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Deficit irrigation differently affects aroma composition in berries of *Vitis vinifera* L. (cvs Sangiovese and Merlot) grafted on two rootstocks

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Abstract

Background and Aims: Water deficit modifies the concentration of the aroma compounds of grape berries, but little information is available on the effect of deficits applied at different phenological stages. We evaluated the effect of deficit irrigation on glycosylated volatile organic compounds (VOCs) responsible for the aroma of berries of Sangiovese and Merlot cultivars grafted on 1103P or SO4 rootstocks.

Methods and Results: Vines were subjected to either pre- or post-veraison water stress, and berry composition compared against that of fruit of fully irrigated vines. At harvest, a higher concentration of glycosylated VOCs was measured in berries from vines stressed pre-veraison, but while it increased as water deficit increased in Sangiovese, this occurred only at a low or moderate level of stress in Merlot. Post-veraison water stress had a negative or negligible effect on the concentration of glycosylated VOCs in berries at harvest. The rootstock affected the concentration of glycosylated VOCs, particularly in vines stressed pre-veraison, with higher glycosylated VOCs observed for SO4 grafted vines than for 1103P grafted vines.

Conclusions: Pre-veraison water deficit enhanced the concentration of berry glycosylated VOCs, while post-veraison deficit did not. The rootstock–scion interaction might amplify the irrigation effect on berry glycosylated VOCs.

Significance of the Study: Modifying the timing and volume of irrigation might allow management of berry flavour for improved fruit and wine composition. Irrigation protocols should be tailored for specific cultivar–rootstock combinations.

Keywords: *aroma compound, glycosylated volatile organic compound, grapevine, terpene, water deficit*

Introduction

The sensory profile of wines depends on berry characteristics which, in turn, are affected by the cultivar and its interaction with environmental factors and cultural practices. Among secondary metabolites present in grapes, volatile organic compounds (VOCs) contribute to define wine composition and its aroma features. Despite some common characteristics in the composition of berry VOCs of many cultivars, there are also distinct aroma differences that identify cultivars. These differences are often related to small changes in specific compounds or their ratios within the VOC profile (Styger et al. 2011). For instance, among monoterpenes, berries and wines of cv. Sangiovese are reportedly characterised by a higher concentration of monoterpenes, especially *trans*-8-hydroxy-linalool and 7-hydroxy-α-terpineol (D'Onofrio et al. 2018). Benzene derivatives and pyrazines are prevalent in Merlot wines, as well as compounds responsible for fruity flavours, such as β-ionone and β-damascenone (Kotseridis and Baumes 2000, Ruiz et al. 2019). The majority of the aroma compounds found in grape berries are present at higher concentration in bound rather than in free form (Gunata et al. 1985, Williams and Allen 1996, Darriet et al. 2012). Usually, bound VOCs are glucosides or disaccharides comprising glucose and a second sugar moiety and the aglycone can be easily released chemically during winemaking and wine ageing through acid hydrolysis or enzymatically in the presence of oxidase activity. The concentration of glycosylated VOCs is typically high for the key aroma classes of terpenes and C_{13}-norisprenoids (Wilson et al. 1984, Winterhalter et al. 1990, D'Onofrio et al. 2017, Yue et al. 2020). The glycosylated fractions are particularly important in cultivars such as Sangiovese and Merlot where the free fraction is low (Bureau et al. 2000, Papini et al. 2010, Song et al. 2012).

Although grape aroma depends on the cultivar, it can be somewhat controlled by appropriate cultural practices if we reach a good understanding of the biochemistry of VOCs and how these compounds change during berry development (Kalua and Boss 2009, Matarese et al. 2013). Irrigation plays a key role in determining grape and wine composition (Gambetta et al. 2020). Managing irrigation allows preservation of the optimal grape characteristics which ensure wine quality (Romero et al. 2019, Lizama et al. 2021). The effect of vine water status on berry and wine sensory traits and aroma precursors have been previously reported (Chapman et al. 2005, Bindon et al. 2007, Koundouras et al. 2009). More recently, the effect of water deficit was investigated on terpenes, including several key compounds that contribute to floral and fruity notes. A high concentration of glycosylated and free monoterpenes was, respectively, found in Merlot and Viognier berries derived from deficit-irrigated vines (Song et al. 2012, Wang et al. 2019). A significant effect of water stress on the up-regulation of terpene synthases was reported for Cabernet Sauvignon and Tocai Friulano berries (Deluc et al. 2009, Savoi et al. 2016). C_{13}-Norisoprenoids, derived

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from the degradation of carotenoids, also contributed to the aroma of grapes (Baumes et al. 2002), and water deficit induced the production of carotenoid precursors and up-regulated genes associated with the biosynthesis of C_{13}-norisoprenoids (Bindon et al. 2007, Song et al. 2012, Savoi et al. 2016). Other VOCs, such as C_6 aroma compounds (e.g. 1-hexanol, hexanal, *trans*-2-hexenal), responsible for green fruity notes, were apparently lower in Cabernet Sauvignon berries from vines subjected to water deficit (García-Esparza et al. 2018), while they increased in Verdejo berries (Vilanova et al. 2019).

The effect of timing and intensity of water deficit on VOCs has been poorly investigated so far. Severe water stress (pre-dawn leaf water potential about −1.0 MPa) negatively affected Sauvignon Blanc aroma potential, which was instead enhanced under mild water deficit (Peyrot des Gachons et al. 2005). The concentration of free grape α-terpineol and linalool was higher for Viognier vines subjected to pre-veraison water deficit, but no effect was reported when drought conditions were prolonged over the whole growing season (Wang et al. 2019). In contrast, a higher concentration of glycosylated terpenes was measured in berries from Gewürztraminer vines that were subjected to prolonged deficit irrigation for the entire growing season (Kovalenko et al. 2021).

It is well known that the use of rootstocks allows the growth of grapevines under different soil water availability conditions, and that canopy structure, leaf area, biomass accumulation, yield and berry composition are influenced through different physiological and metabolic mechanisms (Soar et al. 2006, Alsina et al. 2011, Tramontini et al. 2013). These effects are mediated by the scion and can influence VOCs biosynthesis, thus enhancing or diminishing aroma intensity. For example, the wine quality of deficit irrigated Monastrell vines was higher when vines were grafted on a low vigour rootstock 161-49C, rather than on 140Ru, 1103P, 41B or 110R, due to a lower concentration of unpleasant C_6 alcohols (Romero et al. 2019). A significantly higher concentration of β-damascenone was observed in Shiraz wines derived from vines grafted on Schwarzmann, compared to 1103P and 110R (Olarte Mantilla et al. 2018).

Managing water availability in the vineyard may be an effective practice for improving berry aroma in many cultivars, but it appears important to clarify the combined effect of the scion and the rootstock on both secondary metabolism and the berry aroma profile during different periods of water deficit. Little information is available on the effect of plant water status on the glycosylated VOCs of Sangiovese or Merlot berries, two widely grown cultivars worldwide. Some information is available for Merlot (Song et al. 2012), but none for Sangiovese. Moreover, it is interesting to focus on the glycosylated VOCs which for these cultivars represent the aroma potential of the finished wine.

The aim of the present study was to compare the effect of deficit irrigation imposed at two phenological stages on the glycosylated VOCs of berries from two cultivars grafted onto two rootstocks. Deficit irrigation was therefore imposed either pre-veraison or post-veraison on fully productive potted Sangiovese and Merlot vines, grafted on either 1103P or SO4 rootstocks, during two consecutive growing seasons.

Materials and methods

Plant material and irrigation

The study was carried out on 6-year-old potted (50 L) grapevines (*Vitis vinifera* L. cvs Merlot and Sangiovese) grafted on 1103P or SO4 rootstocks [1103P: 1103 Paulsen (*V. rupestris* × *V. berlandieri*); SO4: Selection Oppenheim n. 4 (*V. riparia* × *V. berlandieri*)] at the experimental farm of the Department of Agriculture Food and Environment of the University of Pisa over 2 years (2018 and 2019). Rows were north–south oriented, and vines were trained according to the Guyot system, leaving one spur with two count buds and one cane with six–eight count buds. Forty-eight vines per cultivar were used for the experiment. Fertilisers were supplied via the irrigation system in spring, before irrigation differentiation (Palai et al. 2021). A modified Eichhorn–Lorenz (E-L) scale (Coombe 1995) was used to monitor fruitset (27 E-L) and veraison (35 E-L). Harvest dates were established on the basis of TSS in berries (22 ± 0.5°Brix). Climatic conditions were monitored with a WatchDog (Spectrum Technologies, Aurora, IL, USA) weather station located on site.

Vines were irrigated twice daily using drip lines (two emitters per container, delivering water at a rate of 2 L/h each). All plants were fully irrigated until fruitset (day of the year 154 and 164 in 2018 and 2019, respectively), when three irrigation regimes were applied to each cultivar–rootstock combination, being full irrigation (FI) and two regulated deficit irrigation (RDI) treatments. Full irrigation delivered 455 and 414 L/vine from fruitset to harvest in 2018 and 2019, respectively, in order to maintain the stem water potential (SWP) above −0.5 MPa. The two different RDI treatments were imposed from fruitset to veraison (RDI-1, 37% of FI) and from veraison to harvest (RDI-2, 49% of FI), respectively; RDI vines were fully irrigated for the remaining irrigation period (Palai et al. 2021, Caruso et al. 2022). The SWP was measured at 7–10 day intervals with a Scholander pressure chamber using standard protocols (Palai et al. 2021). The water stress integral (WSI) was calculated from the SWP values as reported by Myers (1988).

Berry characteristics and determination of VOCs

Grape bunches were harvested separately from each vine, and crop mass, berry fresh mass and berry skin to pulp ratio immediately determined. Berry dry mass was measured after oven-drying at 70°C until constant mass on three samples of 100 berries from each cultivar–rootstock–irrigation combination. The TSS, TA and pH were measured on 30-berry samples from individual vines; that is the juice was extracted from each sample, TSS determined with a hand refractometer, and a 10 mL aliquot titrated with 0.1 N NaOH to an endpoint pH of 8.2 to determine TA. A TSS threshold of 22 ± 0.5°Brix was established for harvest in order to minimise the potential effects of sugar concentration on the concentration of berry VOCs; thus, the harvest date did not coincide for all irrigation treatments (Palai et al. 2021, Caruso et al. 2022).

Three samples of 100 berries each were randomly collected at harvest from each treatment (cultivar–rootstock–irrigation combinations) for determination of glycosylated VOCs by solid-phase extraction, following the protocol developed by Di Stefano (1991) and modified by D'Onofrio et al. (2018). Chromatographic analyses were carried out using an Agilent 7890A GC coupled with an Agilent 5975C quadrupole MS. The capillary column was an HP-Innowax (30 m length, 0.25 mm i.d., 0.25 mm film thickness) (Agilent Technologies, Waldbron, Germany). Helium was the carrier gas, with a constant flow rate of 1 mL/min. The column oven temperature was programmed from 30°C, followed by an isotherm of 60°C for 2 min, a temperature gradient of 2°C/min from 60 to 190°C, a second gradient of

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5°C/min from 190 to 230°C and 15 min of final isotherm at 230°C. The MS detector scanned within a mass range of *m/z* 30–450. Volatile compounds were identified and quantified as previously reported (D'Onofrio et al. 2017).

Eighty glycosylated VOCs were detected. A full list of the correspondence between the VOCs common name and their nomenclature recommended by the International Union of Pure and Applied Chemistry (IUPAC) is reported in Table S1: throughout the text and in tables VOCs are reported with their common name aiming to simplify the reading of the article. The monoterpenes, geraniol, linalool and α-terpineol derivatives, were grouped following the aggregation proposed by D'Onofrio et al. (2017) with some modifications, based on their common biosynthetic derivation by terpene synthases from geranyl diphosphate. In order to avoid concentration or dilution effects due to different irrigation treatments, all glycosylated VOC data were expressed as ng/g of berry dry mass.

Experimental design and statistical analysis

Potted vines were arranged according to a split-plot design within each cultivar (48 vines per cultivar, 24 for each rootstock). The rootstock (R) was the main plot and irrigation (I) the subplot. Vines from each cultivar–rootstock combination were subjected to three irrigation regimes (eight vines for each treatment). Twelve combinations of cultivar–rootstock–irrigation were compared. Significant differences between treatments and rootstocks were determined by two-way ANOVA ($P \leq 0.05$). Principal component analysis (PCA) was performed over the aroma compound classes (2 years, two cultivars, two rootstocks, three irrigation treatments and three vine replicates). Discriminant analysis was implemented on all VOCs through a stepforward analysis. All statistical analyses were performed with JMP (SAS Institute, Cary, NC, USA).

Results

Climatic conditions and vine water status

Annual precipitation (932 and 970 mm in 2018 and 2019, respectively), reference evapotranspiration (927 and 900 mm, respectively), annual mean air temperature (16.3 and 16.0°C, respectively) and summer mean air temperature (24.1 and 24.3°C, respectively) were quite similar in 2018 and 2019 (Figure 1). Mean air temperature of April–May, however, was lower in 2019 (14.7°C) than in 2018 (17.5°C), but 2°C higher than in 2018 during the 30 days after fruitset. The lower temperature measured in May 2019 caused a 14 day delay in flowering and a 13 day delay in the onset of ripening (i.e. veraison), with respect to 2018 (as an average of all treatments). In 2019, Sangiovese and Merlot vines were harvested 12 and 26 days later than in 2018, respectively (as an average of all rootstock–irrigation combinations). In each year, the SWP and daily WSI values for FI were not different between rootstocks of the same cultivar (Table 1). Deficit irrigation significantly affected vine water status in all cultivar–rootstock combinations. The lowest values for daily WSI between fruitset and veraison were measured in 2018 in both cultivars (−1.08 and −1.03 MPa for Sangiovese and Merlot, respectively), whereas after veraison, the lowest daily WSI was measured in 2019 (−1.17 and −1.08 MPa in Sangiovese and Merlot, respectively) (Table 1). The lowest SWP values were observed in RDI-1 vines (being −2.07 MPa in Sangiovese and −2.08 MPa in Merlot, in 2018) and the minimum SWP values observed for RDI-2 were −1.71 MPa for Merlot in 2019 and −1.83 MPa for Sangiovese in 2018 (Table 1).

Yield and berry characteristics

Yields and berry characteristics were previously published (Palai et al. 2021, Caruso et al. 2022) and are reported again here to allow a better appreciation of VOC results. In brief, fruit yield per vine ranged from 1.21 kg (SO4-FI in 2018) to 2.29 kg (1103P-FI in 2019) in Sangiovese, and from 1.05 kg (SO4-RDI-1 in 2019) to 2.24 kg (SO4-RDI-2) in Merlot, but no significant differences were observed between irrigation treatments and rootstocks. In contrast, berry fresh mass was significantly lower in RDI-1 vines of both cultivars. At harvest, berry fresh mass for Sangiovese vines was 2.28, 1.75 and 2.23 g in FI, RDI-1 and RDI-2 berries, respectively (averaged between rootstocks and years), whereas in Merlot vines, it was 1.70, 1.15 and 1.52 g in FI, RDI-1 and RDI-2 treatments, respectively (again, averaged between rootstocks and years). The highest and lowest skin to pulp ratios for Sangiovese were 0.24 and 0.18 in RDI-2 in 2019 and in

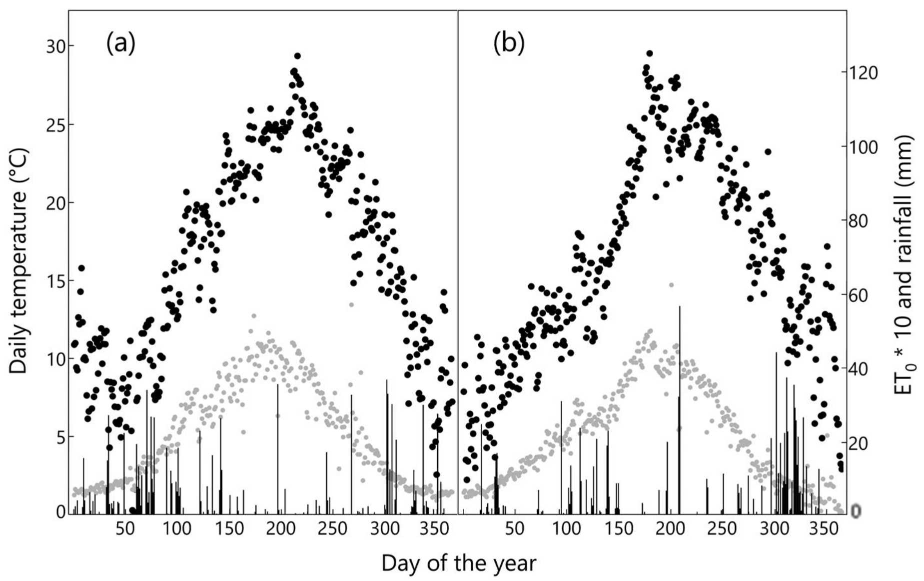

Figure 1. Daily values of mean air temperature (●), evapotranspiration (ET_0) (●) and precipitation (|) at the experimental site in (a) 2018 and (b) 2019.

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Table 1. Effect of the irrigation regimes on the minimum stem water potential and on the daily water stress integral in Sangiovese and Merlot grapevines (*Vitis vinifera* L.) grafted on 1103P and SO4 rootstocks.

Year	Cultivar	Rootstock	Irrigation treatment	Minimum SWP (MPa, DOY)	Daily WSI FS-V (MPa)	Daily WSI V-H (MPa)
2018	Sangiovese	1103P	FI	−0.60 (234)	−0.16	−0.21
			RDI-1	−2.07 (205)	−1.08	−0.17
			RDI-2	−1.58 (221)	−0.14	−0.67
		SO4	FI	−0.60 (234)	−0.11	−0.24
			RDI-1	−1.41 (162)	−0.73	−0.17
			RDI-2	−1.83 (205)	−0.13	−0.81
	Merlot	1103P	FI	−0.58 (234)	−0.14	−0.20
			RDI-1	−2.08 (162)	−1.03	−0.17
			RDI-2	−1.08 (221)	−0.14	−0.47
		SO4	FI	−0.47 (234)	−0.09	−0.16
			RDI-1	−1.62 (185)	−0.92	−0.14
			RDI-2	−1.25 (221)	−0.13	−0.53
2019	Sangiovese	1103P	FI	−0.67 (175)	−0.25	−0.17
			RDI-1	−1.75 (219)	−0.78	−0.21
			RDI-2	−1.73 (247)	−0.33	−1.09
		SO4	FI	−0.65 (175)	−0.26	−0.18
			RDI-1	−1.56 (204)	−0.82	−0.18
			RDI-2	−1.73 (238)	−0.20	−1.17
	Merlot	1103P	FI	−0.73 (175)	−0.29	−0.15
			RDI-1	−1.68 (219)	−0.77	−0.26
			RDI-2	−1.21 (219)	−0.34	−0.86
		SO4	FI	−0.70 (175)	−0.25	−0.15
			RDI-1	−1.48 (219)	−0.68	−0.32
			RDI-2	−1.71 (219)	−0.30	−1.08

DOY, day of the year; FI, full irrigation; FS, fruitset; H, harvest; RDI-1, regulated deficit irrigation 1; RDI-2 regulated deficit irrigation 2; SWP, stem water potential; WSI, water stress integral; V, veraison.

FI in 2019, respectively, while in Merlot they were 0.27 and 0.20 for RDI-1 (2018) and FI (2018) vines, respectively (averaged between rootstocks; differences were not significant). A significant difference in the skin to pulp ratio was observed only between rootstocks for Merlot in 2018 (1103P was 18% > SO4). Some differences due to irrigation were observed in TSS, pH and TA measurements over (Figures S1,S2). Some treatments did not reach the TSS threshold of 22 ± 0.5°Brix: Sangiovese SO4-RDI-1 in both years, and Merlot SO4 RDI-1 and RDI-2 in 2019. The RDI-1 berries had lower TA at harvest irrespective of cultivar, especially in 2019 (Figures S1,S2).

Volatile organic compounds

In Sangiovese, the glycosylated VOC profile mainly comprised benzene derivatives, C_{13}-norisoprenoids and monoterpenes (46, 17 and 13% of total VOCs, respectively) (Table 2). The concentration of total glycosylated VOCs, however, was higher in Merlot berries due to the contribution of benzene derivatives, phenols and vanillins (48, 18 and 13% of total VOCs, respectively) (Table 3). Despite differences between years, there was a clear effect of irrigation in both years. The highest concentration of total glycosylated VOC was measured for RDI-1 berries (+43 and +45% relative to the concentration measured in berries from FI Sangiovese and Merlot vines, respectively, when averaged between years and rootstock), while the lowest concentration was in RDI-2 berries (−10 and −2% relative to FI Sangiovese and Merlot vines, respectively). The effect of rootstock was evident in the RDI-1 treatment, with higher values obtained for SO4-grafted vines than 1103P, in both cultivars and both years.

Linalool and its derived compounds (Tables 2,3) were the most abundant monoterpenes in Sangiovese berries (54% of total monoterpenes) and accumulated in higher concentration under RDI-1 irrigation (+61% than in FI berries, averaged between rootstock and year). Similarly, geraniol and its derived compounds (29% of total monoterpenes), and α-terpineol and its derived compounds (16%), increased by 94 and 42%, respectively, under RDI-1 irrigation, compared to the FI treatment. Water deficit applied after veraison was detrimental, especially for the accumulation of geraniol and its derived compounds (−27%). The concentration of total monoterpenes in Merlot berries was lower than in Sangiovese berries (5.3 vs 12.8% of total VOCs in Merlot and Sangiovese, respectively), but the proportion of linalool and geraniol derived compounds was similar (being 40 and 43%, respectively). Pre-veraison water deficit caused an increase in all three groups of monoterpene derivatives in Merlot berries, in both years and regardless of the rootstock (+28, +56 and +28%, for linalool, geraniol and α-terpineol derivatives, respectively). Unlike Sangiovese, accumulation of monoterpenes in Merlot berries was enhanced by RDI-2 irrigation in 2018; in particular, the accumulation of α-terpineol, (*E*)-pyranoid linalool oxide C and 2,6-dimethyl-3,7-octadiene-2,6-diol 1, for vines grafted onto the SO4 rootstock. The effect of rootstock on monoterpene concentration was more evident in Sangiovese than in Merlot berries. In both years, a higher concentration of citronellol, myrtenol and 6,7-dihydro-7-hydroxylinalool was measured in Sangiovese berries sampled from vines grafted onto SO4 than in berries from Sangiovese vines on 1103P. In Merlot vines, a positive and consistent effect of the SO4 rootstock in both years was observed only for (*E*)-pyranoid linalool oxide C. Figure 2 shows the general relationship between the

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Table 2. Effect of irrigation on the glycosylated aroma compounds measured in 2018 and 2019 in Sangiovese (*Vitis vinifera* L.) grapevines grafted on 1103P and SO4 rootstocks.

	Concentration (ng/g of berry dry mass)																	
	2018									2019								
	1103P			SO4						1103P			SO4					
	FI	RDI-1	RDI-2	FI	RDI-1	RDI-2	*R*	*I*	*R × I*	FI	RDI-1	RDI-2	FI	RDI-1	RDI-2	*R*	*I*	*R × I*
Isoamyl alcohol	98.7 ± 37.4	236.2 ± 113.7	89.1 ± 11.8	83.2 ± 13.8	201.3 ± 52.6	67 ± 10	n.s.	**	n.s.	80.2 ± 14.5	118.4 ± 14.9	77.7 ± 26.3	76.7 ± 16.2	139.8 ± 25	76.5 ± 6.1	n.s.	***	n.s.
1-Pentanol	25 ± 2.4	29.1 ± 25.2	28 ± 3.8	33.5 ± 4.2	44.2 ± 6	26.2 ± 2.6	n.s.	n.s.	n.s.	42 ± 1.2	49.2 ± 6.1	33.7 ± 3.9	36.4 ± 2.2	51.8 ± 5.5	32.2 ± 2.8	n.s.	***	n.s.
2-Buten-1-ol, 3-methyl	76.2 ± 15.2	128.7 ± 31.1	74.7 ± 5.7	98.1 ± 4.5	139 ± 5.8	74 ± 1.3	n.s.	***	n.s.	104 ± 12.2	130.2 ± 18.1	104 ± 7.7	99.5 ± 2.4	140.4 ± 19.4	87 ± 7.3	n.s.	***	n.s.
1-Hexanol	120 ± 8.8	233.8 ± 66.6	190.9 ± 10.1	156.8 ± 31.5	202.8 ± 22	192.1 ± 29.7	n.s.	**	n.s.	98.6 ± 11.3	153.6 ± 28.8	107.5 ± 5.6	101.5 ± 17.3	164.7 ± 26.8	126.6 ± 9	n.s.	***	n.s.
trans-2-Hexenol	21.7 ± 2.5	32.6 ± 9.4	36.8 ± 3.3	33.4 ± 3.7	40.4 ± 9.2	30 ± 1.9	n.s.	n.s.	*	20 ± 1.3	23.6 ± 1.8	23.4 ± 2.4	20.2 ± 4.3	24.8 ± 3.5	24.3 ± 2.6	n.s.	n.s.	n.s.
1-Octen-3-ol	10.5 ± 2.7	26.3 ± 5.7	6.2 ± 5.6	17.7 ± 3.7	36.3 ± 4.6	14.1 ± 3.8	**	***	n.s.	4.2 ± 0.6	5.3 ± 2.1	5.4 ± 1.6	3.9 ± 0.9	5.3 ± 2.2	4.1 ± 0.2	n.s.	n.s.	n.s.
1-Octanol	5.4 ± 0.8	12 ± 1.5	3.4 ± 0.5	9 ± 1.1	11.5 ± 2.2	6.5 ± 2.4	*	***	n.s.	4.2 ± 1.1	4.7 ± 1.3	3.4 ± 0.7	5.3 ± 1.4	8.2 ± 1.7	3.5 ± 0.7	*	**	n.s.
(*E*)-2-Octen-1-ol	3.8 ± 1.4	8.8 ± 3.6	2.4 ± 0.5	6.7 ± 1.2	18.8 ± 5.8	6.2 ± 1.7	**	***	n.s.	4.5 ± 0.9	4.1 ± 0.9	4.2 ± 0.6	6.2 ± 1.6	7.1 ± 1	3.4 ± 0.3	*	*	*
3-Penten-1-ol, 4-methyl	49.1 ± 5.6	64.2 ± 30.4	108.9 ± 4.4	52.3 ± 7.5	67.8 ± 6.7	126.9 ± 8.4	n.s.	***	n.s.	34.5 ± 5.2	44.5 ± 4.7	61.9 ± 2.5	37 ± 7.3	47.7 ± 5.4	56.7 ± 1.5	n.s.	***	n.s.
Total aliphatic alcohols	411 ± 56	772 ± 158	541 ± 24	491 ± 69	762 ± 9	544 ± 60				393 ± 40	534 ± 74	422 ± 42	387 ± 41	590 ± 86	415 ± 20			
Benzaldehyde	4.6 ± 1.5	9 ± 2.7	7.1 ± 1.4	12.1 ± 2.4	20.6 ± 9.9	10.9 ± 5	**	n.s.	n.s.	17.6 ± 10.1	6.5 ± 0.4	8 ± 2.1	15.2 ± 6.1	18.1 ± 14.1	9.6 ± 4.3	n.s.	n.s.	n.s.
Methyl benzoate	13.78 ± 3.96	15.19 ± 2.34	13.08 ± 2.53	12.68 ± 0.64	21.71 ± 3.96	10.69 ± 0.43	n.s.	**	*	0.1 ± 0.09	0.18 ± 0.01	0.15 ± 0.01	0.14 ± 0.01	0.13 ± 0.11	0.09 ± 0.01	n.s.	n.s.	n.s.
Acetophenone	0.41 ± 0.35	0.24 ± 0.42	0.8 ± 0.11	0.79 ± 0.04	2.18 ± 0.59	1.26 ± 0.12	***	*	**	1.22 ± 0.08	1.15 ± 0.07	0.97 ± 0.09	1.22 ± 0.17	1.58 ± 0.14	1.13 ± 0.09	**	**	*
Ethyl benzoate	0.86 ± 0.18	1.37 ± 0.14	0.77 ± 0.08	1.22 ± 0.09	1.96 ± 0.11	1.02 ± 0.06	***	***	n.s.	0.37 ± 0.03	0.53 ± 0.01	0.37 ± 0.05	0.45 ± 0.12	0.61 ± 0.08	0.4 ± 0.02	n.s.	**	n.s.
Methyl salicylate	4.6 ± 2.3	16.6 ± 7.7	10.6 ± 5.8	16.4 ± 10.3	44.4 ± 23.5	34.8 ± 19.3	n.s.	**	n.s.	28.1 ± 13.6	37.5 ± 6.1	28.1 ± 10.7	40.2 ± 14.6	101.6 ± 66.5	23.8 ± 9.4	n.s.	n.s.	n.s.
Benzyl alcohol	2145 ± 57	2428 ± 147	2136 ± 160	2327 ± 89	2741 ± 383	2309 ± 167	n.s.	**	n.s.	1179 ± 167	2279 ± 230	1693 ± 152	1435 ± 259	2535 ± 148	1949 ± 409	n.s.	**.	n.s.
2-Phenylethanol	1842 ± 212	2636 ± 626	1626 ± 241	2660 ± 86	4083 ± 289	1803 ± 163	***	***	*	2406 ± 231	2456 ± 202	2028 ± 94	2331 ± 413	2849 ± 132	1673 ± 14	n.s.	***	*
3,5-Dimethoxyacetophenone	1.3 ± 0.8	1.9 ± 1.1	1 ± 0.2	1.6 ± 0.2	3.4 ± 0.6	2.1 ± 0.4	**	*	n.s.	14.6 ± 1.6	16.1 ± 0.7	22.1 ± 1.4	14.7 ± 4	16.9 ± 0.3	13.2 ± 4.9	n.s.	n.s.	*
3,4-Dimethoxybenzyl alcohol	147 ± 53.1	111.1 ± 26.7	160.6 ± 66.6	90.7 ± 5.5	202.2 ± 78.6	110.8 ± 19.6	n.s.	n.s.	*	181.8 ± 50.3	181.8 ± 71	191.9 ± 34.2	154.3 ± 49.1	228.1 ± 18.8	193.2 ± 46.2	n.s.	n.s.	n.s.
2,3,4-Trimethoxybenzyl alcohol	23.2 ± 4.1	36.8 ± 3.3	16.3 ± 4.2	29 ± 0.8	37.8 ± 14.3	27.5 ± 0.4	n.s.	**	n.s.	55.2 ± 7.7	67.1 ± 6.6	54.5 ± 1.9	55.1 ± 16.5	64.7 ± 18.4	40.8 ± 1.1	n.s.	*	n.s.
Total benzene derivatives	4185 ± 153	5253 ± 628	3972 ± 294	5152 ± 103	7160 ± 256	4312 ± 96				3885 ± 404	5047 ± 230	4029 ± 389	4049 ± 529	5817 ± 249	3905 ± 490			
Guaiacol	11.4 ± 0.2	21.3 ± 6.2	9.4 ± 4.2	14.2 ± 0.3	20.1 ± 1.5	11.4 ± 0.9	n.s.	***	n.s.	8.7 ± 0.4	10.5 ± 0.6	9.8 ± 0.4	10 ± 1.8	16.1 ± 4.2	8.3 ± 1.2	n.s.	**	*
Phenoxyethanol							–	–	–	3.7 ± 0.7	6.9 ± 0.7	5.3 ± 0.7	4.5 ± 1.1	7.1 ± 0.8	3.6 ± 0.4	n.s.	***	n.s.
4-Vinylguaiacol	214 ± 65.1	89 ± 59.2	86 ± 103.2	169 ± 85.8	478 ± 35.1	122 ± 65.5	**	**	***	812 ± 86.2	1151 ± 65.9	1217 ± 240.6	1461 ± 390.5	1759 ± 305.9	812 ± 332.8	*	*	**
Syringol	95 ± 1.9	185.9 ± 66.1	91.9 ± 47.2	100.4 ± 7.7	132.8 ± 27.7	75.3 ± 12.2	n.s.	**	n.s.	20.9 ± 1.4	34 ± 4.9	29 ± 4.1	18.6 ± 12.2	42.2 ± 7.1	26.7 ± 9.5	n.s.	**	n.s.
Eugenol	3.6 ± 0.2	7.9 ± 2.1	2.2 ± 0.7	4.9 ± 0.9	14.3 ± 4.7	4.2 ± 0.2	**	***	n.s.	5.7 ± 1.1	6.9 ± 0.8	4.9 ± 0.6	5.5 ± 0.5	9 ± 0.7	3.6 ± 0.3	n.s.	***	**
Methoxyeugenol							–	–	–	10 ± 3.3	6.2 ± 0.2	6.4 ± 0.7	8.8 ± 1	7.1 ± 1.2	6.4 ± 2	n.s.	*	n.s.
γ-Hydroxyeugenol	8.2 ± 0.8	19.5 ± 2.5	6.5 ± 1.8	11.8 ± 2.5	23.8 ± 8.2	11.8 ± 1.4	*	***	n.s.	23.5 ± 1.9	29.7 ± 1.3	23.7 ± 1.4	32.4 ± 6.8	38.9 ± 1.1	18 ± 2.5	*	***	**
Phenol-3,4,5-trimethoxy	64.8 ± 6.5	82.6 ± 23.2	58 ± 12.2	65.2 ± 2.7	89.3 ± 7.5	65.4 ± 7.4	n.s.	**	n.s.	77.3 ± 8.2	76.7 ± 6.5	71.5 ± 1.4	65.1 ± 4.5	68.8 ± 6.5	64.9 ± 13.7	*	n.s.	n.s.
Total phenols	398 ± 68	407 ± 153	254 ± 166	366 ± 81	759 ± 56	291 ± 86				962 ± 88	1323 ± 71	1368 ± 247	1607 ± 408	1949 ± 312	944 ± 361			
Vanillin	63.9 ± 2	100.8 ± 32.7	57.3 ± 15	72.4 ± 3	106.7 ± 9.8	72.5 ± 6	n.s.	**	n.s.	39.7 ± 1.7	50.5 ± 3.7	44.9 ± 2.7	45 ± 8.2	58.1 ± 8.4	39.3 ± 7.1	n.s.	**	n.s.
Methyl vanillate	147 ± 53.1	111.1 ± 26.7	160.6 ± 66.6	90.7 ± 5.5	202.2 ± 78.6	110.8 ± 19.6	n.s.	n.s.	*	181.8 ± 50.3	181.8 ± 71	191.9 ± 34.2	154.3 ± 49.1	228.1 ± 18.8	193.2 ± 46.2	n.s.	n.s.	n.s.
Acetovanillone	80.2 ± 9.9	132.1 ± 20.5	69 ± 19.5	87.6 ± 5.8	168.4 ± 7.2	99.7 ± 30.6	*	**	n.s.	208.3 ± 66	147.9 ± 14.1	189.6 ± 47.6	155.5 ± 15.7	193 ± 42.3	175.4 ± 75.4	n.s.	n.s.	n.s.
Zingerone	32.6 ± 7.6	37.9 ± 5.7	19.4 ± 4.4	37.3 ± 4.1	59.6 ± 7.1	35.4 ± 4.7	***	***	n.s.	56.2 ± 6.4	59.7 ± 12.5	50.9 ± 6.3	57.7 ± 6.1	86.3 ± 15.9	47.3 ± 9.9	n.s.	**	n.s.
Homovanillyl alcohol	350.9 ± 52.1	406.6 ± 122.7	173.3 ± 34.4	516.5 ± 161.1	613 ± 51	248.4 ± 30.2	**	***	n.s.	592.8 ± 187.8	231.7 ± 12.3	219.3 ± 44.4	486 ± 135.4	315.3 ± 43.8	235.1 ± 38.7	n.s.	***	n.s.
3,4,5-Trimethoxybenzyl methyl ether	75.5 ± 56.3	23.6 ± 25.1	96.6 ± 65.7	10 ± 2	52.1 ± 25.6	19.8 ± 6.4	n.s.	n.s.	n.s.	77.9 ± 50.7	98.5 ± 81.9	58.2 ± 37.9	38.2 ± 23.5	128.2 ± 21.8	104.9 ± 42.4	n.s.	n.s.	n.s.

(*Continues*)

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Table 2. Continued

	Concentration (ng/g of berry dry mass)																		
	2018									2019									
	1103P			SO4						1103P			SO4						
	FI	RDI-1	RDI-2	FI	RDI-1	RDI-2	*R*	*I*	*R* × *I*	FI	RDI-1	RDI-2	FI	RDI-1	RDI-2	*R*	*I*	*R* × *I*
Homovanillic acid	63.7 ± 7.7	213 ± 44.7	52 ± 14.2	122.3 ± 77.6	598.7 ± 301.4	114.1 ± 28.3	*	**	n.s.	7.5 ± 2.7	8 ± 7.2	2.4 ± 4.2	4.6 ± 4	13 ± 0.4	9 ± 2.7	n.s.	n.s.	n.s.
Acetosyringone	14.9 ± 4.2	22.5 ± 4.7	13.7 ± 6.4	16 ± 3.1	29 ± 7.8	19.9 ± 4.5	n.s.	*	n.s.	79.5 ± 9.3	96.2 ± 7.5	81.7 ± 5.1	85.2 ± 5.6	114.2 ± 12.2	77.8 ± 20.9	n.s.	**	n.s.
Total vanillins	829 ± 139	1048 ± 219	642 ± 201	953 ± 189	1830 ± 430	720 ± 90				1244 ± 117	874 ± 145	839 ± 31	1027 ± 112	1136 ± 71	882 ± 241			
(*E*)-Furanoid linalool oxide A^{L,†}	7.2 ± 0.8	11 ± 2.1	3.6 ± 3.2	11.2 ± 2.8	11.1 ± 2	10.2 ± 1.1	**	*	n.s.	24.6 ± 2.5	19.1 ± 2.1	26.9 ± 4.8	25.1 ± 4.3	24.6 ± 1.8	20.4 ± 4.3	n.s.	n.s.	*
(*Z*)-Furanoid linalool oxide B^{L}	3.3 ± 0.5	4.7 ± 4.3	1.4 ± 2.5	6.2 ± 1.3	7.1 ± 0.4	6 ± 0.5	**	n.s.	n.s.	14.5 ± 2.1	13.2 ± 1.7	16.4 ± 2.7	15.7 ± 2	17.7 ± 1.2	12.6 ± 1.8	n.s.	n.s.	*
Linalool^{L}	9 ± 0.9	39.6 ± 21.6	5.9 ± 0.8	5.7 ± 1.2	35.1 ± 17.9	4.4 ± 0.6	n.s.	***	n.s.	8 ± 2.5	13.9 ± 1.6	12.4 ± 1.2	13.7 ± 2.9	22.6 ± 9.7	5.4 ± 0.8	n.s.	**	*
Hotrienol^{L}							–	–	–	1.9 ± 1.3	5.4 ± 0.5	8.9 ± 0.7	15.5 ± 2.3	33.5 ± 11.1	3.2 ± 0.7	***	***	***
Ocimenol							–	–	–	13.2 ± 4.8	13.5 ± 2.2	10.5 ± 1	13.5 ± 3.1	18.1 ± 1.4	11.8 ± 1.6	n.s.	*	n.s.
p-Cymen-7-ol	1.2 ± 0.2	3.3 ± 0.8	0.6 ± 0.3	3 ± 0.1	4.4 ± 1.4	2.2 ± 0.3	**	***	n.s.	3.9 ± 0.7	4.8 ± 0.5	3.3 ± 0.2	3.9 ± 0.6	5.9 ± 0.6	3.4 ± 0.3	n.s.	***	n.s.
α-Terpineol^{T}	7.1 ± 1.1	16.4 ± 2.7	5.5 ± 1.6	22.5 ± 5.1	23.5 ± 15.4	15.5 ± 1.5	**	n.s.	n.s.	17.1 ± 6.3	17.4 ± 2.9	13.5 ± 1.4	17 ± 3.8	22.9 ± 1.6	15.3 ± 2	n.s.	*	n.s.
α-Citral^{G}					7.4 ± 1.8	0.3 ± 0.6				4.9 ± 1	6.2 ± 0.2	5.6 ± 0.3	8 ± 1.4	10.8 ± 1.1	3.5 ± 0.1	***	***	***
(*E*)-Pyranoid linalool oxide C^{L}	19.1 ± 1.8	22.7 ± 2.8	14.3 ± 2.6	28.6 ± 4.9	28.1 ± 7.3	24.2 ± 3.2	**	n.s.	n.s.	53.1 ± 9.1	46.5 ± 4.7	69.1 ± 8.1	47 ± 6.2	57 ± 3.2	47.8 ± 7.7	n.s.	n.s.	**
(*Z*)-Pyranoid linalool oxide D^{L}	4.7 ± 0.6	9.1 ± 4.2	3.2 ± 1.8	6.2 ± 1.3	10.5 ± 0.7	5.5 ± 0.7	n.s.	**	n.s.	21.4 ± 3.7	17.8 ± 2.8	23.5 ± 4.4	22.6 ± 3.9	25.6 ± 1.8	16 ± 2	n.s.	n.s.	**
Citronellol^{G}	6 ± 2.5	26 ± 2.9	6.1 ± 2	9.3 ± 1.7	35.1 ± 2.6	8.8 ± 2.5	***	***	n.s.	8.6 ± 0.8	14.3 ± 1.1	24.1 ± 2.7	28.1 ± 8.4	38.4 ± 7.9	9.7 ± 1.4	**	*	***
Lilac alcohol A^{L}	14.9 ± 4.5	49.8 ± 4.4	11.2 ± 13.8	14.8 ± 12.8	68.6 ± 13.9	14.1 ± 13.2	n.s.	***	n.s.	17.5 ± 1.4	22.7 ± 1.7	20.2 ± 0.8	24.7 ± 5.4	32.6 ± 4.4	12.5 ± 0.5	*	***	***
Myrtenol^{T}	1.6 ± 1.4	3.6 ± 3.8	1.2 ± 1.3	5.3 ± 0.6	5 ± 0.4	3.3 ± 0.4	*	n.s.	n.s.	4.6 ± 0.8	5.7 ± 0.4	4.5 ± 0.2	5.4 ± 1.1	7.9 ± 0.5	3.9 ± 0.3	*	**	*
Nerol^{G}	19.5 ± 1.9	55.2 ± 1.8	15.6 ± 7.1	37.8 ± 2.4	69.6 ± 8	40.4 ± 7.7	***	***	n.s.	34.2 ± 11.1	57.7 ± 5.5	37.7 ± 5.8	39.5 ± 10.4	61.1 ± 4.7	25.9 ± 2.1	n.s.	***	n.s.
Isogeraniol^{G}	3.5 ± 0.1	8.3 ± 0.5	2.7 ± 0.9	6.1 ± 0.1	13.1 ± 4.1	5.4 ± 0.3	**	***	n.s.	3.2 ± 0.5	4.3 ± 0.3	3.9 ± 0.1	4.4 ± 0.7	4.7 ± 0.7	2.7 ± 0.1	n.s.	**	**
Lilac alcohol B^{L}	2 ± 0.2	3.2 ± 2.7	0.9 ± 0.9	3.3 ± 0.2	7.9 ± 7.1	2.9 ± 0.8	n.s.	n.s.	n.s.	6.3 ± 0.9	8.2 ± 0.6	14.5 ± 2.8	19.9 ± 3.6	23.1 ± 3.1	4.9 ± 0	***	**	***
Geraniol^{G}	49.4 ± 4.9	133.8 ± 16.9	32.4 ± 12.2	95.2 ± 5.4	171.8 ± 37.3	77.2 ± 10.4	***	***	n.s.	77.8 ± 23.1	112.1 ± 5.4	79.4 ± 9.7	84.3 ± 3.8	131.3 ± 11.6	59.6 ± 1.2	n.s.	***	*
Exo-2-hydroxycineole^{T}							–	–	–	39.1 ± 6	49.8 ± 6.6	37.1 ± 4.8	35.7 ± 6	48.4 ± 4	33.5 ± 3	n.s.	**	n.s.
2,6-Dimethyl-3,7-octadiene-2,6-diol 1^{L}	3.3 ± 0.8	8.6 ± 2.9	2 ± 0.8	6 ± 0.1	7.5 ± 3.1	5.6 ± 1.5	n.s.	**	n.s.	7.9 ± 2	7.3 ± 0.8	15.8 ± 1.6	9.3 ± 2.8	7 ± 2.5	6 ± 0.5	**	*	***
6,7-2OH-7-Hydroxylinalool^{L}	3.6 ± 0.9	12.9 ± 1	2.7 ± 1.4	5.4 ± 0.6	17 ± 2.1	5.6 ± 1	***	***	n.s.	5.5 ± 0.6	7.9 ± 1.3	9.6 ± 1	10.6 ± 2.3	13.1 ± 1.5	4.6 ± 0.3	*	**	***
2,6-Dimethyl-1,7-octadiene-3,6-diol 2^{L}	1.5 ± 0.3	4.6 ± 0.5	1.2 ± 0.8	2.8 ± 0.2	5.1 ± 0.1	3.4 ± 2	*	***	n.s.	8.1 ± 1.3	10.6 ± 0.2	9.5 ± 0.8	10.2 ± 1.7	11.9 ± 1	7.4 ± 1.1	n.s.	**	*
2,3-Pinanediol							-	-	-	18.7 ± 16.6	26 ± 18.5	15.3 ± 6.6	12.2 ± 2.6	18.4 ± 1.7	17.9 ± 15.5	n.s.	n.s.	n.s.
OH-Citronellol^{G}	23.3 ± 4.6	57.5 ± 11.2	16.6 ± 11.6	44.1 ± 6.8	84.9 ± 11.6	48.8 ± 3.3	***	***	n.s.							-	-	-
trans-8-Hydroxylinalool^{L}	156.4 ± 30	280.2 ± 22.2	100.1 ± 34	237.6 ± 7.4	353.3 ± 77.4	247 ± 27.4	***	***	n.s.	189.7 ± 1.1	247.1 ± 37.1	258.1 ± 46.4	169 ± 12.7	254.6 ± 30.6	166.1 ± 8	*	**	*
cis-8-Hydroxylinalool^{L}	73.7 ± 6.2	172 ± 43.1	40.8 ± 14.3	80.4 ± 4.8	160 ± 53.8	68.8 ± 7.9	n.s.	***	n.s.	98.6 ± 26.4	163.6 ± 1.2	99.2 ± 12.1	113.1 ± 27	159.4 ± 55.5	70.4 ± 6.8	n.s.	**	n.s.
Geranic acid^{G}	119.6 ± 18.8	304 ± 31.9	61 ± 43.1	200.8 ± 13.6	476.8 ± 75.3	105.3 ± 11.6	***	***	*	150.5 ± 43	218.7 ± 22.5	122.8 ± 3.6	165.9 ± 15.8	277.7 ± 60.7	97 ± 3.5	n.s.	***	n.s.
cis-2,7-Dimethyl-4-octene-2,7-diol^{L}	43.2 ± 13.9	103.9 ± 54.6	33.1 ± 8.8	138.2 ± 11	108.6 ± 64.4	98.5 ± 21.1	**	n.s.	n.s.							-	-	-
7-OH-α-Terpineol^{T}	131.4 ± 20.7	265.3 ± 58.9	137.6 ± 18.6	294.7 ± 50.6	316.3 ± 156.5	243.4 ± 33.1	**	n.s.	n.s.	71.1 ± 13.6	147.6 ± 43.7	130.5 ± 15.7	82 ± 26.4	115.8 ± 18.3	64.2 ± 19.4	*	**	n.s.
2,6-Dimethyl-6OH-2,7-Octadienoic acid^{L}	162 ± 25.6	293 ± 32.9	82.6 ± 29.7	163.4 ± 30.3	392.3 ± 69.3	155.2 ± 14.4	**	***	n.s.	122.2 ± 19	184.4 ± 29.2	155 ± 29.6	95.2 ± 15	158.9 ± 39.5	91.8 ± 16.7	**	**	n.s.
Total monoterpenes	869 ± 128	1889 ± 272	583 ± 212	1430 ± 68	2421 ± 587	1202 ± 140				1028 ± 149	1448 ± 134	1230 ± 86	1093 ± 127	1605 ± 256	820 ± 51			

(Continues)

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Table 2. Continued

	Concentration (ng/g of berry dry mass)																	
	2018									2019								
	1103P			SO4						1103P			SO4					
	FI	RDI-1	RDI-2	FI	RDI-1	RDI-2	*R*	*I*	*R* × *I*	FI	RDI-1	RDI-2	FI	RDI-1	RDI-2	*R*	*I*	*R* × *I*
Damascenone							-	-	-	34.1 ± 10.9	57.6 ± 6	37.5 ± 5.6	39.3 ± 10.4	61.2 ± 4.6	25.8 ± 2.1	n.s.	***	n.s.
Actinidol A	0.9 ± 0.2	2.4 ± 0.1	0.3 ± 0.1	1.8 ± 0.3	3.8 ± 0.3	1.4 ± 0.3	***	***	n.s.	3.9 ± 0.4	5.5 ± 0.8	2.8 ± 0.2	3.6 ± 0.6	5.8 ± 0.4	2.4 ± 0.2	n.s.	***	n.s.
Actinidol B	1.7 ± 0.5	3.8 ± 0.2	0.5 ± 0.2	2.9 ± 0.5	6.1 ± 0.7	2.3 ± 0.4	***	***	n.s.	7 ± 1	9.8 ± 1.3	4.8 ± 0.4	6.6 ± 1.3	10.4 ± 0.9	4.2 ± 0.7	n.s.	***	n.s.
3,4-Dihydro-3-oxo-α-ionol (I)	71.4 ± 41.2	102.4 ± 10.5		98.5 ± 7	140.5 ± 35.3	80.5 ± 8.6	***	***	n.s.	79.4 ± 14.4	92.1 ± 5.2	80.1 ± 7.8	91.7 ± 22.1	106.1 ± 9.8	61.8 ± 1.8	n.s.	**	n.s.
3,4-Dihydro-3-oxo-α-ionol (II)	197.6 ± 33	222.3 ± 11.4	110.3 ± 39.6	217.2 ± 18.6	324.4 ± 121.5	175.6 ± 20.1	*	**	n.s.	215.5 ± 35.5	227.4 ± 11.4	203.5 ± 28.4	221 ± 18.8	262.7 ± 31.8	160.7 ± 6.3	n.s.	**	n.s.
3,4-Dihydro-3-oxo-α-ionol (III)	235 ± 8.1	293.7 ± 12.6	139.7 ± 48.8	300.5 ± 27.9	430.3 ± 157	225.9 ± 25.6	*	**	n.s.	273.9 ± 45.6	271.6 ± 12.8	238.9 ± 29.1	254.2 ± 21	318.6 ± 38.9	195.6 ± 5.8	n.s.	**	*
3-Hydroxy-β-damascone	72.5 ± 3.9	108.8 ± 28.8	71.6 ± 15.9	71 ± 4.4	130.2 ± 0.6	72 ± 4.7	n.s.	***	n.s.	10.9 ± 2.5	12.1 ± 0	11.7 ± 1	15.9 ± 4.8	15.7 ± 9	8.2 ± 1.9	n.s.	n.s.	n.s.
3-Oxo-α-damascone							-	-	-	26.9 ± 4.9	37.5 ± 3.3	28.9 ± 3.3	30.1 ± 7.2	40.5 ± 3.9	19.9 ± 2.8	n.s.	***	n.s.
4-Hydroxy-β-ionol	13.1 ± 1.8	24.4 ± 3	11.2 ± 3	14.8 ± 2.2	28.6 ± 3.8	14.5 ± 1.3	*	***	n.s.	6 ± 0.6	7.6 ± 0.7	6.7 ± 1.1	5.7 ± 1	8 ± 1.4	4 ± 0.5	n.s.	**	*
3-Oxo-α-ionol	512 ± 37	1054 ± 270	317 ± 127	593 ± 52	1313 ± 609	554 ± 66	n.s.	**	n.s.	829 ± 252	1485 ± 34	925 ± 90	716 ± 93	1485 ± 192	663 ± 35	n.s.	***	n.s.
2,3-2OH-4-Oxo-7,8-2OH-β-ionon	28.7 ± 16.7	45.1 ± 3.4	9.7 ± 10.5	41.5 ± 4.3	64.5 ± 21.6	28 ± 3.4	**	**	n.s.	62.2 ± 5.6	62.2 ± 4.3	48.5 ± 4.6	74.5 ± 21.1	74.8 ± 6.7	44.9 ± 0.7	n.s.	**	n.s.
Epimanool							-	-	-	9.4 ± 1	13.2 ± 1.2	10.2 ± 0.9	9.4 ± 1.7	14.2 ± 2.3	7.6 ± 0.6	n.s.	***	n.s.
3,9-Dihydroxy-megastigman-5-en	22.4 ± 2.2	45.7 ± 6.1	17.3 ± 4.2	21.6 ± 3.4	48.5 ± 15.8	22.5 ± 2.6	n.s.	***	n.s.	12.7 ± 3.3	19.1 ± 0.6	13.5 ± 0.6	11.8 ± 3.1	18.1 ± 3.5	8.1 ± 0.4	n.s.	***	n.s.
Blumenol C	9.8 ± 0.3	20 ± 4.8	7.2 ± 2.7	10.6 ± 0.7	22 ± 6.7	10.1 ± 0.9	n.s.	***	n.s.	4.2 ± 0.8	4.1 ± 1.5	3.3 ± 0.3	4.2 ± 0.6	6.3 ± 1.6	2.5 ± 0.6	n.s.	*	n.s.
3-Hydroxy-7,8-dihydro-β-ionol	31.8 ± 1.4	56.5 ± 11.4	19.1 ± 8.1	33.7 ± 3	72.3 ± 5.5	28.4 ± 3.3	*	***	n.s.	4.1 ± 0.6	6.1 ± 0.6	4.9 ± 1.3	4.7 ± 0.9	6.4 ± 0.2	3.2 ± 0.2	n.s.	***	n.s.
7,8-dihydrovomifoliol	101.9 ± 12.3	176.9 ± 25.5	73.1 ± 20.8	100.4 ± 15.5	248.6 ± 39.9	109.6 ± 8.8	**	***	n.s.	57.2 ± 13.4	114.9 ± 12.3	96.6 ± 18.9	76.5 ± 18.3	117.2 ± 13.7	44.2 ± 8.1	n.s.	***	**
Total C_{13}-norisprenoids	1243 ± 32	2158 ± 292	778 ± 276	1509 ± 136	2834 ± 1014	1326 ± 140				1637 ± 379	2427 ± 65	1718 ± 188	1567 ± 159	2542 ± 275	1258 ± 62			
Total VOCs	7932 ± 144	11 530 ± 91	6770 ± 1102	9901 ± 520	15 766 ± 1838	8395 ± 175				9149 ± 722	11 654 ± 99	9606 ± 710	9730 ± 1256	13 640 ± 606	8224 ± 1112			

Values are means +/- SD ($n = 3$); *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; n.s., not significant, $P > 0.05$, respectively. †The superscript letter on monoterpenes indicates the biosynthetic origin, where G, geraniol, L, linalool and T, α-terpineol. FI, full irrigation from budburst through harvest; RDI-1, water deficit applied from fruitset through veraison; RDI-2, water deficit applied from veraison through harvest.

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Table 3. Effect of irrigation on the glycosylated aroma compounds measured in 2018 and 2019 in Merlot (*Vitis vinifera* L.) grapevines grafted on 1103P and SO4 rootstocks.

	Concentration (ng/g of berry dry mass)																	
	2018									2019								
	1103P			SO4						1103P			SO4					
	FI	RDI-1	RDI-2	FI	RDI-1	RDI-2	*R*	*I*	*R* × *I*	FI	RDI-1	RDI-2	FI	RDI-1	RDI-2	*R*	*I*	*R* × *I*
Isoamyl alcohol	67 ± 8.7	73.6 ± 9.3	70.6 ± 17.4	38.8 ± 1.1	87.3 ± 22.2	47.3 ± 17.6	n.s.	*	n.s.	74.1 ± 5.9	80.8 ± 13.8	46 ± 7.6	95.3 ± 38.8	125.9 ± 1.7	108 ± 30.2	*	n.s.	n.s.
1-Pentanol	37.6 ± 1.8	40.1 ± 6.1	34.3 ± 7.6	22.8 ± 2.1	43.1 ± 6.5	20.9 ± 4.8	**	**	*	54.4 ± 7.3	53.2 ± 6.4	27.4 ± 3.5	59.8 ± 11	70.2 ± 1.5	62.7 ± 3.8	***	**	**
2-Buten-1-ol, 3-methyl	105.9 ± 20	101.2 ± 16.5	74.5 ± 15.6	63.4 ± 5.6	97 ± 16.9	46 ± 6.7	**	**	n.s.	125.5 ± 22.4	92 ± 1.6	53.4 ± 1.3	115.4 ± 25.7	130.2 ± 10.6	99.5 ± 6.4	**	***	*
1-Hexanol	144.9 ± 4.6	124.8 ± 20.1	158.7 ± 29.6	88.2 ± 8.1	123.8 ± 11	113.3 ± 21.1	**	n.s.	*	116.4 ± 21.9	136 ± 13.7	110.7 ± 2.9	84.8 ± 13.5	148.6 ± 14.5	126.4 ± 16.3	n.s.	**	*
trans-2-Hexenol	29 ± 4.9	18.1 ± 6.7	32.3 ± 7.3	21.6 ± 3.8	18.8 ± 5.1	29.5 ± 5.5	n.s.	**	n.s.	30 ± 6.8	15.6 ± 3.3	18.9 ± 1.3	12.2 ± 2.2	13.3 ± 1.4	15.3 ± 1	***	*	**
1-Octen-3-ol	15 ± 1.1	25.2 ± 5.0	16 ± 3.5	9.9 ± 0.6	30.2 ± 8.1	12.3 ± 1.2	n.s.	***	n.s.	7.4 ± 1.7	4.6 ± 0.4	6.5 ± 2.1	5.4 ± 1.6	3.3 ± 1	8.8 ± 2.9	n.s.	*	n.s.
1-Octanol	6.8 ± 0.5	14.5 ± 2.2	9.2 ± 1.7	6.7 ± 1.1	14.4 ± 1.4	7.2 ± 0.9	n.s.	***	n.s.	3.8 ± 0.1	5.7 ± 1.4	3.8 ± 0.4	5.2 ± 1.3	12.7 ± 1.7	6.2 ± 0.8	***	***	**
(*E*)-2-Octen-1-ol	5.4 ± 1.4	10.2 ± 0.8	6.4 ± 1	3.8 ± 0.6	14.2 ± 4.1	4.7 ± 0.5	n.s.	***	*	3.1 ± 0.1	4.8 ± 1.1	2.4 ± 0.3	4 ± 0.6	8.8 ± 0.6	4.7 ± 0.5	***	***	**
3-Penten-1-ol, 4-methyl	152.1 ± 21.4	59.7 ± 7.5	129.3 ± 26.7	58.3 ± 3.1	68.9 ± 14.8	185.8 ± 36.2	n.s.	***	**	80.9 ± 14.2	100.4 ± 4.2	91.5 ± 5.5	40.1 ± 7.4	55.8 ± 6.7	65.3 ± 1.9	***	**	n.s.
Total aliphatic alcohols	564 ± 54	468 ± 58	532 ± 107	314 ± 20	498 ± 81	467 ± 77				496 ± 74	493 ± 9	361 ± 12	423 ± 94	569 ± 26	497 ± 50			
Benzaldehyde	11.9 ± 5	23.1 ± 1.7	6.1 ± 3.1	7.6 ± 1.3	36.8 ± 7.2	5.2 ± 2.3	n.s.	***	**	12.8 ± 0.5	23.9 ± 4.1	3.5 ± 1	17.7 ± 4.2	36.4 ± 6.4	6.6 ± 1.3	**	***	n.s.
Methyl benzoate	21.9 ± 6.2	33.3 ± 11.4	20.5 ± 5.9	14.8 ± 1.5	34.9 ± 8.4	17.9 ± 3.5	n.s.	**	n.s.							-	-	-
Acetophenone	1.16 ± 0.2	1.5 ± 0.3	1.58 ± 0.16	0.73 ± 0.06	2.44 ± 0.71	1.39 ± 0.08	n.s.	**	**	1.46 ± 0.08	2.1 ± 0.06	1.18 ± 0.21	1.73 ± 0.15	1.99 ± 0.1	1.32 ± 0.17	n.s.	***	n.s.
Ethyl benzoate	1.29 ± 0.1	2.1 ± 0.6	1.3 ± 0.17	1.07 ± 0.08	2.19 ± 0.33	1.3 ± 0.12	n.s.	n.s.	n.s.	0.44 ± 0.04	0.66 ± 0.1	0.33 ± 0.08	0.41 ± 0.08	0.67 ± 0.04	0.51 ± 0.09	n.s.	***	n.s.
Methyl salicylate	350.8 ± 121.7	189.8 ± 96.0	84.8 ± 76.6	220.7 ± 80.1	546 ± 498	65.7 ± 34.8	n.s.	n.s.	n.s.	86 ± 34.2	221.9 ± 60.6	254.3 ± 126	146.8 ± 37.5	240.5 ± 105.9	94.4 ± 23.6	n.s.	n.s.	n.s.
Benzyl alcohol	2255 ± 57.9	3014 ± 77.9	2275 ± 96.7	2298 ± 31.6	3523 ± 115	2224 ± 62.1	**	***	***	2111 ± 46	2113 ± 32	2106 ± 20	2111 ± 64	2110 ± 58	2114 ± 97	n.s.	n.s.	n.s.
2-Phenylethanol	1948 ± 662	4464 ± 462	3850 ± 456	2761 ± 372	5389 ± 233	3603 ± 417	n.s.	**	n.s.	4357 ± 644	5963 ± 916	3389 ± 530	4964 ± 785	6724 ± 398	5212 ± 475	**	**	n.s.
3,5-Dimethoxyacetophenone	8.9 ± 4.1	10.1 ± 0.9	10.8 ± 0.4	5.7 ± 1.2	15.1 ± 3.4	9.2 ± 2.8	n.s.	*	*	19.9 ± 4.9	32.7 ± 3.9	19.9 ± 1.6	34 ± 1.9	67.6 ± 6.8	34.7 ± 3.7	***	***	**
3,4-Dimethoxybenzyl alcohol	156.3 ± 78.9	178.2 ± 38.5	155.9 ± 67.6	94.1 ± 39.9	194.3 ± 82.6	83.8 ± 23.4	n.s.	n.s.	n.s.	224.1 ± 71.1	310.5 ± 168.5	231.3 ± 80.8	284.2 ± 107.2	371.7 ± 43.5	205.1 ± 18.8	n.s.	n.s.	n.s.
2,3,4-Trimethoxybenzyl alcohol	57.1 ± 10.7	60.5 ± 6.6	60 ± 8.8	43.4 ± 16.9	54.2 ± 12	52.4 ± 15.6	n.s.	n.s.	n.s.	65.9 ± 15.7	66.1 ± 3.4	42.8 ± 10.2	84.8 ± 24.9	97 ± 15	75.4 ± 7.6	*	n.s.	n.s.
Total benzene derivatives	4522 ± 744	7987 ± 605	6466 ± 485	5447 ± 387	9799 ± 217	6064 ± 497				6880 ± 599	8734 ± 915	6049 ± 499	7646 ± 804	9650 ± 452	7744 ± 475			
Guaiacol	30.3 ± 3.9	63.8 ± 25.5	24 ± 3.6	22.4 ± 1.6	54.6 ± 4.9	22.8 ± 9.8	n.s.	**	n.s.	15.2 ± 1	17.6 ± 0.8	9.5 ± 1.9	18.7 ± 2.4	42.7 ± 5.8	19.2 ± 2.2	***	***	***
Phenoxyethanol							-	-	-	3.8 ± 0.2	4.2 ± 0	2.2 ± 0.3	4.3 ± 0.1	6 ± 1	4.2 ± 0.6	***	***	n.s.
4-Vinylguaiacol	381.5 ± 57.7	508.2 ± 146.7	110.4 ± 75	232 ± 143.9	554.7 ± 225.9	361.1 ± 275.3	n.s.	*	n.s.	2635.5 ± 456.7	4641.3 ± 780.6	2372 ± 427.7	3546 ± 361.2	5818.9 ± 260.2	3837 ± 435.8	***	***	n.s.
Syringol	600.8 ± 127	988.3 ± 316.6	524.1 ± 129.6	444.5 ± 138.9	593.1 ± 38.4	754.8 ± 439.3	n.s.	n.s.	n.s.	116 ± 6.4	204.9 ± 30.4	146.2 ± 43.6	238.8 ± 6.9	481 ± 87.1	458.2 ± 59.2	***	***	*
Eugenol	5.5 ± 1	5.6 ± 0.5	4.5 ± 0.6	4.6 ± 0.5	7.1 ± 0.8	5.4 ± 1	n.s.	*	n.s.	6.4 ± 0.5	6.5 ± 0.7	5.7 ± 0.1	10.2 ± 3.5	10.4 ± 1.1	9.4 ± 1.2	***	n.s.	n.s.
Methoxyeugenol							-	-	-	11.7 ± 1.6	8.8 ± 1.1	7.8 ± 0.6	21.7 ± 4.3	18 ± 2.9	15.6 ± 2.1	***	*	n.s.
γ-Hydroxyeugenol	12 ± 1.5	16.5 ± 5.0	7.9 ± 7.8	6.2 ± 0.6	20.1 ± 4.6	7.7 ± 2.5	n.s.	**	n.s.	14.1 ± 1.2	22.5 ± 1.2	10.2 ± 3.5	16.8 ± 1.9	28.9 ± 2.4	18.9 ± 4.8	***	***	n.s.
Phenol-3,4,5-trimethoxy	247.8 ± 24.4	205.4 ± 47.9	172.1 ± 10.5	145.4 ± 37.4	181.9 ± 30.4	153.4 ± 71.9	*	n.s.	n.s.	232.3 ± 40.6	160.7 ± 26	90.7 ± 14.5	246.1 ± 22.8	273 ± 31.4	274.3 ± 17	***	*	***
Total phenols	1278 ± 211	1788 ± 160	843 ± 207	855 ± 199	1411 ± 228	1185 ± 798				3035 ± 499	5066 ± 779	2644 ± 482	4103 ± 365	6679 ± 371	4637 ± 424			
Vanillin	102.9 ± 14.7	154.4 ± 49.6	74.9 ± 12.9	70.7 ± 13.6	125.6 ± 23.5	72.8 ± 27.2	n.s.	**	n.s.	55.5 ± 5.8	70.8 ± 8.9	40.4 ± 7.1	66.2 ± 4.4	84.5 ± 10.1	57.6 ± 4	**	***	n.s.
Methyl vanillate	156.3 ± 78.9	178.2 ± 38.5	155.9 ± 67.6	94.1 ± 39.9	194.3 ± 82.6	83.8 ± 23.4	n.s.	n.s.	n.s.	224.1 ± 71.1	310.5 ± 168.5	231.3 ± 80.8	284.2 ± 107.2	371.7 ± 43.5	205.1 ± 18.8	n.s.	n.s.	n.s.
Acetovanillone	102.9 ± 6.7	156.7 ± 27.4	78.3 ± 11	67.2 ± 23.2	179.2 ± 57.1	64.5 ± 36.6	n.s.	**	n.s.	123.8 ± 18.2	206.2 ± 37.9	62.4 ± 12.4	160.8 ± 16.7	360.2 ± 104.2	126.2 ± 11.3	**	***	n.s.
Zingerone	41.7 ± 15.2	73.9 ± 7.9	42.6 ± 1	28.8 ± 6.2	83.1 ± 23.4	39.7 ± 11.2	n.s.	**	n.s.	36.4 ± 3.5	122.8 ± 27.5	42.6 ± 13.6	65 ± 2.3	175 ± 46.5	74 ± 11.8	**	***	n.s.
Homovanillyl alcohol	1597 ± 818	1289 ± 374	931 ± 261	1052 ± 403	1409 ± 604	638 ± 314	n.s.	n.s.	n.s.	1314 ± 482	688 ± 87	391 ± 98	1743 ± 817	1435 ± 276	1203 ± 351	**	*	n.s.
3,4,5-Trimethoxybenzyl methyl ether	92 ± 95.4	152.6 ± 62.3	169.5 ± 127.2	29 ± 16.3	129.6 ± 142.5	55.5 ± 19.3	n.s.	n.s.	n.s.	187.3 ± 106.7	387.8 ± 242.2	439 ± 152.2	273.8 ± 156.9	348.5 ± 87.4	405.1 ± 173	n.s.	n.s.	n.s.
Homovanillic acid	120.1 ± 7.2	237.4 ± 50.0	82.7 ± 21.8	58.3 ± 11.3	262 ± 22.9	95.3 ± 24.6	n.s.	***	*	14.4 ± 5.6	27.5 ± 12.6	27.6 ± 8.1	21.1 ± 8.9	29.4 ± 1.6	27 ± 8.3	n.s.	n.s.	n.s.

(Continues)

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Table 3. Continued

	Concentration (ng/g of berry dry mass)																	
	2018									2019								
	1103P			SO4						1103P			SO4					
	FI	RDI-1	RDI-2	FI	RDI-1	RDI-2	*R*	*I*	*R* × *I*	FI	RDI-1	RDI-2	FI	RDI-1	RDI-2	*R*	*I*	*R* × *I*
Acetosyringone	36.7 ± 10.2	74.3 ± 9.6	28.5 ± 5.6	22.6 ± 7.2	77.4 ± 13.4	22.8 ± 10.1	n.s.	***	n.s.	113.8 ± 17.3	168.1 ± 17.3	74.2 ± 12.5	155.2 ± 10	302.4 ± 57.8	125.7 ± 20.5	***	***	*
Total vanillins	2250 ± 872	2317 ± 200	1564 ± 477	1424 ± 492	2461 ± 574	1073 ± 453				2069 ± 651	1982 ± 559	1309 ± 265	2770 ± 987	3107 ± 258	2224 ± 245			
(*E*)-Furanoid linalool oxide A[L,†]	5.9 ± 0.6						-	-	-	7.9 ± 2.5	5.9 ± 1.3	6.2 ± 0.6	7.6 ± 2.2	6.2 ± 1.3	8.4 ± 1.6	n.s.	n.s.	n.s.
(*Z*)-Furanoid linalool oxide B[L]	10.6 ± 0.7	6.4 ± 0.8	6.8 ± 2.1	7.4 ± 1.9	8.4 ± 1.2	11.4 ± 1.6	n.s.	n.s.	**	12.6 ± 3.8	11 ± 1.4	10.4 ± 0.8	13.1 ± 3.2	10.4 ± 2.3	14.8 ± 1.9	n.s.	n.s.	n.s.
Linalool[L]							-	-	-	4.01 ± 0.77	4.63 ± 1.24	3.59 ± 0.63	3.16 ± 0.24	5.67 ± 0.53	4.35 ± 0.06	n.s.	**	n.s.
Hotrienol[L]							-	-	-	5.3 ± 0.46	7.23 ± 2.52	4.54 ± 0.76	4.95 ± 0.57	6.68 ± 0.6	4.89 ± 0.42	n.s.	*	n.s.
Ocimenol							-	-	-	15.79 ± 7.15	15.39 ± 5.1	10.76 ± 2.66	17.91 ± 8.76	16.58 ± 2.47	18.56 ± 3.94	n.s.	n.s.	n.s.
p-Cymen-7-ol	1.14 ± 0.03	1.77 ± 0.5	1.17 ± 0.19	0.53 ± 0.51	1.12 ± 1	0.31 ± 0.54	n.s.	n.s.	n.s.	2.3 ± 0.17	2.61 ± 0.5	1.6 ± 0.29	2.67 ± 0.52	3.74 ± 0.13	2.82 ± 0.13	***	***	n.s.
α-Terpineol[T]	9 ± 2.2	10.7 ± 2.9	8.5 ± 3.7	9.5 ± 0.8	10.4 ± 2.6	18.8 ± 1	**	*	**	20.4 ± 9.3	19.9 ± 6.5	14.1 ± 3.2	22.8 ± 11.6	21.3 ± 3.2	24.1 ± 5.3	n.s.	n.s.	n.s.
α-Citral[G]							-	-	-	6.1 ± 0.2	6.7 ± 0.8	3.5 ± 0.2	6.7 ± 0.4	8.2 ± 0.4	6.1 ± 0.1	***	***	**
(*E*)-Pyranoid linalool oxide C[L]	9.9 ± 0.9	7.2 ± 1.5	9.5 ± 2.9	8.7 ± 1.4	8.8 ± 1.1	14.5 ± 2.3	n.s.	**	*	17.9 ± 5.1	13.4 ± 2.1	14.2 ± 2.6	19.2 ± 4.4	16.5 ± 3.2	23.6 ± 3.1	*	n.s.	n.s.
(*Z*)-Pyranoid linalool oxide D[L]	9.7 ± 1.3	7.0 ± 0.9	6.8 ± 1.7	6.7 ± 2.4	8.6 ± 2.4	8.5 ± 0.9	n.s.	n.s.	n.s.	14.2 ± 4.1	9.8 ± 1.4	10.1 ± 2.3	13.6 ± 2.9	10.1 ± 0.9	18.2 ± 4.3	n.s.	n.s.	n.s.
Citronellol[G]	6.7 ± 3.9	31.4 ± 2.3	13.7 ± 2.6	6.6 ± 1.6	26.9 ± 6.4	9.1 ± 1.2	n.s.	***	n.s.	13.1 ± 2	16.9 ± 3.4	11.3 ± 2.8	13.4 ± 1.3	21 ± 2.3	14.9 ± 0.6	*	**	n.s.
Lilac alcohol A[L]			24 ± 2.9	12.3 ± 3.9	47.8 ± 8.7	13.5 ± 7.8	-	-	-	14.8 ± 2.8	15.1 ± 1	11 ± 2.6	14.3 ± 0.1	21.6 ± 1	17.7 ± 2.3	***	**	*
Myrtenol[T]							-	-	-	1.5 ± 0.3	1.1 ± 0.9	0.8 ± 0.7	1 ± 0.8	1.4 ± 1.3	1.1 ± 0.9	n.s.	n.s.	n.s.
Nerol[G]	15.7 ± 1.4	35.5 ± 7.2	25.8 ± 4.8	14.3 ± 2.4	26 ± 6.6	17.1 ± 2.1	*	**	n.s.	19.9 ± 0.7	29.8 ± 3.1	15.9 ± 2.8	22 ± 3.5	41.5 ± 2.8	23 ± 1.1	***	***	*
Isogeraniol[G]	4.5 ± 1	8.0 ± 2.5	5 ± 0.1	3.3 ± 0.6	7.2 ± 1.5	4.3 ± 0.5	n.s.	**	n.s.	2.6 ± 0.4	3 ± 0.4	2 ± 0.4	2.9 ± 0.1	3.9 ± 0.2	3 ± 0.3	***	**	n.s.
Lilac alcohol B[L]			2.6 ± 0.4	1.6 ± 0.5		2.2 ± 0.8	n.s.	***	**	5 ± 0.6	5.9 ± 0.5	3.7 ± 0.7	5.7 ± 0.3	7.2 ± 0.9	5.4 ± 0.8	**	**	n.s.
Geraniol[G]	68 ± 8.5	104.5 ± 23.9	87.5 ± 12.8	67.7 ± 13.8	111.6 ± 29.2	80.9 ± 10.9	n.s.	**	n.s.	93.2 ± 1.3	111.3 ± 19.4	66 ± 8.9	103.7 ± 14	152 ± 7.8	106.3 ± 6.5	***	***	n.s.
Exo-2-hydroxycineole[T]							-	-	-	16.1 ± 4.6	19.5 ± 3.7	11 ± 2.2	16.8 ± 5.9	18.9 ± 2.3	19.9 ± 1.8	n.s.	n.s.	n.s.
2,6-Dimethyl-3,7-octadiene-2,6-diol 1[L]	17.2 ± 1.3	8.9 ± 0.7	19.8 ± 9.3	18 ± 3.3	10.1 ± 0.6	33.2 ± 6.9	n.s.	**	n.s.	10.2 ± 3.4	8.2 ± 1.5	11.2 ± 2.6	10 ± 1.6	8.9 ± 2.3	14.1 ± 3.2	n.s.	n.s.	n.s.
6,7-2OH-7-Hydroxylinalool[L]	4.5 ± 0.6	10.0 ± 2.0	4.5 ± 0.5	2.8 ± 0.9	10.9 ± 2.4	3.7 ± 0.9	n.s.	***	n.s.	3.9 ± 0.5	5 ± 0.7	3.4 ± 0.9	5.4 ± 0.5	7.5 ± 0.6	5.7 ± 1	***	**	n.s.
2,6-Dimethyl-1,7-octadiene-3,6-diol 2[L]	12.2 ± 1.1	12.6 ± 3.0	10.8 ± 0.8	6.8 ± 1.6	12 ± 3	7 ± 1.7	**	*	n.s.	24.8 ± 3.1	27.7 ± 2.9	17.4 ± 4.9	25.7 ± 3.4	30.8 ± 2.9	25 ± 1.8	*	**	n.s.
2,3-Pinanediol							-	-	-	11.4 ± 3.8	9.7 ± 0.8	7.9 ± 2.8	10.6 ± 2.1	12.9 ± 2.9	7.5 ± 1.4	n.s.	n.s.	n.s.
OH-Citronellol[G]	24.1 ± 3	39.5 ± 4.4	23.8 ± 3.5	21.4 ± 5.8	50.9 ± 10.5	26.9 ± 6.5	n.s.	***	n.s.							-	-	-
trans-8-Hydroxylinalool[L]	34.1 ± 0.2	31.8 ± 4.3	40.9 ± 9.5	25.3 ± 7.1	29.1 ± 2.9	34.9 ± 9.3	n.s.	n.s.	n.s.	29.1 ± 3.5	27.3 ± 3.7	23.9 ± 5.1	35.6 ± 1.8	34.2 ± 3.7	34.1 ± 2	***	n.s.	n.s.
cis-8-Hydroxylinalool[L]	49.9 ± 4	67.9 ± 11.3	58.9 ± 10.9	42.4 ± 13.6	66.1 ± 9	47.5 ± 12.3	n.s.	*	n.s.	49.8 ± 10	56.5 ± 3.5	34.5 ± 9.1	59.1 ± 5.9	76.2 ± 9.6	54.2 ± 9	**	**	n.s.
Geranic acid[G]	147.6 ± 22.4	238.3 ± 37.5	192.5 ± 30	149.5 ± 36.7	248 ± 52.5	185.3 ± 38.1	n.s.	**	n.s.	132.1 ± 15	185 ± 26.2	107.9 ± 14.4	195.4 ± 27.2	273.4 ± 11.1	188 ± 17.5	***	***	n.s.
cis-2,7-Dimethyl-4-octene-2,7-diol[L]	35.6 ± 31.7	81.1 ± 14.7	59 ± 17.8	50.8 ± 15.2	65.1 ± 22.8	76.5 ± 17	n.s.	n.s.	n.s.							-	-	-
7-OH-α-Terpineol[T]	103.3 ± 18.4	139.2 ± 15.6	94.8 ± 32.9	93.4 ± 22.7	129.2 ± 16.9	162.5 ± 34.4	n.s.	n.s.	*	54.7 ± 11.6	68.2 ± 15.2	42.8 ± 9.6	72.4 ± 22.3	100.8 ± 19	96.9 ± 5.3	***	n.s.	n.s.
2,6-Dimethyl-6OH-2,7-Octadienoic acid[L]	45.9 ± 79.5	129.7 ± 14.3	155.3 ± 31.8	119.9 ± 42.9	143.7 ± 24	115.9 ± 32.5	n.s.	n.s.	n.s.	62.1 ± 8.9	89.5 ± 16.7	59.7 ± 17.7	101.8 ± 24.5	127.2 ± 25.7	99.7 ± 21.7	**	n.s.	n.s.
Total monoterpenes	614 ± 87	971 ± 103	852 ± 156	670 ± 176	1023 ± 194	871 ± 170				652 ± 78	778 ± 115	511 ± 97	809 ± 124	1046 ± 67	844 ± 46			
β-Damascenone							-	-	-	19.9 ± 0.7	29.9 ± 3.1	15.9 ± 2.8	22 ± 3.5	41.6 ± 2.9	23 ± 1	***	***	*

(Continues)

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Table 3. Continued

	Concentration (ng/g of berry dry mass)																	
	2018									2019								
	1103P			SO4						1103P			SO4					
	FI	RDI-1	RDI-2	FI	RDI-1	RDI-2	*R*	*I*	*R* × *I*	FI	RDI-1	RDI-2	FI	RDI-1	RDI-2	*R*	*I*	*R* × *I*
Actinidol A	1.1 ± 0.2	2.0 ± 0.4	1.1 ± 0.2	0.8 ± 0.3	2.2 ± 0.6	0.6 ± 0.1	n.s.	***	n.s.	2.3 ± 0.3	3.9 ± 0.3	1.4 ± 0.3	3.1 ± 0.5	6.3 ± 0.5	2.6 ± 0.5	***	***	*
Actinidol B	1.8 ± 0.4	3.5 ± 0.6	1.9 ± 0.4	1.4 ± 0.4	3.4 ± 0.7	1.1 ± 0.1	n.s.	***	n.s.	4.4 ± 0.6	6.8 ± 0.6	2.6 ± 0.7	5.7 ± 0.9	10.6 ± 1	4.7 ± 1.1	***	***	n.s.
3,4-Dihydro-3-oxo-α-ionol (I)	58.5 ± 51.5	83.4 ± 74.4	88.8 ± 19.4	64.7 ± 15.1	116.1 ± 26.8	67.3 ± 20.5	n.s.	n.s.	n.s.	75.9 ± 13.9	91.5 ± 5	43.9 ± 10.8	94.9 ± 15.8	144.8 ± 10.1	88.1 ± 15	***	***	n.s.
3,4-Dihydro-3-oxo-α-ionol (II)	102.5 ± 16.6	153.7 ± 24.8	87.5 ± 21.4	71.2 ± 19.3	140.7 ± 37.2	69 ± 20.5	n.s.	**	n.s.	85.9 ± 20.9	127 ± 9.1	54 ± 13.7	135.9 ± 20.9	210.7 ± 12.7	113.3 ± 24.8	***	***	n.s.
3,4-Dihydro-3-oxo-α-ionol (III)	142.4 ± 21.4	214.1 ± 38.1	130.7 ± 29.7	104.9 ± 29.4	201.5 ± 58.4	101.8 ± 28.1	n.s.	**	n.s.	125.1 ± 15.1	172.9 ± 17.6	74 ± 17.8	184 ± 28.1	284.4 ± 17.9	151 ± 30.3	***	***	n.s.
3-Hydroxy-β-damascone	163.3 ± 19.7	192.7 ± 6.7	123.1 ± 15.5	88 ± 20.2	192.6 ± 29.9	112.1 ± 41.6	*	**	*	12.3 ± 2.2	8.4 ± 7.3	8.4 ± 2.1	16.5 ± 0.6	17.6 ± 4.9	13.4 ± 4.5	*	n.s.	n.s.
3-Oxo-α-damascone		23.3 ± 20.2	27.7 ± 16	7.5 ± 4.5	35.2 ± 20.3	24.9 ± 9.1	-	-	-	39.3 ± 7.7	58.8 ± 3.5	33.2 ± 8.5	57.3 ± 2.3	91.8 ± 6.2	61.2 ± 7.1	***	***	n.s.
4-Hydroxy-β-ionol		10.1 ± 2.9	3.4 ± 3				-	-	-	4.3 ± 2.1	5.8 ± 1.2	4.9 ± 2.3	5.3 ± 0.1	7 ± 0.3	8 ± 5.5	n.s.	n.s.	n.s.
3-Oxo-α-ionol	1080 ± 210	1474 ± 228	793 ± 152	679 ± 218	1308 ± 367	711 ± 221	n.s.	**	n.s.	947 ± 139	1396 ± 86	653 ± 140	1349 ± 153	2293 ± 180	1014 ± 160	***	***	*
2,3-2OH-4-Oxo-7,8-2OH-β-ionon	23.8 ± 20.8	26.1 ± 23	36.2 ± 6.3	23.5 ± 6.6	44.7 ± 14.6	27.7 ± 10.4	n.s.	n.s.	n.s.	42.5 ± 6.6	55.1 ± 2.6	28.3 ± 5.3	54.5 ± 4.3	82.8 ± 2.6	50.7 ± 6	***	***	*
Epimanool							-	-	-	6.6 ± 1.8	14.1 ± 2.1	8.4 ± 7.5	9.3 ± 0.4	17.6 ± 2.2	12.2 ± 3	n.s.	**	n.s.
3,9-Dihydroxy-megastigman-5-en	12.4 ± 11.5	21.8 ± 19.9	20.7 ± 6.1	14.4 ± 3.2	28.2 ± 8.2	16 ± 5.6	n.s.	n.s.	n.s.	8.6 ± 1.6	14.2 ± 3.5	14.8 ± 16.7	10.2 ± 0.7	18 ± 1.8	22.7 ± 17.5	n.s.	n.s.	n.s.
Blumenol C	45.2 ± 6.6	90.8 ± 11.1	47.1 ± 9.9	36.9 ± 11.3	89.3 ± 24.8	40.3 ± 12.1	n.s.	***	n.s.	4.8 ± 1.7	4.2 ± 1.4	3.2 ± 0.4	4.4 ± 0.8	7.5 ± 2.4	6.4 ± 3.1	*	n.s.	n.s.
3-Hydroxy-7,8-dihydro-β-ionol	81.7 ± 13.8	103.8 ± 5.9	64.3 ± 8.7	43.3 ± 12.9	100.8 ± 20.7	54.6 ± 17.3	*	**	n.s.	12.7 ± 2.8	19.4 ± 3.1	8.9 ± 1.6	18.4 ± 2.6	35.8 ± 2.5	20.6 ± 1.8	***	***	*
7,8-dihydrovomifoliol	24.1 ± 3.7	37.2 ± 8.6	26.3 ± 6.8	18 ± 5.5	33.9 ± 10.6	19.4 ± 5.7	n.s.	**	n.s.	14.8 ± 4.7	20.8 ± 3.6	11.8 ± 3.5	18.4 ± 2.6	34.1 ± 1.8	21.2 ± 4.8	***	***	n.s.
Total C_{13}-norisprenoids	1738 ± 259	2436 ± 307	1444 ± 286	1152 ± 345	2274 ± 586	1247 ± 392				1408 ± 191	2031 ± 127	968 ± 226	1990 ± 234	3305 ± 236	1614 ± 185			
Total VOCs	10 966 ± 1817	15 957 ± 978	11 702 ± 1283	9863 ± 1504	17 467 ± 3709	10 909 ± 2205				14 540 ± 1422	19 085 ± 1701	11 844 ± 1442	17 741 ± 1516	24 359 ± 590	17 562 ± 719			

Values are means ± SD (n = 3); *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; n.s., not significant, $P > 0.05$, respectively. †The superscript letter on monoterpenes indicates the biosynthetic origin, where G, geraniol, L, linalool and T, α-terpineol. FI, full irrigation from budburst through harvest; RDI-1, water deficit applied from fruitset through veraison; RDI-2, water deficit applied from veraison through harvest.

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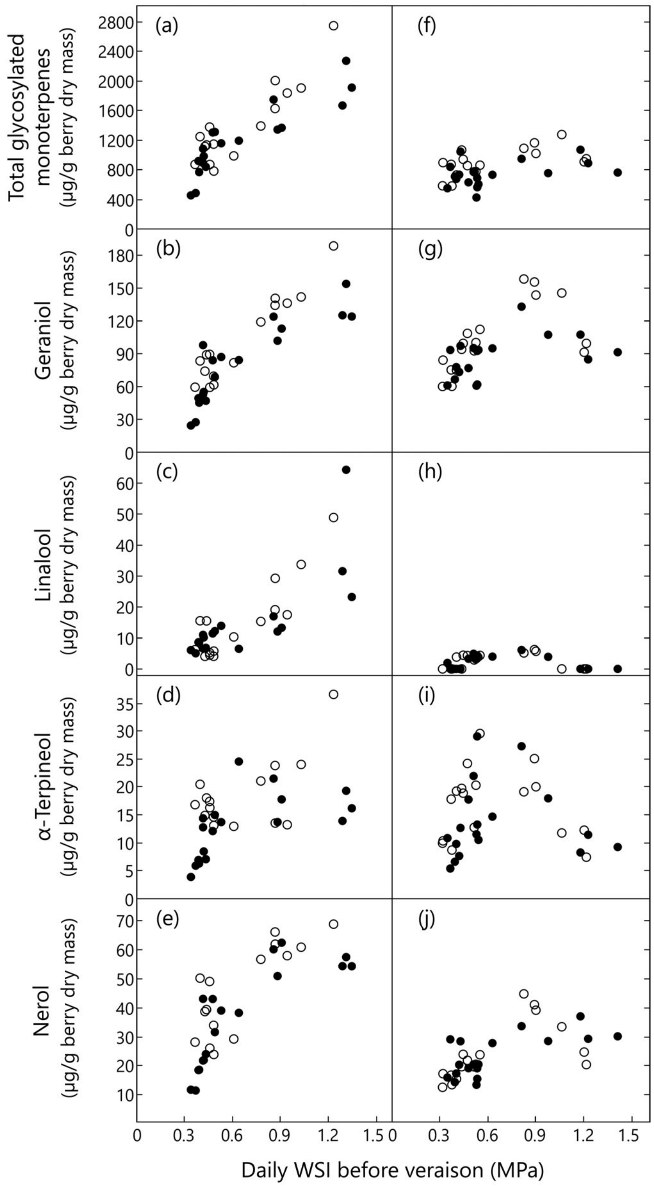

Figure 2. Relationship between (a,f) total glycosylated monoterpenes, (b,g) geraniol, (c,h) linalool, (d,i) α-terpineol, and (e,j) nerol at harvest and the daily water stress integral (WSI) before veraison, in berries from (a–e) Sangiovese and (f–j) Merlot vines grafted onto 1103P (●) and SO4 (○) rootstocks and subjected to different irrigation regimes (2018 and 2019).

water stress experienced by vines from fruitset to veraison (dWSI FS-V) and the concentration of the key monoterpenes at harvest. In Sangiovese there was a positive linear relationship between dWSI and geraniol, linalool and nerol, whereas in Merlot berries the same compounds (as well as α-terpineol) increased up to about −0.8/−0.9 MPa dWSI, and then decreased as water stress became more severe (Figure 2).

C_{13}-Norisoprenoids represented 17% (Sangiovese) and 12% (Merlot) of the total glycosylated VOCs (as an average of both years) (Tables 2,3). In Sangiovese, the concentration of most C_{13}-norisoprenoids was significantly higher in RDI-1 vines in both years (+67% > FI), and in SO4 grafted vines relative to 1103P vines (Table 2). The compound 3-oxo-α-ionol was the most abundant C_{13}-norisoprenoid and its concentration was about twofold higher in berries from the RDI-1 treatment than in Control berries, for both rootstocks and both years. A similar effect of RDI-1 treatment was observed in Merlot berries in both years, but only for a limited number of compounds [actinidol A and B, 3,4-dihydro-3-oxo-α-ionol (II), 3,4-dihydro-3-oxo-α-ionol (III), 3-oxo-α-ionol, 3-hydroxy-7,8-dihydro-β-ionol and 7,8-dihydrovomifoliol]. In Sangiovese, some differences emerged between rootstocks. In fact, while a linear positive relationship was observed between the dWSI and the 3-oxo-α-ionolo and the 2,3-dihydro-4-oxo-7,8-2H-β-ionone in Sangiovese-SO4 vines, a curvilinear relationship emerged in vines grafted on 1103P (Figure 3). In Merlot in 2019, almost all the C_{13}-norisoprenoid compounds had a higher concentration in berries sampled from Merlot–SO4 vines, whereas no difference between rootstocks was measured in 2018. Moreover, the relationship between C_{13}-norisoprenoids and the dWSI before veraison was similar to that observed for monoterpenes (Figure 3).

Benzene derivatives significantly contributed to the concentration of total glycosylated VOCs in berries (Tables 2, 3). 2-Phenylethanol and benzyl alcohol, which are synthesised from aromatic amino acids present in grapes, were the main benzene derivative compounds detected in the two cultivars. The RDI-1 berries accumulated more benzene derivatives. In RDI-1 Sangiovese berries, the concentration of ethyl benzoate, benzyl alcohol, 2-phenylethanol and 2,3,4-trimethoxybenzyl alcohol was higher than that in berries from other treatments in both years (Table 2). In Merlot, a significant and consistent effect of pre-veraison water deficit was observed on benzaldehyde, 2-phenylethanol and 3,4-dimethoxybenzyl alcohol (Table 3). The rootstock affected the concentration of benzene derivatives only slightly, and differences were inconsistent between years. An almost linear relationship between 2-phenylethanol and the dWSI FS-V was evident in Sangiovese berries, whereas a parabolic relationship was apparent in Merlot (Figure 4a,f).

Among the phenols, guaiacol, eugenol and γ-hydroxyeugenol reached a higher concentration in the berries of RDI-1 vines in both cultivars and both years (Tables 2,3). The concentration of 4-vinylguaiacol was higher in each year in berries from Sangiovese-SO4 vines than in 1103P grafted vines (Table 2). In Merlot, the concentration of phenols was higher in SO4 grafted vines, especially in 2019 (Table 3). Eugenol increased at a higher rate in berries corresponding to SO4, than to 1103P, as water stress before veraison increased (Figure 4c,h).

Methyl vanillate, acetovanillone, zingerone and homovanillyl alcohol were the most abundant vanillins, with vanillin and zingerone higher in berries sampled from RDI-1 vines of both cultivars and in both years (Tables 2, 3). Zingerone and acetovanillone showed a curvilinear (Sangiovese) and an almost bilinear relationship (Merlot) in response to dWSI, and a threshold similar to that observed for other aroma compounds (i.e. −0.8/−0.9 MPa) (Figure 4).

Irrigation affected the aliphatic alcohols differently. In Sangiovese, they increased in both RDI treatments (particularly in RDI-1), in both years. The most abundant aliphatic alcohols, isoamyl alcohol, 3-methyl-2-buten-1-ol and 1-hexanol, were present at higher concentration in berries from RDI-1 vines, whereas the concentration of 4-methyl-3-penten-1-ol was higher in vines subjected to water stress between veraison and harvest (Table 2). Differences in the concentration of aliphatic alcohols between irrigation treatments in Merlot vines were inconsistent between years, except for 1-octanol and (*E*)-2-octen-1-ol, which was higher in RDI-1 berries (Table 3). There was no clear effect of rootstock in both cultivars on the concentration of aliphatic alcohols.

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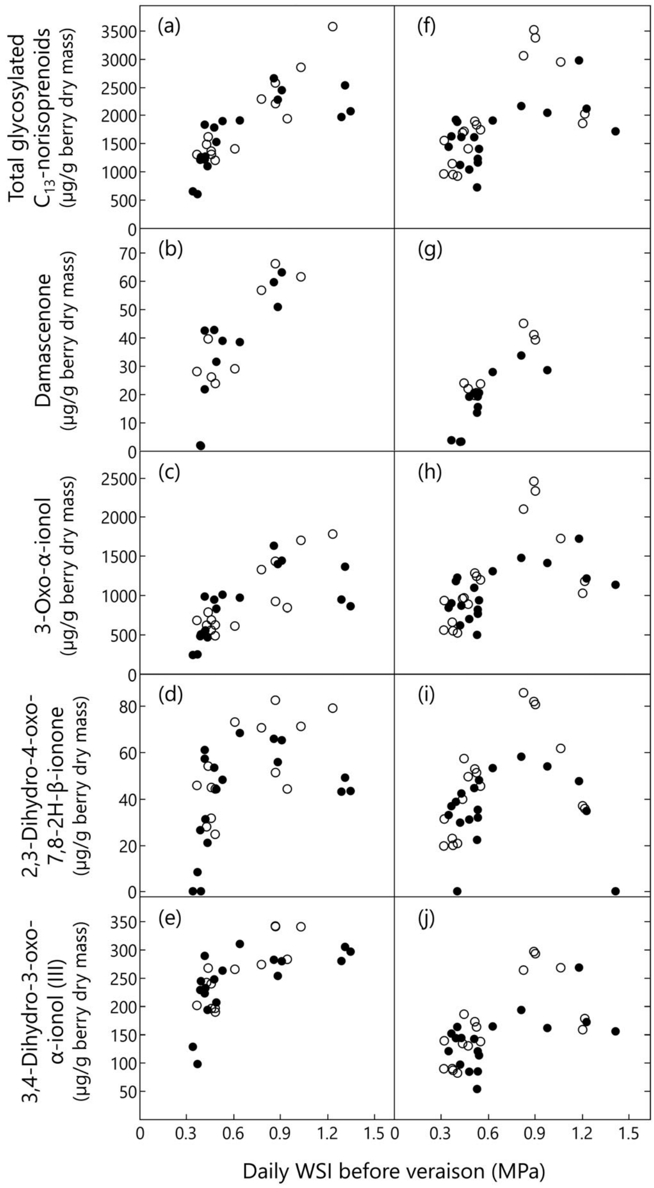

Figure 3. Relationship between (a,f) total glycosylated C_{13}-norisoprenoids, (b,g) damascenone, (c,h) 3-oxo-α-ionol, (d,i) 2,3-dihydro-4-oxo-7,8-2H-β-ionone, and (e,j) 3,4-dihydro-3-oxo-α-ionol at harvest and the daily water stress integral (WSI) before veraison, in berries from (a–e) Sangiovese and (f–j) Merlot vines grafted onto 1103P (●) and SO4 (○) rootstocks and subjected to different irrigation regimes (2018 and 2019).

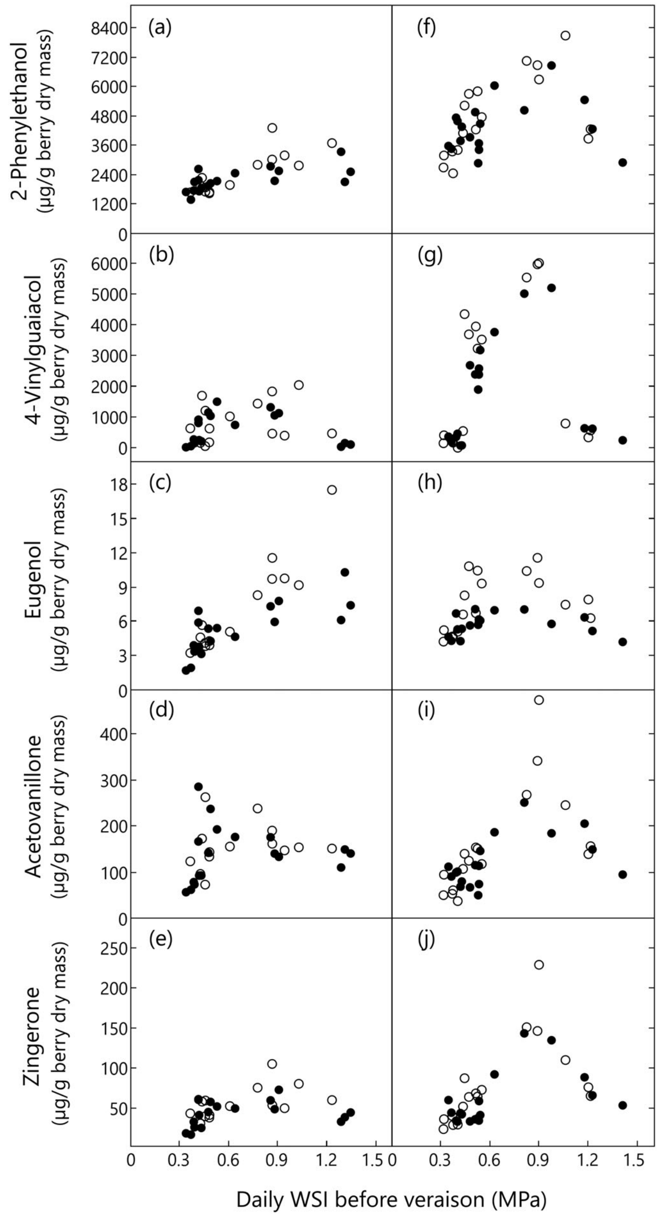

Figure 4. Relationship between (a,f) glycosylated 2-phenylethanol, (b,g) 4-vinylguaiacol, (c,h) eugenol, (d,i) acetovanillone, and (e,j) zingerone at harvest and the daily water stress integral (WSI) before veraison, in berries from (a–e) Sangiovese and (f–j) Merlot vines grafted onto 1103P (●) and SO4 (○) rootstocks and subjected to different irrigation regimes (2018 and 2019).

The PCA provides a general overview of the distribution of the classes of VOCs over the 2 years, with respect to cultivar, irrigation treatment and rootstock (Figure 5). Principal component (PC)1 and PC2 described 66% of the total variation and explained most of the variation due to cultivar or to irrigation. Loadings of the corresponding two eigenvectors are the weights of the linear combination of the initial variables from which PCs are constructed. The PC1 had eigenvalues of 4.00 and described 44.5% of the total variance. It clearly discriminated the effect of irrigation on the concentration of glycosylated VOCs at harvest. The effect of water deficit before veraison correlated with all volatile classes, whereas post-veraison water deficit did not. The score plot confirmed that total glycosylated VOCs were higher in SO4 RDI-1 treatments. The PC2 described 21.5% of the variance and had an eigenvalue of 1.94. The PC2 separated the cultivars on the basis of their typical VOC classes. Vintage affected the total concentration of several VOCs (Figure S3, Table S2). In fact, the step-forward analysis discriminated between 2018 and 2019 using 65 VOCs as a set of independent variables, as summarised by their respective scoring coefficients in Table S2.

Discussion

The composition of the glycosylated VOCs of the berries of the Sangiovese and Merlot cultivars was different, in that, the main groups in Sangiovese were benzene derivatives, C_{13}-norisoprenoids and monoterpenes, confirming previous findings by D'Onofrio et al. (2018), whereas benzene derivatives, vanillin derivatives and phenols were the most abundant glycosylated VOCs in Merlot berries.

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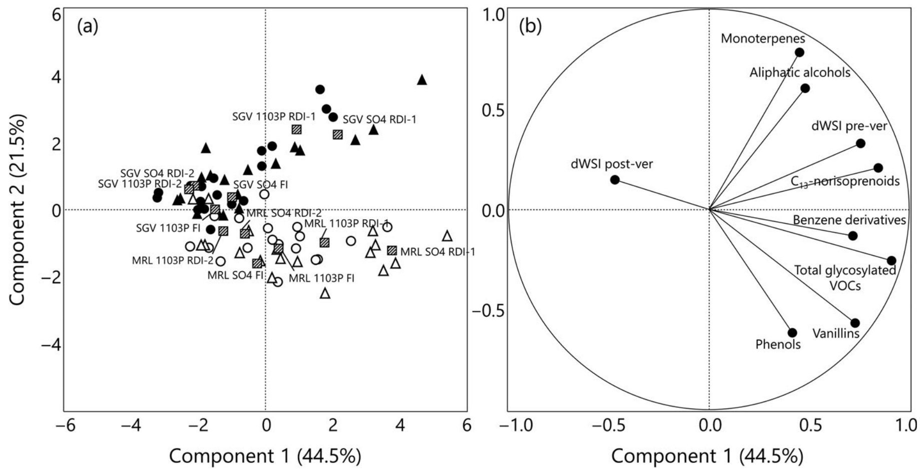

Figure 5. (a) Score plot and (b) loadings plot for principal component (PC)1 and PC2 of principal component analysis performed using classes of aroma compounds and deficit irrigation treatments from 2018 and 2019. In the score plot Sangiovese SO4 (▲), Sangiovese 1103P (●), Merlot 1103P (○) and Merlot SO4 (△) and average of the scores of observations for each cultivar–rootstock–irrigation combination (▨).

The different climatic conditions between the two growing seasons (especially mean air temperature) affected vine phenology and physiology (Palai et al. 2021, Caruso et al. 2022), as well as the total amount of glycosylated VOCs in berries (Figure S3, Tables 2,3). The crucial role of climatic conditions on glycosylated VOC profiles has been widely reported in previous studies (Bureau et al. 2000, Song et al. 2012, D'Onofrio et al. 2018, Kovalenko et al. 2021), but interestingly, results herein showed that the relationship between the different VOC classes that characterise berry aroma, and the effect of irrigation, remained consistent over both growing seasons. In particular, the water deficit applied from fruitset to veraison (RDI-1) enhanced the concentration of glycosylated VOCs at harvest, whereas post-veraison water deficit (RDI-2) was detrimental or did not greatly influence the accumulation of glycosylated VOCs. Pre-veraison proved to be a critical stage during which the biosynthesis of berry glycosylated VOCs could be regulated, in agreement with what has been suggested in previous studies (Kalua and Boss 2010, Martin et al. 2012, Matarese et al. 2013). In contrast, post-veraison is reported to be more important for the accumulation of VOCs (García et al. 2003, Yang et al. 2009), and VOCs are negatively affected by water deficit, probably due to the lower availability of biosynthetic resources or their modulation through different metabolic pathways (Degu et al. 2019, Gambetta et al. 2020).

Post-veraison water deficit also caused rapid accumulation of TSS in berries of both cultivars. A possible relationship between the TSS increment and the low concentration of glycosylated VOCs in RDI-2 berries cannot be excluded. However, the higher values of glycosylated VOCs, measured in RDI-1 berries, which had the lowest TSS, appears to confirm the negligible impact of sugar concentration on glycosylated VOCs accumulation. In a previous study, Böttcher et al. (2018) suggested that once berries have reached a modest sugar concentration (i.e. 18°Brix), the effect of further accumulation of sugars has a minimal impact on the free VOC composition of the resulting wines.

In both cultivars, a higher concentration of most glycosylated VOC classes was measured in berries from SO4 grafted vines, especially under the RDI-1 irrigation regime (although results were not always statistically significant), suggesting a direct effect of rootstock on the accumulation of glycosylated VOCs in berries. Plant vigour expressed as canopy volume or trunk diameter increment was greater in 1103P grafted vines relative to SO4 grafted vines (Palai et al. 2021, Caruso et al. 2022). In turn, vigour might have modified the leaf area to fruit mass ratio affecting accumulation of glycosylated VOCs in berries. The influence of rootstocks, however, on the molecular mechanisms which affect the berry skin transcriptome and berry chemical composition at harvest (Zombardo et al. 2020), cannot be excluded. For instance, the promoters of many deficit-induced genes involved in VOC biosynthesis are enriched for abscisic acid (ABA)-related *cis*-regulatory elements (Savoi et al. 2016), which in turn are differently modulated by each rootstock under water scarcity conditions (Soar et al. 2006). It should be noted, however, that plant water status, leaf gas exchange, yield components and berry characteristics were similar between rootstocks in both years (Palai et al. 2021, Caruso et al. 2022).

In both years, irrigation significantly affected the concentration of glycosylated monoterpenes which increased following pre-veraison water deficit, but not due to post-veraison water stress. Savoi et al. (2016) reported that pre-veraison water deficit enhanced the accumulation of free nerol, linalool, hotrienol and α-terpineol, and the expression of several key genes, in berries of Tocai Friulano. Transcriptional modulation also enhanced monoterpene accumulation in Viognier berries where terpene synthases were overexpressed in vines subjected to pre-veraison deficit irrigation (early deficit) and sustained deficit irrigation (Wang et al. 2019). The same authors reported that a higher concentration of free α-terpineol and linalool was observed only with early water deficit, whereas prolonging stress until ripening did not have the same effect, similar to observations for RDI-2 berries in the current study. Linalool and α-terpineol (and their derivatives) were also higher in RDI-1 berries (in both cultivars) with linalool derivatives prevalent in Sangiovese, and geraniol and linalool derivatives prevalent in Merlot. Likewise, Song et al. (2012) observed an increase in glycosylated geraniol and some bound terpenes, such as nerol, in deficit irrigated (35–70% ET_c) Merlot. Qian et al. (2009), studying the same cultivar, reported a higher concentration of linalool and geraniol in wines derived from vines subjected to prolonged water deficit (35% ET_c). Geraniol, linalool, α-terpineol (and their derivatives) are

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biosynthetically independent, starting from geranyl pyrophosphate (Martin et al. 2012, Matarese et al. 2013). The greater accumulation of linalool derivatives in Sangiovese vines under the RDI-1 irrigation treatment, and for geraniol derivatives in Merlot, support the hypothesis for a different modulation of linalool and geraniol synthases between the two cultivars. Furthermore, in Sangiovese there was a linear and positive relationship between the concentration of monoterpenes and the amount of water stress experienced before veraison, whereas in Merlot berries, monoterpenes increased as SWP decreased to about −0.9 MPa, and then declined at higher levels of water deficit (Figure 2). Cultivars with a different sensitivity to water scarcity have been shown to respond differently in terms of fruit composition when subjected to deficit irrigation (Hochberg et al. 2015). Dal Santo et al. (2016) reported some evidence for differences in the transcriptome response and ABA-related gene modulations following water stress. Thus, the different VOCs accumulation pattern observed in Merlot and Sangiovese may provide further evidence of a specific cultivar response to water deficit.

Berries from SO4 grafted vines subjected to a similar level of water deficit contained more geraniol (Merlot and Sangiovese), nerol (Merlot) and α-terpineol (Sangiovese), but a higher concentration was also found for other monoterpenes (Tables 2, 3). Similarly, a higher concentration of free terpenes was observed in wines obtained by Summer Black vines grafted onto SO4 compared to those grafted onto 5BB or 101-14, or to own-rooted vines (Jin et al. 2016), whereas in Carignan Noir wines, α-terpineol and linalool were significant higher in berries from ungrafted vines, relative to those grafted onto Païs (Gutiérrez-Gamboa et al. 2018).

The effect of irrigation on glycosylated C_{13}-norisoprenoids was clearly enhanced by the RDI-1 treatment, in both cultivars. Our results indicate that pre-veraison water deficit increased C_{13}-norisoprenoids, particularly 3-oxo-α-ionol, 3,4-dihydro-3-oxo-α-ionol (I, II and III), β-damascenone, 3-OH-β-damascone and both actinidols (A and B). Song et al. (2012) also reported a significantly higher concentration of 3-oxo-α-ionol and β-damascenone (both free and bound forms) in Merlot grapes grown under water deficit conditions. C_{13}-Norisoprenoids originate from the biodegradation of carotenoids via chemical or photochemical-oxidase coupled degradation, or by enzymatic cleavage [carotenoid cleavage dioxygenase (CCD)] (Mendes-Pinto 2009); a clear correlation was found between the concentration of berry carotenoids and of wine C_{13}-norisoprenoids (Oliveira et al. 2006, Crupi et al. 2010). The CCD transcript abundance was reported to be higher in Chardonnay and Cabernet Sauvignon under partial root-zone drying, particularly before and around veraison (Deluc et al. 2009). Savoi et al. (2016) also reported that water deficit triggered the accumulation of carotenoids (e.g. violaxanthin and zeaxanthin), which are the precursors of C_{13}-norisoprenoids. In our experiment, the RDI-1 treatment may have contributed indirectly, since the loss of basal leaves exposed the fruiting zone to sunlight radiation, and this might have increased both carotenoids and C_{13}-norisoprenoids (Razungles et al. 1998, Bureau et al. 2000). The modulation induced by water deficit, however, on diverse stress-related signals may have activated alternative carotenoid biosynthetic pathways, such as the MEP plastidial pathway (Bindon et al. 2007). There was a different relationship between the concentration of C_{13}-norisoprenoids and daily WSI before veraison in Merlot and Sangiovese. In Merlot berries, the concentration of damascenone, 3-oxo-α-ionol, 2,3-dihydro-4-oxo-7,8-2H-β-ionone and 3,4-dihydro-3-oxo-α-ionol was higher in SO4 grafted vines. A different concentration of norisoprenoids, especially β-damascenone, was measured in Shiraz wines obtained from vines grafted on different rootstocks (Olarte Mantilla et al. 2018).

In Merlot 1-octen-3-ol was higher in RDI-1 berries compared to that of the other treatments, while the concentration of 1-hexanol (characterised by herbaceous and grassy odours which relate to a deleterious effect) was inconsistent between years and irrigation, confirming previous results reported for the same cultivar (Song et al. 2012). Isoamyl alcohol was strongly enhanced by deficit irrigation before veraison in Sangiovese, as was 1-hexanol. The latter compound is produced from the degradation of linoleic acid via the lipoxygenase pathway, which is more dominant than the degradation of linolenic acid after veraison, as reported in Cabernet Sauvignon (Kalua and Boss 2009). Although the accumulation of 1-hexanol steadily increased toward maturation, our results suggest a major effect of water stress before veraison. Nevertheless, the higher concentration of aliphatic alcohols often associated with RDI-1 berries could represent a positive attribute due to: (i) their ability to form fruity esters during vinification in the presence of carboxylic acid; and (ii) their higher herbaceous odour threshold than related aldehydes (Kalua and Boss 2009). The effect of the rootstock was irrelevant in Sangiovese, while in Merlot, SO4 grafted vines had a higher concentration of total aliphatic alcohols relative to that of 1103P vines, when subjected to RDI-1 treatment. Olarte Mantilla et al. (2018) reported a significantly different concentration of aliphatic alcohols (e.g. 1-hexanol, 1-pentanol, 1-octen-3-ol) in Shiraz wines obtained from vines grafted onto different rootstocks. Romero et al. (2019) studied Monastrell vines under deficit irrigation and observed an improvement in wine quality using a low vigour rootstock (161-49C), due to a significantly lower concentration of unpleasant VOCs (e.g. propanol, 3-methyl-ethyl-butanoate, diethyl succinate, 2-octanone).

Among the benzene derivatives measured, 2-phenylethanol and benzyl alcohol, which are responsible for fruity and floral/rose-like scents, were the principal benzene derivatives found in both cultivars, and both compounds increased in RDI-1 berries. 4-Vinylguaiacol was among the more interesting phenols detected, and is known to confer spicy notes that are particularly appreciated in Sangiovese wines. In Verdejo, the same compound was enhanced in wines derived from rain-fed vines, compared to that of deficit irrigated vines (Vilanova et al. 2019), and a higher concentration of 4-vinylguaiacol and guaiacol was observed in wines from deficit irrigated (35% ET_c from fruitset to harvest) Merlot grapevines (Qian et al. 2009). Syringol imparts wood and creamy notes, while eugenol is responsible for clove aroma, and these compounds were particularly affected by pre-veraison water deficit of Merlot and Sangiovese vines, respectively, while methyl vanillate, acetovanillone, vanillin and zingerone, which all exhibit vanilla notes, increased in RDI-1 berries from both cultivars. Despite little information being available on the biosynthesis of these compounds, Kalua and Boss (2009) observed an increase in benzene derivatives during late stages of ripening, and attributed this to protein solubilisation or up-regulation operated by flavonoids. Although our results showed some compounds were affected by deficit irrigation after veraison (e.g. alcohol 3,4-dimethoxybenzyl and homovanillyl alcohol), they still suggest there is a direct effect of water deficit before

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veraison, resulting in an increased concentration of benzene derivatives, phenols and vanillins at harvest.

Conclusions

In conclusion, our comprehensive experiment (three irrigation regimes, two rootstocks and two cultivars) afforded a wide range of treatments to investigate the individual and combined effects of these factors on glycosylated VOCs in grape berries. Despite variation in glycosylated VOCs between growing seasons, the typical profiles observed for each cultivar were maintained, and the accumulation of glycosylated VOCs in berries was affected by water deficit. In particular, the clear effect of water deficit applied from fruitset until veraison to increase the final concentration of glycosylated VOCs in berries, and in contrast, the minimal effect of deficit irrigation post-veraison indicates the potential for deficit irrigation to be managed to enhance glycosylated VOCs so as to increase berry aroma. At the same time, Merlot and Sangiovese vines showed different responses toward the magnitude of imposed pre-veraison irrigation treatments: Sangiovese increased glycosylated VOCs in berries, when pre-veraison water stress increased, whereas Merlot exhibited a peak in accumulation of glycosylated VOCs, followed by a decrease under more severe water stress. These results suggest cultivar sensitivity to water deficit, which affects the biosynthesis of glycosylated VOCs at different levels of water stress severity, suggesting vine water status and irrigation need to be managed differently depending on cultivar. Finally, the rootstock choice also proved to be important for berry quality, although further work is needed to confirm these findings, since the rootstock effect (SO4 appeared to be more sensitive to early water deficit than 1103P, enhancing the accumulation of glycosylated VOCs in berries) was not consistent for many VOCs, in both years. Overall, these results suggest a potential role of the rootstock in determining berry aroma profiles, but further investigations should be conducted to identify and characterise the metabolic and molecular responses involved.

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Figure S1. (a,c,e) Total soluble solids (TSS) and (b,d,f) TA from veraison to harvest measured in (a,c,e) 2018 and (b,d,f) 2019 in Sangiovese (*Vitis vinifera* L.) grapevines grafted on

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1103P (□, ▵) and SO4 (●, ○) rootstocks and subjected to the following irrigation regimes: (a,b) full irrigation (FI), full irrigated from budburst through harvest; (c,d) regulated deficit irrigation 1 (RDI-1), and (e,f) regulated deficit irrigation 2 (RDI-2), water deficit applied from fruitset through veraison and from veraison through harvest, respectively. Values are means ± SD of three replicates per treatment ($n = 3$).

Figure S2. (a,c,e) Total soluble solids (TSS) and (b,d,f) TA from veraison to harvest measured in (a,c,e) 2018 and (b,d, f) 2019 in Merlot (*Vitis vinifera* L.) grapevines grafted on 1103P (□, ▵) and SO4 (●, ○) rootstocks and subjected to the following irrigation regimes: full irrigation (FI), full irrigated from budburst through harvest; (e,f) regulated deficit irrigation 1 (RDI-1), and regulated deficit irrigation 2 (RDI-2), water deficit applied from fruitset through veraison and from veraison through harvest, respectively). Values are means ± SD of three replicates per treatment ($n = 3$).

Figure S3. Effect of year on the accumulation of glycosylated volatile organic compounds (VOCs) in berries on Sangiovese and Merlot cultivars. Discriminant analysis was performed using different glycosylated VOCs as a set of independent variables. Lines refer to variables considered in the model. Their arrangement indicates how they are related to the discriminated years. Stepforward analysis was performed using 65 aroma compounds. Canonical details calculated from the overall pooled within-group covariance matrix are reported in the tables. The ID number and the respective glycosylated VOC is listed in Table S2.

Table S1. Correspondence between International Union of Pure and Applied Chemistry (IUPAC) nomenclature for volatile organic compounds (VOCs) and the relative common name used in the manuscript.

Table S2. Scoring coefficients of the 65 glycosylated volatile organic compounds selected in the stepforward analysis which characterises the year as reported in the discriminant analysis (Figure S3).

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