with a 15 % slope, featuring Epileptic Rendzic Phaeozems (Hypercalcaric, Skeletic). The vines were not irrigated during the growing season. Meteorological data relevant to the trial can be found in the supplementary Fig. S2. Three-hundred and sixty plants were selected and divided in four groups (I, II, III, IV), with each group composed of 90 plants subdivided in three biological replicates (30 plants for each replicate). Two bunches per plant were collected at different times: a) at TH, which occurred at the first week of September (I group), b) at 21 days after TH (DATH) corresponding to LH berries (over-ripened in plant, II group), c) at 8 (PDMR1), 15 (PDMR2), and 21 DATH (PDMR3) (III group). These PDMR berries collected from clusters located below the cut; d) at TH and maintained in a drying cell up to a 10 % (reached 17 DATH and named W1) and 30 %, (reached 36 DATH and named W2) of water loss (IV group). Other PDMR-berries collected at 21 DATH were transferred in a drying cell up to 10 and 30 % of water loss (named PDMRW1 and PDMRW2, respectively) (Table 1). The bunches were selected from the middle part of the canopy on both sides and were in excellent sanitary condition. No defoliation of the canopy was performed during the trial period (Supplementary Fig. S3). At each sampling date, to reduce variability both within and between clusters, the berries were sorted using a flotation method as described by Rolle et al. (2012). The most representative berries, with a density rang between 1081 and 1094 kg/m^3, were selected for the following studies. The sorted berries were visually inspected before analysis; those with damaged skins were discarded. Then the berries were separated in two groups: the first to be used immediately for biochemical and sensory analyses, and the second (frozen in liquid nitrogen and stored at −80 °C) for transcript and metabolite analysis. One hundred kg of TH, LH, PDMR3, W2 and PDMRW2 berries were used to produce wines following a microvinification protocol previously developed (Tomasi et al., 2013). The bunches, which underwent a withering process, were carefully selected and placed in perforated plastic boxes under controlled conditions. They were stored in a dehydration tunnel (Marvil Engineering SpA, Egna-Ora, Bolzano, Italy) with the following environmental settings: temperature at 20±1 °C, relative humidity (RH) at 40±5 %, and air flow between 1 and 1.5 m/s (Rizzini et al., 2009).

2.2. Basic juice analysis

The juice from fifty homogenized berries was used to measure total acidity (g/L), malic and tartaric acid (g/L), pH and sugars content (°Brix) concentration, using a WineScan™ Basic (FOSS, Italia) analyzer following the manufacturer's instructions.

2.3. Analysis of aromatic compounds

2.3.1. Extraction from berries

Sample preparation and analyses for volatile was performed according to Tomasi et al. (2013). Briefly, skins of 10 frozen berries were extracted using 30 mL of methanol for 4 h at room temperature. After homogenization and centrifugation, the pellet was resuspended in 30 mL of water, and the resuspension was centrifuged again. The first methanolic supernatant was vacuum evaporated at 30 °C and mixed with the second supernatant. The resulting solution was then transferred to a flask and brought to volume (250 mL) with water containing 1 g of PVPP, agitated for 1 hour, and filtered. 200 µL of 1-heptanol (164 mg/L) were added to the sample, which was then loaded into a 10 g C18 columns activated with 10 mL methanol, washed with 100 mL water, and eluted with 50 mL dichloromethane into 50 mL flasks chilled with ice. After this step, the column was washed with 30 mL methanol to recover glycosylated aroma compounds. The resulting solution was evaporated, resuspended in citrate-phosphate buffer (pH 5) containing 20 mg/mL pektolase 3PA (Grinsted) and 10 mg/mL hemicellulase (Gist-Brocades). The mixture was incubated at 40 °C for 16 h Then, after the addition of 200 µL of 1-decanol (166 mg/L), the resulting mixture was flowed through a 1 g C18 Sep-Pak cartridge. Compounds were eluted with 6 mL

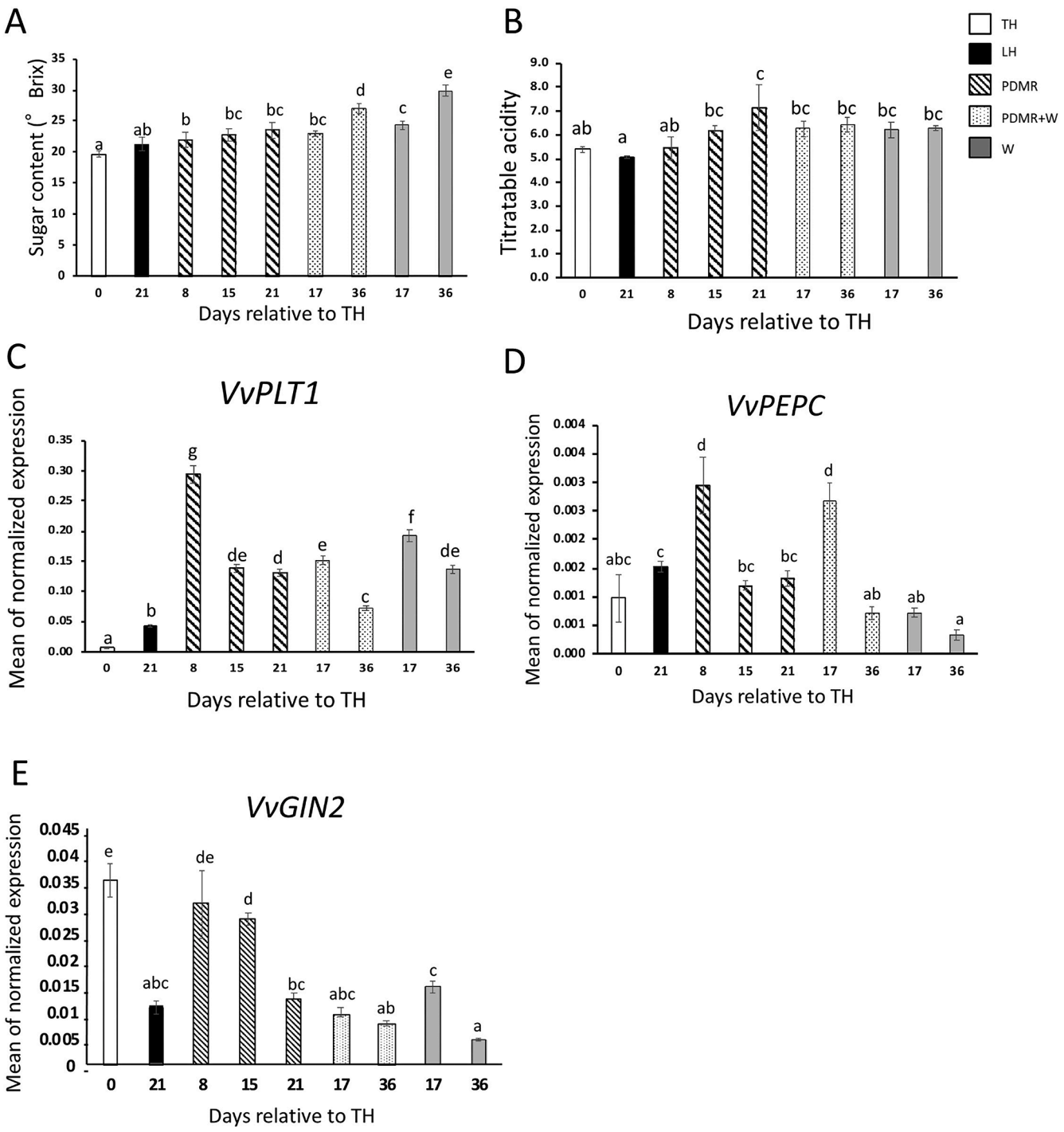

Fig. 1. Analysis of biochemical and molecular parameters in Yellow Muscat berries. Sugar content (°Brix) (A), Titratable acidity (B), and gene expression of VvPTL1 (C), VvGIN2 (D) and VvPEPC (E) across the samples of traditional harvest (TH), late harvest (LH), poly double reasoned maturation (PDMR1, PDMR2 and PDMR3 sampled 8, 15 and 21 DATH), PDMR3 + withering 1 and 2 (PDMR+W1 and +W2 sampled at 17 and 36 DATH) and withering 1 and 2 (W1 and W2 sampled at 17 and 36 DATH). Significant differences among samples ($p < 0.01$) are indicated by different letters as determined by appropriate statistical analysis. Error bars represent standard errors of the mean.

dichloromethane and concentrated under nitrogen to 200 µL. Chilled dichloromethane samples were treated with anhydrous sodium sulfate and paper filtered into rotary evaporator flasks. The filter was washed with dichloromethane to recover aromas, then the solution was evaporated using a Vigreux column (50–60 °C). The resulting volume (~5 mL) was further concentrated to 200 µL under nitrogen flow.

2.3.2. Extraction from wine

50 ml of wine were added of 400 ml of a solution of 1-heptanol at 445 mg/L as the internal standard. The sample was extracted with 15 ml of dichloromethane, repeating the extraction 3 times. The organic phases were combined and washed with a 5 % sodium bicarbonate solution. The solution was dehydrated using anhydrous sodium sulfate, concentrated to 3 ml by distillation with a Vigreux column, and finally brought to 0.5 ml using a nitrogen flow.

2.4. Gas chromatography/mass spectrometry analysis (GC/MS)

A Hewlett-Packard (HP) system (Palo Alto, CA, USA) was used, consisting of an HP 5890 gas chromatograph equipped with an HP Innowax fused silica column (Supelco, Milan) (30 $m \times 0.25$ mm; film thickness 0.25 mm) interfaced with an HP5971A mass spectrometer and a 6890 Series Injector autosampler. Experimental conditions were as follow: injector temperature 200 °C; splitless injection mode; injected sample volume 1 ml; transfer line temperature 280 °C; helium carrier gas at constant pressure of 12 psi. The temperature program of the oven for analysis of fermentative origin was 4 min at 38 °C, increase of 5 °C/min to 180 °C, 10 °C/min to 230 °C, 10 min at 230 °C. The temperature program of the oven for analysis of volatile compounds of grape origin (varietal aroma) was 1 min at 32 °C, 2 °C/min to 160 °C, 3 °C/min to 230 °C, 5 min at 230 °C. Compound identification was performed by comparison with the fragmentation spectra of the NIST98 database (Version 1.6) and the ESTRATTI database of the CENTRO DI RICERCA PER LA VITICOLTURA" of Council for research and experimentation in Agriculture (CRA-VIT).

2.5. Gene expression analysis

RNA extraction and Real Time-PCR analysis were performed as described by Corso et al., 2013.

Specific primers utilized in RT-PCR have been listed in Supplementary Table 1.

2.6. Microvinification and wine sensory analysis

Experimental wines were produced starting from TH, PDMR3, and W2 grape berries by using the standard microvinification protocol developed by CRA-VIT (Alessandrini et al., 2017). Briefly, berries were crushed and pressed using a membrane press at 1.2 atm. Then, 100 mg L^{-1} of potassium metabisulfite and 3 mg L^{-1} of pectolytic enzyme were added to the must. Clarification was performed for 12 h, and the juice was then separated from the lees. Alcoholic fermentation was conducted at 18 °C for 18–20 days. After fermentation completion, the wines were filtered and bottled. The obtained wines were used for sensory analysis performed by a panel formed by twelve members who were considered as experts. The panel members were either winemakers or equally experienced laboratory staff members selected for their consistent assessments. The sessions consisted of presenting the three types of wines to the judges for comparative purposes. Exactly 50 mL of wine was poured into a tasting glass (UNE-EN ISO 3591:1977) fitted with a lid to minimize aroma losses. Each glass was identified by a 3-digit code. The room temperature was set at 22 °C and the samples were presented randomly.

The sensory analysis considered two different evaluation phases: 1) Olfactory profile, and 2) general evaluation. In the first evaluation phase, the most common descriptors for sensory analysis of the olfactory profile of a wine were considered, including aromaticity, fruity, floral, herbaceous, fragrant, and spicy notes. Specific scents typically associated with Yellow Muscat Fior d'Arancio DOCG were added to the evaluation sheet, including muscat grape, lemon, orange, apricot, pineapple, banana, wisteria, rose, lime tree, vanilla, and cinnamon. Moving on, the "general evaluation" of the wine was performed, using parameters summarizing color, taste, phenolic maturity, retro-olfactory persistence, and providing an overall judgment of the product under evaluation with particular attention to mouthfeel descriptors. The wine samples were quantitatively assessed using a 10-point interval scale, where 1 indicated none, 5 indicated moderate intense, and 10 indicated extremely intense.

2.7. Statistical analysis

All experiments were performed in randomized blocks with three biological replicates. Blocks distribution have been reported in Fig. S1. Data were statistically analyzed with SPSS (Statistical Package for Social Scientists) software of 26 version. One-way ANOVA ($p < 0.01$) and Duncan's multiple range tests were conducted to measure the differences between treatments. PCA analysis has been carried out by using the PAST software (version 4.16) (Hammer et al., 2001). Heatmaps were obtained uploading data in a web server tool called ClustVis, a web tool for visualizing clustering of multivariate data, which is available in https://biit.cs.ut.ee/clustvis/.

3. Results and discussion

3.1. Composition of Muscat berries are deeply modified by PDMR

The weather conditions, although in the presence of a moderate drought in September (Fig. S2), slightly modified the content of sugar and titratable acidity in LH berries (Fig. 1 and B). This outcome was somewhat expected, given that studies have indicated that water scarcity in the initial stages has a more significant impact on sugar and acidity levels than during later stages (Geng et al., 2022). The use of PDMR and W (both separately and in combination) leads to a significant increase in sugar content (Fig. 1A) and, partially, titratable acidity increased in Yellow Muscat berries (Fig. 1B, particularly in PDMR3 at 21 DATH). This is in agreement with has been reported in berries of *Vitis vinifera* cv. Raboso Piave subject to W (Rizzini et al., 2009) or LH and PDMR (Corso et al., 2013; Giacosa et al., 2019). The variations in sugar and organic acid content primarily result from the dehydration processes during on-plant and off-plant drying. Observing the PDMR, PDMR+W, and W berries reveals significant differences in their water loss rates. These variations are thought to have a considerable impact on the distinct kinetics of sugar and organic acid concentration (Rizzini et al., 2009).

However, the level of sugars in PDMR and W berries could also be the result of an increase of biosynthesis/transport of osmoprotective molecules, such as sorbitol, into the berries (Conde et al., 2011). To support this view, it must be highlighted that the expression of the polyol transporter gene (*VvPTL1*) was most up-regulated in PDMR1 and W1 berries in comparison to TH (Fig. 1C). A similar result was found by Conde et al. (2018), wherein several other sugar transporter genes exhibited heightened expression following a dehydration process in grapes. According to Conde et al. (2015), *VvPLT1*, functions as an H^+-dependent transporter for polyols/monosaccharides, with its transcription being regulated by environmental stressors such as water deficit and dehydration. This result suggests that postharvest dehydration stimulated the capacity for accumulation of polyols into berry cells as a molecular response.

Molecular analysis also suggests that the higher level of organic acids observed in PDMR berries in comparison to TH, could be due to both malic acid synthesis and the detriment of its catabolism. Actually, transcript phosphoenolpyruvate carboxylase (*VvPEPC*), whose product catalyzes the synthesis of oxaloacetate (precursor of malic acid) from phosphoenolpyruvate (Sweetman et al., 2009), showed high expression in PDMR1 and PDMRW1 berries (Fig. 1D). This observation suggests that in PDMR berries could somehow not be obliged to consume malic acid instead of sugar, nor utilize it as substrate for neoglucogenesis. A synthesis of malic acid uncoupled with increased sugar content was observed in ripe grape berries undergoing alternate warm/cold temperature regimes (Rienth et al., 2016). This behavior has been associated with a better carbon status of plants exposed to cool conditions (Luchaire et al., 2023). Whether the application of PDMR can alter the carbon status remains to be demonstrated, although early pruning (4–10 days after harvest) did not interfere with the global vine performances (Falginella et al., 2022).

The vacuolar invertase *VvGIN2* was highly expressed at TH and at PDMR1, followed by PDMR2 (Fig. 1E). GIN2 is a pivotal enzyme in sucrose hydrolysis, catalyzing the conversion of sucrose into glucose and

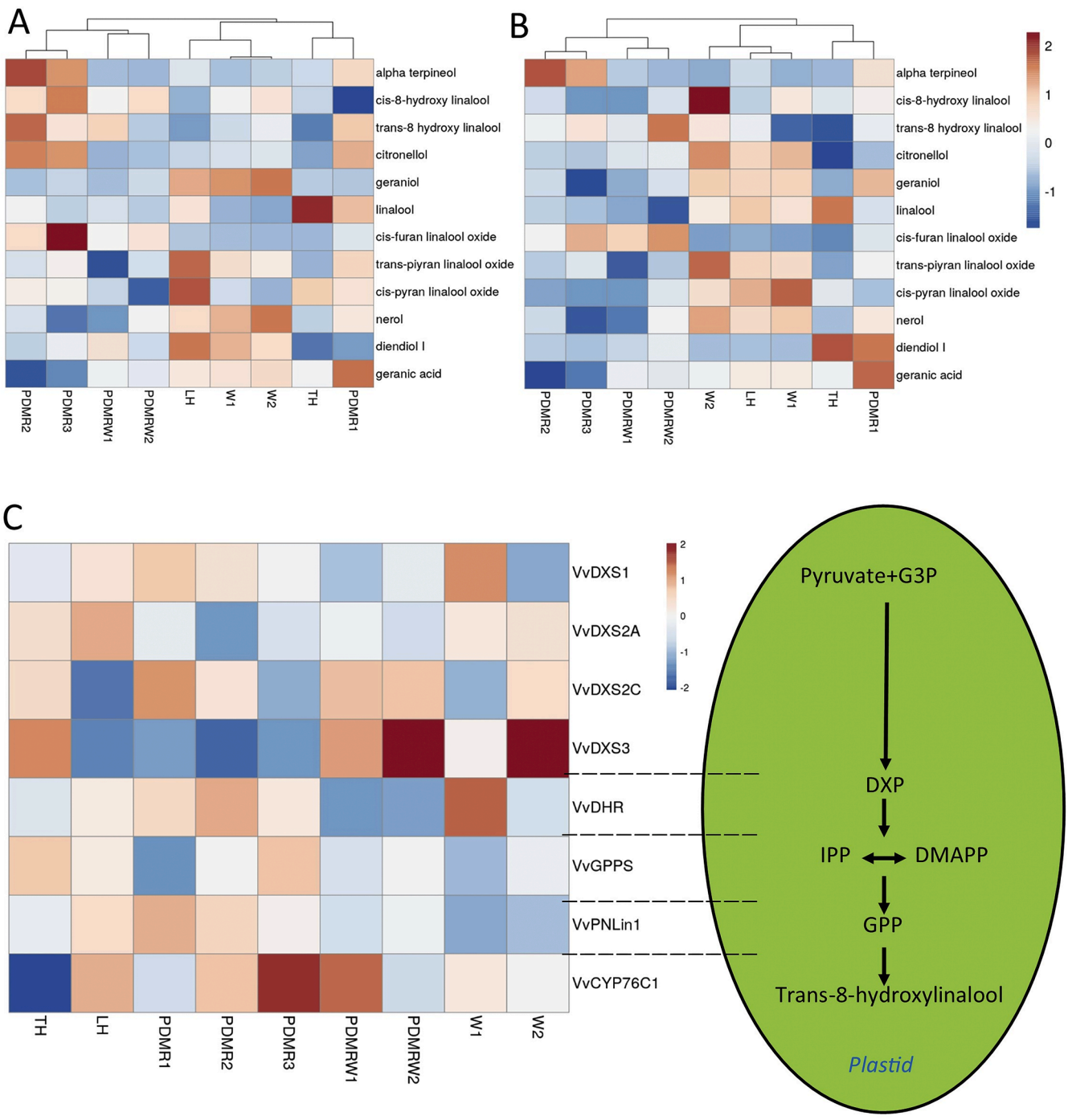

Fig. 2. Heatmaps showing the accumulation profiles of free (A) and conjugate (B) terpene. and expression of key genes involved in linalool synthesis and the MEP pathway (C) in Yellow Muscat berries. The rows in the heatmap represent compounds (A and B) or genes (C) and the columns indicate samples. The colours of the heatmap cells indicate the abundance of compounds or transcripts across different samples. The colour gradient, ranging from dark blue through white to dark red, represents low, middle and high abundance of a compound.

fructose (Kim et al., 2000), thus playing a critical role in supplying carbon nutrients to plants and influencing sugar signaling significantly (Ruan, 2014). In numerous plant species, elevated vacuolar invertase activity often correlates with increased hexose accumulation (Chen et al., 2022; Ruan, 2014). Our findings corroborate with those of Savoi et al. (2019), who showed that the expression of vacuolar invertase *VvGIN2* was elevated in berry shrivel, a condition that negatively affected sugar accumulation and, hence, fruit quality (Griesser et al., 2024).

3.2. PDMR shapes monoterpenoid compositions

In addition to the effect on sugar and organic acids, an impact on aroma of Yellow Muscat berries was also expected taking into account that volatile and aroma compounds profile are deeply affected by the harvest date (Reynolds et al., 1993). Given that the aroma of Muscat wine is predominantly impacted by terpene composition (Fenoll et al., 2012), we addressed our attention towards this category of compounds.

A total of 12 monoterpene compounds present in free or conjugated form were identified in Yellow Muscat grape berries. The application of

PDMR1 induced an increase of total terpenes level due to a positive variation of both conjugated and free compounds (Supplementary Table 2). According to Giacosa et al. (2019), the application of cane-cut on-vine led to a considerable rise in the total terpenes (particularly in the conjugated forms) in Muscat Blanc grape berries. Nevertheless, it should be noted that this increase was observed after 24 days, a time-frame that is longer than the 8 days it took to detect the increase in total terpenes in PDMR1 berries. Fig. 2 presents a heatmap illustrating the level of monoterpenes in berries for both free (Fig. 2A) and conjugated (Fig. 2B) forms following the application of different harvesting time and postharvest dehydration levels. Notably, within the free fraction, linalool exhibits high concentration levels in TH berries, followed by PDMR1. This terpene, together with geraniol, alfa-terpinol and nerol, is associated with the distinctive taste and flavor of Muscat grape varieties (Li et al., 2023; Wilson et al., 1984; Yang et al., 2009). PDMR1 also induces the accumulation of geranic acid, citronellol, *trans*-pyran linalool oxide, *alpha*-terpineol, and *trans*-8-hydroxy linalool, while *alpha*-terpineol, *trans*-8-hydroxy linalool, *cis*-8-hydroxy linalool, citronellol, and *cis*-furan linalool oxide are predominantly found in PDMR2 and PDMR3. The main linalool oxidation products are *trans/-cis*-8-hydroxy-linalool and *trans/cis* pyran/furan linalool oxides (Liu et al., 2022). LH, on the other hand, appears to be characterized by the presence of diendiol I, *cis*-pyran linalool oxide, *trans*-pyran linalool oxide, and geraniol. Additionally, geraniol, alongside nerol, distinguishes W1 and W2 samples (Fig. 2A). The accumulation profiles of conjugated terpenes (Fig. 2B) are similar to those of the free forms. LH, W1, and W2 berries contain the muscat-typical conjugated monoterpenes (Park et al., 1991), with W2 berries standing out due to the high level of *cis*-8-hydroxy linalool. In PDMR1 berries, geranic acid remained the dominant compound, as seen in the free fractions. Additionally, the glycosylated forms were characterized by the terpenes diendiol I and geraniol. In comparison to PDMR1, PDMR2 and PDMR3 showed a lower concentration for all the terpenes, except the *alpha*-terpineol. These data reinforce the observation that water losses impact the monoterpenes accumulation in grape berries, still attached to the vine or detached from it, with variable trends of specific molecule. In the present study, linalool was the main monoterpene alcohol detected and its concentration was significantly decreased by withering, in agreement with previous findings (Giacosa et al., 2019; Zenoni et al., 2016). On the other hand, there are observations that indicate an increase in geranic acid, citronellol, nerol, *cis*-furan-linalool oxide, and *cis*-pyran-linalool oxide in dehydrated grapes (Urcan et al., 2017) consistent with the expression patterns of genes involved in terpene biosynthesis (Fig. 2B).

The initial steps of terpenoid biosynthesis is controlled by *Deoxy-d-xylulose 5-phosphate synthase* (DXS) genes (Battilana et al., 2011, 2009). Alongside DXS, DHR catalyzes the final step of the 2-C-methyl-d-erythritol 4-phosphate (MEP) pathway, synthesizing isopentenyl pyrophosphate (IPP) and dimethylallyl diphosphate (DMAPP) (Ma et al., 2017). These substrates are then converted to geranyl diphosphate (GPP) by geranyl diphosphate synthases (GPPS). Terpene synthases subsequently catalyze the formation of monoterpenes from GPP (Wang et al., 2020). Moreover, enzymes can significantly enhance the carbon structure of terpenes, resulting in a remarkable diversity of terpene profiles observed in plants. Most terpene modifications are catalyzed by cytochrome P450 monooxygenases (CYPs) (Bosman and Lashbrooke, 2023) . Notably, the heat map is marked mainly by two genes, *VvDXS3* and *VvCYP76C1*. *VvDXS3* was highly expressed at W2 and PDMRW2. DXS acts as a rate-limiting enzyme in the methylerythritol phosphate (MEP) pathway, catalyzing the condensation of pyruvate and glyceraldehyde-3-phosphate into 1-deoxy-d-xylulose 5-phosphate (DXP) (Yue et al., 2020). The accumulation of *VvDXS* transcripts is positively correlated with the concentration of monoterpenes in grapes (Zhou et al., 2022). Specifically, VvDXS1 catalyze the conversion of 2-C-methyl-d-erythritol 4-phosphate into isopentenyl pyrophosphate (IPP), and its accumulation may serve as a crucial determinant in monoterpene accumulation, given that the levels of compounds such as linalool, nerol, and geraniol depend on isopentenyl pyrophosphate (Battilana et al., 2011, 2009). Together with *VvDXS1, VvDXS3* has been identified as an important player in diversifying the monoterpenoids profiles in table grape varieties (Zhou et al., 2022). Data presented in this research claims a role for DXS3 also in the different accumulation of monoterpenes following the application of different harvest timing and postharvest dehydration strategies.

While Cytochrome P450 (*VvCYP76C1)* was highly expressed in PDMR3 and PDMRW1 berries, the accumulation of *VvCYP76C1* transcripts was very low in TH, and W2 berries (Supplementary Table 3). CYP76C1 is the main linalool metabolizing oxygenase in Arabidopsis flowers (Boachon et al., 2015), and play a key role in the control of linalool emission and in the formation of most linalool oxides detected in vivo, both as volatile and soluble conjugated compounds, including 8-hydroxy, 8-oxo, and 8-COOH- linalool, as well as lilac aldehydes and alcohols. In grapevine, *VvCYP76C1* is highly expressed in small green and ripening berries (Jiu et al., 2020). Moreover, the ABA application to ripe grape berries induced a *VvCYP76C1* down-regulation (Jiu et al., 2020). This result is note of worthy by considering that it has been reported an increase in ABA content in Malvasia berries undergoing postharvest dehydration (Costantini et al., 2006). These pieces of evidence suggest that the levels of linalool in dehydrated berries are likely resulting both from a concentration process and a reduction in oxidative metabolism.

Furthermore, a higher expression of 4-Hydroxy-3-methylbut-2-enyl diphosphate reductase (*VvDHR*) transcripts was observed in W1 and PDMR2 berries (Fig. 2B).

VvPNLin1 was expressed mainly in PDMR1. Zhang et al. (2017), showed that *VvPNLin1* was a key gene responsible for linalool biosynthesis in berry ripening, and its transcription was affected by sunlight exposure. Linalool oxides are generated via linalool oxidation, which is generally triggered by water loss (Sanmartin et al., 2021). Our results agree with Matarese et al. (2013) and Wen et al. (2015) where *VvPNLin1* was highly expressed in ripening berries of Muscat blanc.

3.3. Volatiles and sensorial analysis of yellow Muscat wines

The GC/MS analysis was conducted on wines obtained from TH, LH, PDMR3 (referred in this section with just PDMR), PDMRW2 and W2 berries. The volatile compounds found in grapes encompass a variety of categories such as monoterpenes, C13-norisoprenoids, benzene derivatives, and aliphatic alcohols. Muscat grapes are distinguished by a unique aroma, with terpenols being the predominant aromatic components (Bayonove, 1993). Among these, the most prevalent are monoterpenes like linalool, geraniol, nerolidol, citronellol, geranic acid, and *alpha*-terpinol (Caffrey and Ebeler, 2021). Analyses on volatiles pointed out that PDMRW2 and W2 wines had higher values of conjugated terpenes and norisoprenoids than that observed for TH wine (Supplementary Table 4).

A total of 19 compounds of conjugated terpenes were found in Yellow Muscat wine. Most of them show a high concentration in PDMRW2 and W2 wines, especially geranic acid (8 times higher in PDMRW2 and 7 times higher in W2 in comparison to TH), diendiol I, hydroxycitronellal and *trans*-8 hydroxy linalool (Supplementary Table 4). However, linalool concentration decreases in LH, PDMR, PDMRW2, and W2 wines compared to TH. Similar results were observed for linalool and *trans*-8 hydroxy linalool levels detected in berries (Fig. 2 AB). The decrease of linalool was counterbalanced by a strong increase of geranic acid. The higher levels of geranic acid could be related to the elevated *VvDSX3* gene expression, as observed in plants overexpressing *VvDXS*, where this volatile is notably accumulated (Battilana et al., 2011), while the increase of diendiol I could be due to the oxidation of linalool (Wilson et al., 1984).

Several glycoside aliphatic alcohols were identified in high concentrations in PDMRW2 wine, such as, 1-butanol, benzyl alcohol, homovanillic alcohol, homovanillic acid and 3-methoxy-1-propanol.

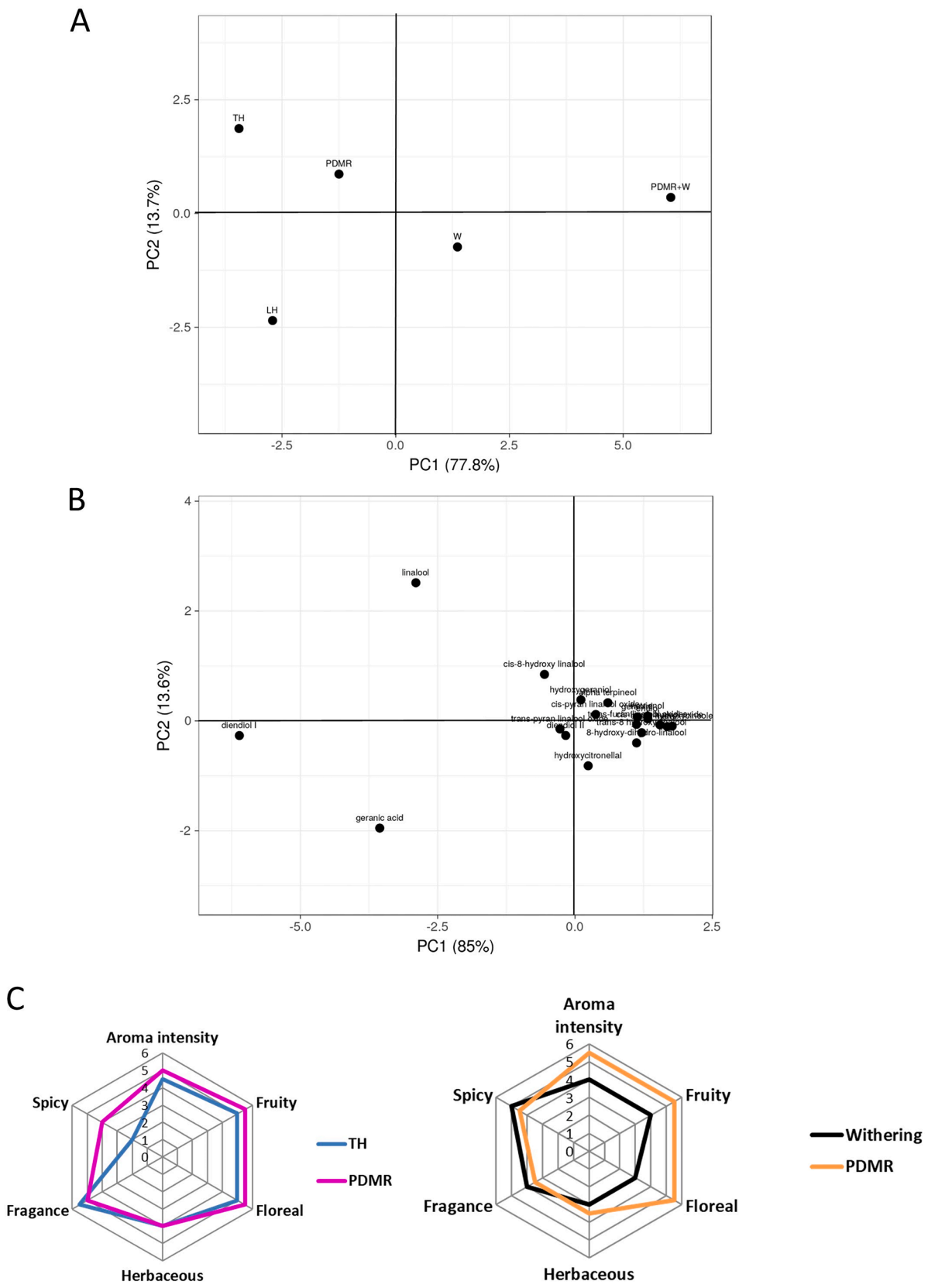

Fig. 3. Principal Component Analysis (PCA) of terpenes distributed across TH (Traditional Harvest), LH (Late Harvest), PDMR (Poly double Maturation Reasoned), PDMR-W2 (Poly double Maturation Reasoned combined with Withering) and W2 (Withering) wine samples (A) and individual terpene compounds distribution (B). Sensory analysis radar chart of TH, PDMR and W wine samples (C).

Withering induces accumulation of these aroma compounds (Tomasi et al., 2021) and, in general, these compounds account for herbaceous and unripe fruit aromas (Flamini and De Rosso, 2019).

C13-Norisoprenoids have been associated with the development of floral and spicy aromas in red wines, particularly following aging (Flamini et al., 2010). We observed an elevation in vomifoliol levels at PDMRW2. A similar result was reported by Tomasi et al. (2021) in the Corvina grape variety, correlating with the progression of withering processes. Vomifoliol potentially serves as a precursor to volatile compounds that contribute positively to the aroma profile of wines, such as β-damascone (imparting fruity notes), β-damascenone, and 3-oxo--α-ionone (offering floral and tobacco nuances).

A multivariate analysis, specifically Principal Component Analysis (PCA), applied to the wine terpenes revealed that the PC1 and PC2 explains 77.8 % and 13.7 % of the variability between different harvest time and postharvest dehydration techniques, respectively. PDMR wine flavors appear to be more like TH wine, compared to LH, PDMR+W and W wines (Fig. 3A).

Examination of individual terpene compounds indicates that most of them cluster together. However, linalool significantly impacts TH and PDMR wines distribution in the PCA. Geranic acid and diendiol I instead indicated similarity to LH wines (Fig. 3B).

A sensory analysis has confirmed discernible differences among the wines. Specifically, PDMR wine exhibited pronounced fruity, floral, and spicy notes compared to TH and W wines (Fig. 3C). Spicy notes in PDMR can be explained by higher content of aromatic compounds such as homovanillic acid and benzyl alcohol that was higher in PDMR3 and PDMRW samples (Supplementary Table 4). Benzyl alcohols were found to be the responsible for the notes of spice also in the study conducted by Tomasi et al. (2021).

4. Conclusions

The application of PDMR (alone or combined with W) to Yellow Muscat allows to change the quantity and profile of aromatic compounds and volatiles while maintaining their correct ratio between acidity and sugar content, essential factors for obtaining dessert wines. The right balance between the PDMR wine components is supported by their higher score obtained in the sensory analysis for taste and mouthfeel (phenolic maturity) descriptors (Supplementary Fig. S4). On the other hand, the positive effect of PDMR on polyphenols maturity of grape berries and derived wines has been already reported for red and white cultivars (Corso et al., 2013; Jahnke et al., 2023; Reščič et al., 2016). Considering this result, it can be concluded that the PDMR technique can be an extremely versatile because can be either applied to preserve Yellow Muscat "Fior d'Arancio" typicity also when the environmental conditions are not favorable (e.g. excess of humidity or warming) or, in relation to winemarker's choices, to produce new wine types with distinctive character.

CRediT authorship contribution statement

Monica Canton: Writing – review & editing, Writing – original draft, Data curation. **Alessandro Botton:** Data curation. **Massimiliano Corso:** Writing – review & editing, Visualization, Methodology, Investigation, Data curation. **Giovanni Cargnello:** Writing – review & editing. **Gianni Teo:** Writing – review & editing. **Andrea Curioni:** Writing – review & editing. **Simone Vincenzi:** Writing – review & editing. **Claudio Bonghi:** Writing – review & editing, Writing – original draft, Supervision, Funding acquisition, Data curation, Conceptualization.

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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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.scienta.2024.113817.

Data availability

Data will be made available on request.

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