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Effects of interaction of UV-B radiation and water deficit on phenolic compounds in 'Pinot Noir' fruit

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Summary

Environmental issues (high UV-B radiation and water deficit) can challenge 'Pinot Noir' growth in New Zealand. The aim of this work is to determine separated and combined UV-B and water deficit effects on phenolic composition of 'Pinot Noir' fruit. In 2016-2017 vintage, two rows of 'Pinot Noir' grapevines in the West Vineyard at Lincoln University were chosen for the study. In comparison to exposure to natural UV-B in the vineyard, the potted vines were put into a glasshouse for the experiments. When berries were directly exposed to UV-B and water deficit, skin anthocyanin and skin total phenolics accumulated to a greater degree in the berry skins. The combined stresses caused larger increases in contents of skin total phenolics than the water deficit in the vineyard and glasshouse. Skin tannin contents were increased by UV-B and water deficit, but there were no consistent changes in seed tannin contents between treatments during ripening and no statistically significant differences between treatments at harvest. This research reported that canopy management (UV-B exposure) interacting with a moderate water deficit may be a good way for vineyard management to increase the accumulation of anthocyanins and tannins in berry skins.

Key words: UV-B radiation; water deficit; skin total phenolics; skin anthocyanin; skin tannins; seed tannins; V*itis vinifera* 'Pinot Noir'.

Introduction

UV can be divided by wavelength into UV-A (315-400 nm), UV-B (280-315 nm) and UV-C (100-280 nm). UV-C and much of UV-B cannot penetrate the stratospheric ozone layer; therefore, the ozone layer protects life on earth from the most dangerous UV radiation. When a fraction of UV-B reaches the Earth's surface, as a highly energetic form of radiation, it can, however, cause damage to the biosphere (Jordan 1996, Matsumi and Kawasaki 2003). In New Zealand, UV radiation levels are 30-40 % higher compared to similar latitudes in the Northern Hemisphere (Seckmeyer and McKenzie 1992, McKenzie *et al.* 1999 and 2007). UV-B causes changes in plant growth and development, regulation of primary and secondary metabolism and alterations in the molecular responses of plant cells (Jordan 1996, Wargent and Jordan 2013). The specific effects of UV-B on plants show changes in leaf area, loss of fresh and dry weight, the inhibition of photosynthesis (Jordan 1996) and alterations in flowering and reproduction (Jansen 2002, Jordan 2002, Strid *et al.* 1990). It causes damage to DNA, proteins and lipids, changes in gene expression and pigment biosynthesis and produces antioxidants (Jordan 2002 and 2017). In addition, the mean annual rainfall in regions where 'Pinot Noir', is low, and long dry spells can occur, especially in summer. Consequently, water deficit challenges 'Pinot Noir' growth in New Zealand (Central Otago, Waipara, Marlborough and Wairarapa). Water deficit has multifaceted effects on grapevine growth and metabolism (Bertamini *et al.* 2006, Cramer *et al.* 2007).

Phenolic compounds are a class of the most important plant secondary metabolites and significantly contribute to grape and wine quality. The biosynthesis of flavonoids, an important subset of phenolics, results in three major classes of compounds in grapevines: flavonols, anthocyanins and flavan-3-ols (the latter class is also referred to as tannins with respect to grapes and wine). Flavonols, which can act as UV protectants and antioxidants, are a ubiquitous class of flavonoids in grape skins and the cell walls of seeds, but not in the pulp (Teixeira *et al.* 2013). Flavonol synthesis primarily begins at an early stage of berry development through to veraison (Downey *et al.* 2003). Anthocyanins are dominant pigments in red grape skins, and include delphinidin, cyanidin, petunidin, peonidin and malvidin (Revilla *et al.* 2013). Accumulation of anthocyanins occurs from veraison to ripening in red grape skins. Flavan-3-ols are another important class of flavonoid compound in berry skins and seeds (Downey *et al.* 2003). Flavan-3-ol monomers in grapes are catechin, epicatechin, gallocatechin, epigallocatechin and catechin-3-O-gallate (Kennedy *et al.* 2001). The polymeric structure of flavan-3-ols is referred to as proanthocyanidins or tannins. Tannins can be composed of chains of almost identical subunits. Skin tannins (4 to more than 100 subunits) tend to be longer than seed

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tannins (2 to 20 subunits) (KELLER 2015). The highest level of catechins is in grape skins with epicatechin and epigallocatechin providing most of the extension subunits, while epicatechins are the major flavan-3-ol in grape seeds. Skin and seed tannins are synthesised from fruit set to veraison or before anthocyanin accumulation and then decline post veraison. The soluble flavan-3-ols and tannins are associated with grape quality and contribute to bitterness and astringency in grape skins and wines (CONDE *et al.* 2007).

Based on this knowledge, UV-B and water deficit are environmental issues for vineyard management in New Zealand. However, there has been only very limited research into the effects of a combination of UV-B radiation and water deficit on the phenolic compounds in grapevines. The aim of this study was to determine effects of the separate and combined UV-B and water deficit on phenolic composition of fruit in *Vitis vinifera* L. var. 'Pinot Noir'.

Material and Methods

Glasshouse experiments: This study was conducted in 2016-2017 in the Horticulture Nursery at Lincoln University. 'Pinot Noir' clone 115 cuttings were collected in August 2013 and rooted on a heating pad before being transferred to 20 L pots and grown outdoors at the Nursery. The vines were pruned in the dormant season of 2014 to one cane on which two shoots, but no fruit, were allowed to grow. In both experiments, 2015 and 2016, the vines were pruned similarly and grown with fruit. The potting mix was 80 % composted bark and 20 % pumice with fertilisation (Osmocote Exact 16-3.9-9.1, horticultural lime and Hydraflo).

The grapevines were moved into the glasshouse for preparation for the experiments in September, prior to budbreak. From October (fruit-set) to December (veraison), the grapevines were uniformly irrigated and were exposed to natural local daylength hours in the glasshouse. All clusters were harvested in February.

Vines of similar leaf area and crop weight were divided into two groups of 18 vines each. In each group treatments were applied from veraison to harvest (Tab. 1): (i) UV-B control treatment (-UV): the vines were moved into the glasshouse; (ii) UV-B treatment (+UV): the vines were put in the same glasshouse, but UV was supplied by UVB-313 UV fluorescent tubes (Q-Lab Company, Westlake, OH, USA). The fluence rates of UV-B (280-313 nm) were measured by a UVB Biometer model 501 radiometer (Solar Light Company, Glenside, PA, USA). The glasshouse was maintained to the following specifications: 28 °C/18 °C, day/night, humidity 70-80 % and, in the UV-area, the intensity of UV-B was kept at UVI-6 for 8 h/d (9:00-17:00).

Table 1

Glasshouse treatments (three wines in a block)

Water treatment	UV-B treatment	Natural light
Well-watered	+W+UV (9 vines)	+W-UV (9 vines)
Water deficit	-W+UV (9 vines)	-W-UV (9 vines)

Vines were exposed to a water treatment in combination with the UV-B treatment. Both UV-B treatment groups were divided into two with two irrigation levels, each one consisting of nine vines. There was a: (i) well-watered control treatment where vines are regularly irrigated to soil water volume content (+W); and a (ii) water-deficit treatment where vines received half that amount of water (-W) (Tab. 1). Soil in the water deficit treatment was dry to the touch at re-watering and the grapes had visible shrivelling. Time domain reflectometry (TDR) (Hydrosense™, Campbell Scientific, Inc) were used to evaluate the percentage of substrate soil moisture for each pot.

Vineyard experiments: In the field trial, this study was conducted at Lincoln University in 2016-2017 vinetage. The vineyard was located at 43°39'S, 172°28'E, which is considered a cool climate winegrowing area (average growing season temperature of 13 to 15 °C; Winkler Index: 850-1389 growing degree-days). The 'Pinot Noir' vines (clone 777 on 3309 rootstock) were planted in 1999 in a north-south row orientation with 1.2 m between vines and 2.5 m between rows. Vines were trained to two bilaterally-opposed canes in a vertical shoot positioned system (VSP). All the grapes were harvested by hand in April 2017.

The trial design was three UV-B treatments interaction with two water treatments in two rows of four replicated blocks (Tab. 2). All vines were randomly selected in the vineyard, and buffer vines were used to avoid the impact of UV-B and water treatments on each vine.

Grapevines across two rows were divided into six groups (each group including four vines), each vine with visually similar canopy size and crop load. UV-B exclusion was achieved using the method of GREGAN *et al.* (2012). A-frame-mounted transparent screens (240 cm × 60 cm) containing UV-B exclusion materials were placed over individual vines to cover the fruiting zone of the test vine and buffer on either side. In each group of vines, the following treatments were applied from veraison to harvest: (i) shade cloth treatment (SC)- leaves around the fruiting zone were removed and clusters were covered by shade cloth (Ultra-Pro 70 % shadecloth, Cosio Industries Ltd); (ii) leaf removal treatment (LR)- all leaves and lateral shoots were removed in the bunch zone leaving clusters fully exposed; (iii) PETG (glycol-modified polyethylene terephthalate, Mulford Plastics, Christchurch New Zealand)- all leaves and lateral shoots were removed in the bunch zone and clusters were covered by a PETG screen to exclude UV-B. In all treatments leaves in the fruiting zone were removed to maintain the same leaf areas across treatments.

16 TDR rods (40 cm) were installed into the soil to evaluate soil moisture in each block. Every UV-B treatment was divided into two groups with two irrigation levels and each one consisted of four vines from veraison to harvest: (i) no irrigation treatment; (ii) standard irrigation treatment.

Sample collection: Glasshouse experiments were carried out on potted vines (36 vines) from veraison (12 weeks post bud burst) to harvest (17 weeks post bud burst). Sampling time points were selected at veraison, 1-week post-veraison, 2-weeks post-veraison, 3-weeks

Table 2

Vineyard experimental design
SC: Shade cloth treatment; LR: Leaf removal treatment; PETG: Polyethylene terephthalate screen treatment. WW, well-water; WD, water deficit

Treatment (52 row)	Rep	Treatment (53 row)	Rep
	Buffer vines		Buffer vines
WW + SC	R1	WD + SC	R3
	Buffer vines		Buffer vines
WW + PETG	R1	WD + LR	R3
	Buffer vines		Buffer vines
WW + LR	R1	WD + PETG	R3
	Buffer vines		Buffer vines
WD + SC	R1	WW + SC	R3
	Buffer vines		Buffer vines
WD + PETG	R1	WW + LR	R3
	Buffer vines		Buffer vines
Wd + LR	R1	WW + PETG	R3
	Buffer vines		Buffer vines
WW+ LR	R2	WD + PETG	R4
	Buffer vines		Buffer vines
WW + PETG	R2	WD + LR	R4
	Buffer vines		Buffer vines
WW + SC	R2	WD + SC	R4
	Buffer vines		Buffer vines
WD + LR	R2	WW + PETG	R4
	Buffer vines		Buffer vines
WD + PETG	R2	WW + LR	R4
	Buffer vines		Buffer vines
WD + SC	R2	WW + SC	R4
	Buffer vines		Buffer vines

post-veraison, 4-weeks post-veraison, 5-weeks post-veraison and 6-weeks post-veraison (harvest).

For the UV and water deficit trials in the Lincoln University Research Vineyard in 2017, berry sampling was performed weekly from veraison until harvest for 5 consecutive weeks. At each time point, samples from four replicates were randomly collected from all treatments and immediately stored in a walk-in freezer (-20 °C). 20 berries each per replicate were randomly collected from different sides of clusters for the analysis of phenolic composition. At harvest, sample collection of 20 berries per replicate each per treatment were used for the analysis of berry parameters. Then, the berries were immediately stored in plastic bags in a walk-in freezer (-20 °C).

°Brix, pH and titratable acidity in grape juice: Fruit °Brix, TA and the pH of the grape juice were measured using the method of Iland *et al.* (2000): A small volume of juice from the berries was used to measure °Brix using a digital refractometer (PAL-1 ATAGO, Tokyo, Japan).

Grape juice pH was measured by a Suntex pH/mV/temperature meter (SP-701; Suntex, Taiwan) with a Eutech Instruments probe (EC 620133; Eutech Instruments Pte Ltd, Singapore). Before the analyses, two standard buffer solutions of pH 4.0 and 7.0 were used to calibrate the pH meter. Titratable acidity (TA) was determined by titration to pH 8.2 using 0.1 mol·L^{-1} NaOH (LabServ, 97 % min; Biolab (Australia) Ltd.). TA was measured on 10 mL of juice for the samples. NaOH (0.1 mol/L) was carefully added into the grape juice under constant stirring using a burette and the volume (mL) used for titration until pH 8.2 was recorded and used for calculations:

$$\text{Titratable acidity } (^{gL}/_{as}\ H2T) = 75 \times \text{molarity of NaOH} \times \text{Titrevalue (mL)} \div \text{Volume of juice (mL)}$$

Berry phenolic compounds analysis: Grape phenolic substances were extracted and analysed following the procedures described by Bonada *et al.* (2015) and Iland *et al.* (2000). Skins were separated from the pulp of berries using tweezers and scalpels. Skins were extracted into 20 mL conical flasks containing 10 mL of 50 % v/v ethanol. Freeze-dried seeds from 10 berries were ground in mortars. The seed powder was extracted in 20 mL conical flasks containing 10 mL of 50 % v/v aqueous ethanol. Flasks were filled in nitrogen before being sealed. The flasks were then placed into a warm bath shaker (100 rpm, 22 °C) for 24 h in the dark. The extracts were transferred into centrifuge tubes and then centrifuged for 5 min at 1960 g.

Skin total phenolic compounds and skin anthocyanins analysis: The collected juice (1 mL) was added into 10 mL of 1 mol/L HCl. Measurements of skin total phenolic compounds and skin anthocyanins at 280 nm and 520 nm were carried out on a Shimadzu UV-1800 Spectrophotometer (Shimadzu Corporation, Kyoto, Japan), using UV semi-micro 1.5 mL disposable cuvettes. The results were reported on the content of total phenolic substances per berry:

$$\text{Skin phenolic substances } (^{au}/_{berry}) = A280\ nm \times DF \times EV \times 0.001$$

where DF was the dilution factor of the extract in 1 mol·L^{-1} HCl, EV was the extracted volume after maceration with 50 % ethanol.

$$\text{Skin anthocyanins } (^{mg}/_{berry}) = A520\ nm \div 500 \times DF \times EV$$

where DF was the dilution factor of the extract in 1 mol·L^{-1} HCl and EV was the extracted volume after maceration with 50 % ethanol. The value of 500 was based on a previous report that estimated the extinction coefficient of malvidin-3-glucose in g·100 mL^{-1} of solution.

Skin and seed tannins analysis: Before the analyses, epicatechin was used as a standard for each batch of samples. Aqueous (–)-epicatechin (Sigma-Aldrich E1753) solutions (10, 25, 50, 75, 100, 150 mg·L^{-1} epicatechin) were used to establish a standard curve for reporting tannin absorbance. All A280 (tannin) values were reported in mg·L^{-1} or g·L^{-1} epicatechin equivalents of the original sample (Fig. 1).

Skin and seed tannins were measured by the methylcellulose precipitation (MCP) tannin assay using the

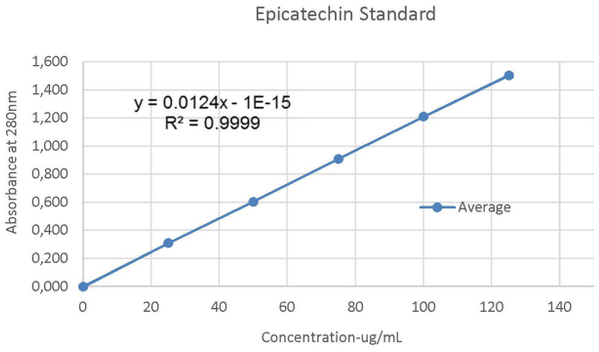

Fig. 1: Epicatechin equivalent calibration curve

1 mL assay in 1.5 mL disposable tubes (SARNECKIS *et al.* 2006). For the treatment samples, 0.3 mL of methylcellulose solution (0.04 % w/v, 1500 cP viscosity at 2 %, M-0387, Sigma-Aldrich, USA) was added to 0.1 mL of skin or seed extract solution. After 3 minutes, 0.2 mL of saturated ammonium solution (Sigma-Aldrich, Auckland) was added into the mixed solution and made up to 1 mL with deionised water. The solution was mixed well, left to stand for 10 min, then centrifuged at 8936 g for 5 min (Tab. 3). Measurements at 280 nm were carried out on a Shimadzu UV-1800 Spectrophotometer (Shimadzu Corporation, Kyoto, Japan), using UV (methacrylate) semi-micro 1.5 mL disposable cuvettes. For the control samples, 0.2 mL of saturated ammonium solution was added to 0.1 mL of the extract solutions and made up to final volume 1 mL with deionised water (Tab. 3). The solution was mixed well, stood for 10 min, then centrifuged at 8936 g for 5 min and measured at 280 nm.

Table 3

Volumes of sample and reagents for MCP tannin assay for grape extractions

	Sample (mL)	MCP (mL)	$(NH_4)_2SO_4$ (mL)	Water (mL)
Treatment	0.1	0.3	0.2	0.4
Control	0.1	0	0.2	0.7

A280 of the tannin in the sample solutions can be calculated by subtracting A280 (treatment) from A280 (control). Epicatechin solution was calculated by epicatechin equivalent calibration curve, ranging from 0 $mg \cdot L^{-1}$ to 150 $mg \cdot L^{-1}$. The dilution factor for the skin or seed extract solutions was 10. The conversion to $mg \cdot g^{-1}$ and mg/berry in seeds and skins from $mg \cdot L^{-1}$ in the extract is shown below:

$$\text{Tannin content of seed or skins (mg/berry)} = \frac{[\text{Tannin}]\,e \times Ve)}{\text{No.}}$$

[Tannin]e = tannins concentration in extraction ($mg \cdot L^{-1}$ epicatechin eq.); Ve = final volume of extraction (L); No. = initial number of berry samples.

Statistical analyses: Statistical analysis was undertaken using IBM SPSS Statistics 22. The data were subjected to two-factor analyses (ANOVA) to partition the variance into the interaction among UV-B and water deficit. In the case of significant interactions among factors, treatments were compared using the least significant difference (LSD) at the 5 % level ($P < 0.05$).

Results

Berry parameters at harvest: In the glasshouse and vineyard trials, °Brix was influenced by water treatments (Tab. 5). Well-watered treatments had a lower °Brix than the water deficit treatments (20.1 in -UV+W vs. 21.7 in -UV-W). A significant difference in TA was shown between UV treatments, with UV-B causing a decrease. The combination of UV-B and water deficit resulted in a significant difference in pH between treatments. UV-B treatments significantly increased the pH compared with no UV-B treatments. +UV-W (3.30) caused a smaller increase in pH than +UV+W (3.41). The effects of UV-B

Table 4

Monthly rainfall and solar irradiance of the west vineyard in 2016 and 2017

		Rainfall (mm)	Rad (MJm^2)	Tmax	Tmin	Avg
Monthly values for 1971-2000	January	42	678.9	22.6	11.4	17.0
	February	39	526.4	21.7	11.0	16.3
	March	54	437.1	20.1	9.9	15.0
	April	54	291.0	17.5	6.7	12.2
	Total	189	1933.4	/	/	/
2017	January	42	705.5	23.2	11.3	17.2
	February	3	550.4	23.0	11.4	17.2
	March	73	380.2	19.2	10.6	14.9
	April	123	260.0	16.5	8.1	12.3
	Total	241	1896.1	/	/	/

Table 5

Berry parameter at harvest in the glasshouse and vineyard

Treatment	°Brix	TA ($g \cdot L^{-1}$)	pH
+UV+W	21.0	6.1	3.41
+UV-W	21.0	6.6	3.30
+UV+W	20.1	7.3	3.23
+UV-W	21.7	7.5	3.23
P_{UV}	n.s.	**<0.001**	**0.001**
P_{water}	**0.010**	n.s.	n.s.
$P_{UV*water}$	n.s.	n.s.	**0.040**
WP	16.4	10.5	3.62
DP	17.9	10.2	3.64
WL	18.2	10.4	3.76
DL	18.4	10.1	3.71
WS	17.1	11.4	3.65
DS	17.4	10.4	3.68
P_{UV}	n.s.	n.s.	n.s.
P_{water}	n.s.	**0.050**	n.s.
$P_{UV*water}$	n.s.	n.s.	n.s.

exposure/exclusion interactions with water treatments on berry parameters are shown in Tab. 5. There were no statistical differences between treatments. At harvest, °Brix ranged from 16.4 to 18.4 in treatments. pH also was not affected by treatments. TA was changed by water treatments. TA in the combination of UV-B exposure/exclusion and well-watered (WP, WL and WS) were below 10.4 $g \cdot L^{-1}$, while in water deficit treatments they were over 10.4 $g \cdot L^{-1}$ of TA.

Skin total phenolic substances: The combination of UV-B radiation and water deficit changed some aspects of phenolic composition in 'Pinot Noir' fruit from veraison to harvest in the 2016-2017 glasshouse trials (Fig. 2). In the glasshouse, the accumulations of skin total phenolics were affected by both UV-B and water deficit (Fig. 2a). There are sharp increases at the first week, and then decreases in the following week. The increases in skin total phenolics are shown again from 3 to 5 weeks post-veraison. At the last week, there are slight decreases between all treatments. In general, all treatments showed the substantial increases during ripening. Compared with the control, the separated or combined UV-B and water deficit caused increases in skin total phenolics after 2-weeks treatment. At harvest, the content of skin total phenolics in +UV-W was 0.354 au/berry higher than the 0.312 au/berry in -UV-W but lower than the 0.397 au/berry in +UV+W. The skin total phenolics increased by 102.6 %, 97.8 %, 58.5 % and 49.3 % in +UV+W, +UV-W, -UV+W and -UV-W, respectively, at harvest.

To determine the effects of UV-B exposure/exclusion interactions with water deficit on 'Pinot Noir' berries, samples from veraison to harvest in 2017 were analysed for skin total phenolics (Fig. 3a). The contents of skin total phenolics in treatments started at around 0.150 au/berry at 0 week post-veraison (veraison) and increased to over 0.200 au/berry at 5 weeks post-veraison (harvest), except for DS, and reached their peaks at 4-weeks post-veraison. At harvest, the shading treatments (WS and DS) had the lowest contents of skin total phenolics, which were 0.207 au/berry and 0.200 au/berry, respectively. Compared to WS and DS, the contents of skin total phenolics were significantly increased by WL and DL. DL and WL had higher values, reaching up to 0.217 $au \cdot berry^{-1}$ and 0.292 $au \cdot berry^{-1}$, respectively.

Skin anthocyanins: The skin anthocyanins in the glasshouse treatments accumulated from veraison to harvest and showed a sharp increase after 1 week post-veraison (Fig. 2b). None of the UV treatments (-UV+W and -UV-W) reached their peaks at harvest, while there were the maximum values of +UV+W (0.702 $mg \cdot berry^{-1}$) and -UV-W (0.739 $mg \cdot berry^{-1}$) at 4 and 5 weeks post-veraison. With respect to the control, the individual or combined UV-B and water deficit significantly increased the skin anthocyanins from 2 to 6 weeks post-veraison. Both +UV+W and +UV-W had more skin anthocyanins than -UV-W from 4 to 6 weeks post-veraison. At harvest, the skin anthocyanin content (0.679 $mg \cdot berry^{-1}$) in +UV-W was the highest value in treatments.

The situation was similar in the field experiment (Fig. 3b). The contents of skin anthocyanin peaked at 4 weeks post-veraison and, subsequently, declined at the harvest sampling. At 2 weeks post-veraison, WP and DP accumulated less skin anthocyanins than others. At 4 weeks post-veraison, WL and DL had the highest contents of skin anthocyanins with 0.516 $mg \cdot berry^{-1}$ and 0.522 $mg \cdot berry^{-1}$, respectively. At harvest, WL (0.466 $mg \cdot berry^{-1}$) had the highest contents of skin anthocyanins, while the lowest contents were in DS (0.245 $mg \cdot berry^{-1}$) and WS (0.232 $mg \cdot berry^{-1}$). DL also had high skin anthocyanin contents, reaching 0.317 $mg \cdot berry^{-1}$. Skin anthocyanins in WP and DP had higher contents than in WS and DS but less than in WL and DL.

Skin and seed tannins: In the glasshouse study, skin tannins showed increases from veraison to 2 weeks post-veraison and substantial reductions from 3 weeks post-veraison to harvest in treatments and the control (-UV+W) (Fig. 2c). -UV+W tended to be higher than other treatments in the first four sample periods, but this was reversed after. With respect to -UV+W (the control), +UV and -W treatments caused a reduction in skin tannins from veraison to 3 weeks post-veraison and then increased until harvest. At harvest, the skin tannin contents reached 0.596 $mg \cdot berry^{-1}$ in +UV-W, which was lower than 0.713 $mg \cdot berry^{-1}$ in +UV+W and 0.709 mg/berry in -UV-W, but higher than the 0.464 $mg \cdot berry^{-1}$ in -UV+W. Seed tannins in the treatments showed increases and then decreases during ripening (Fig. 2d). There were no consistent changes in seed tannin contents between treatments during ripening and no statistically significant differences between treatments at harvest. As shown in Fig. 3c, substantial trends were the reduction in skin tannins from -4- to 5-weeks post-veraison (harvest). UV interactions with water deficit significantly affected the contents of skin tannin at harvest.

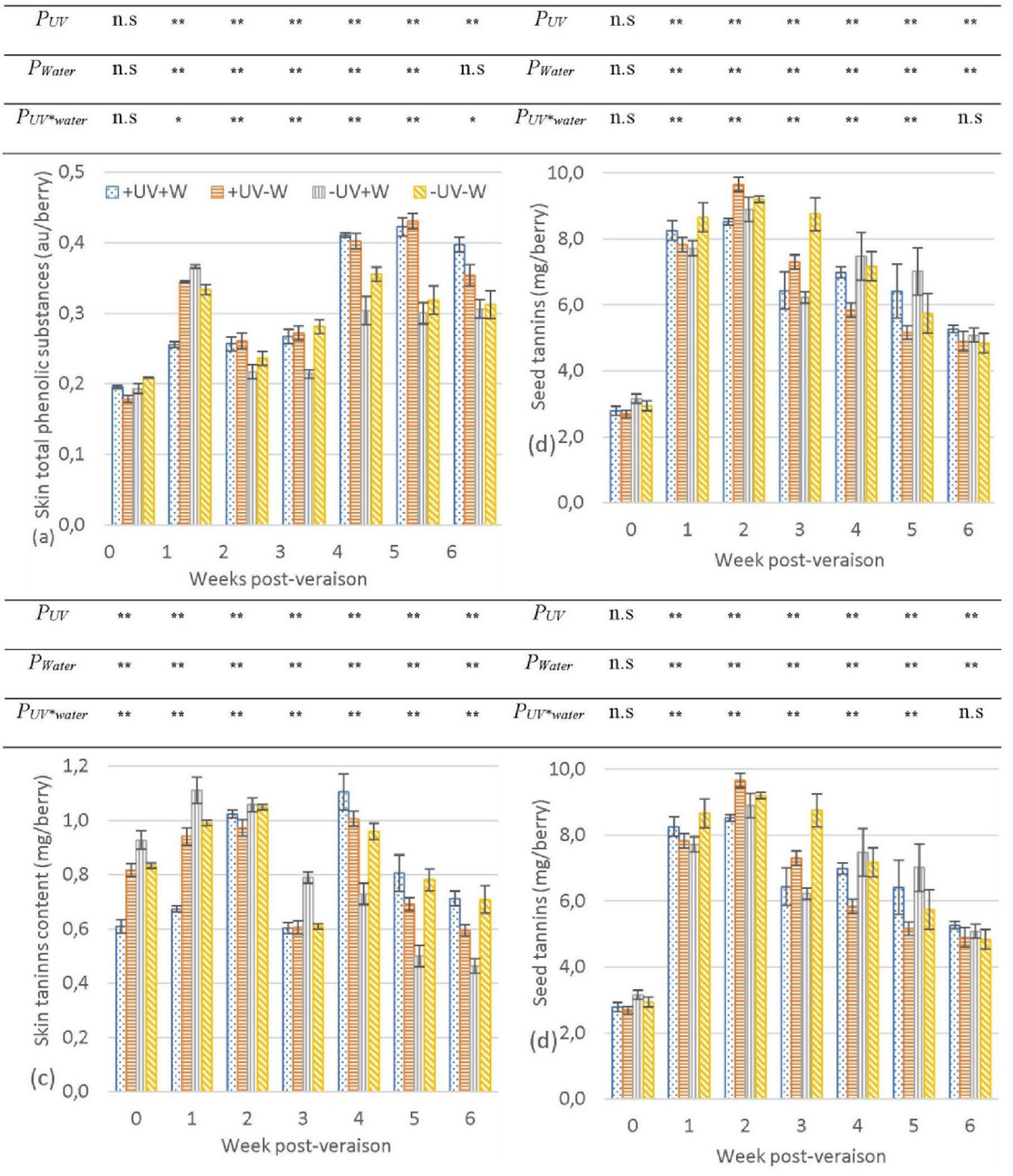

Fig. 2: Effects of UV-B and water deficit on (**a**) skin total phenolic substances, (**b**) skin anthocyanins, (**c**) skin tannins and (**d**) seed tannins in 'Pinot Noir' berries during ripening in glasshouse trials. Data showed the mean ± standard error of four replicates. P-values for statistical significance comparing the different treatments according to Two-factor ANOVA and LSD at the 5 % level; *: $P < 0.05$, **: $P < 0.01$; P_{UV}, UV effects averaged across water treatments; P_{water}, water effects averaged across UV treatments; $P_{UV*water}$, water effects depend on UV treatments and UV effects depend on water treatments; n.s: no significant difference. +W: well-watered, -W: water deficit; +UV: UV-B radiation, -UV: normal light.

In WP and DP, the skin tannin contents were 0.540 mg·berry^{-1} and 0.679 mg·berry^{-1} at harvest, respectively, which were more than in the other treatments. The skin tannin contents in WL and DL were less than 0.520 mg·berry^{-1}, while WS was 0.524 mg·berry^{-1} of skin tannin contents. There were no statistically significant differences in seed tannins between treatments during berry development (Fig. 3d), except for at 1-week post-veraison. DL and DS had the highest seed tannin contents at 7.003 mg·berry^{-1} and 7.195 mg·berry^{-1} than other treatments.

Discussion

Red winegrapes should achieve a value higher than 19 °Brix for commercial harvest of table wines (KELLER 2015). In the glasshouse, °Brix in individual or combined treatments was over 21 and the control reached 20, but there were statistical differences only between well-water and water deficit without UV-B treatments. Water deficit caused the increase in the sugar level in the glasshouse. The accumulation of sugar in berries reflected a portioning

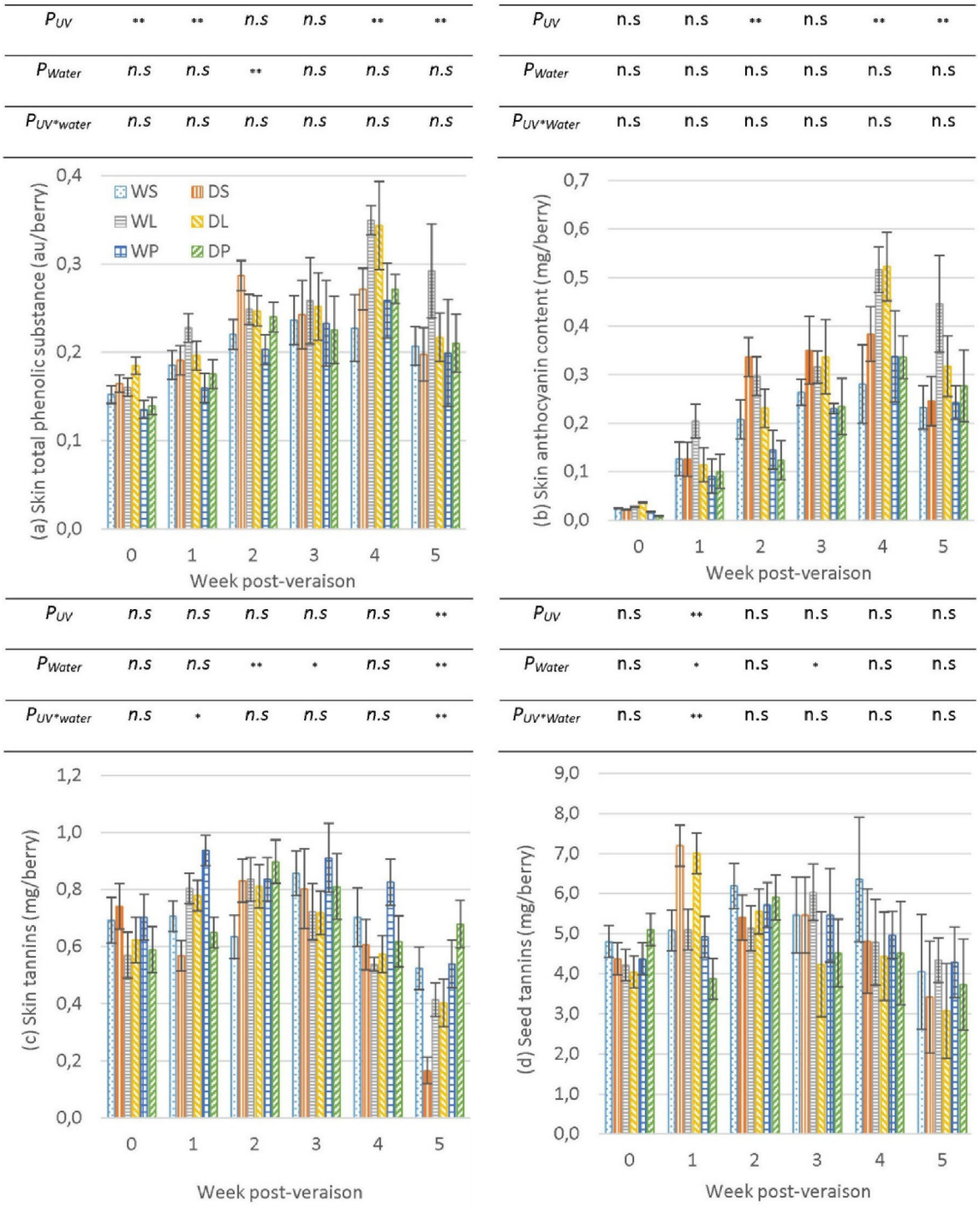

Fig. 3: Effects of UV-B and water deficit on (**a**) skin total phenolic substances, (**b**) anthocyanins, (**c**) skin tannins and (**d**) seed tannins in 'Pinot Noir' berries during ripening in vineyard trials. Data showed the mean ± standard error of four replicates. P-values for statistical significance comparing the different treatments according to Three-factor ANOVA and LSD test at the 5 % level; *: $P < 0.05$, **: $P < 0.01$. Main effects of UV (P_{UV}), water deficit (P_{water}) and the combination of UV and water deficit ($_{PUV*water}$); n.s: no significant difference. P: PETG screen, L: leaf remove, S: shade cloth; W: well-water, D: water deficit.

response to water deficit which increased the allocation of the photosynthate in berries (Roby *et al.* 2004). In the vineyard, all treatments had low (< 19) °Brix, due to the growing conditions (Tab. 4). After veraison, heavy rainfall with low light intensities may prevent photosynthesis producing carbohydrate, resulting in less conversion to glucose and fructose in berries (Jackson and Lombard 1993). Thus, the condition significantly caused this to be an effect on the berry maturity and no significant difference between treatments in the vineyard trials. The composition of phenolics in 'Pinot Noir' berries changed at different stages during ripening in the glasshouse and vineyard. The contents of skin total phenolics and anthocyanins showed developmental trends in 'Pinot Noir' berries during berry development in the treatments (Figs 2a/b and 3a/b). The berries collected at veraison had significantly higher levels of skin tannins

than at harvest (Figs 2c and 3c). These results are consistent with previous findings that skin anthocyanins and total phenolics are mainly produced from veraison to harvest (MARTÍNEZ-LÜSCHER *et al.* 2014b, ROBY *et al.* 2004, THEODOROU *et al.* 2019). In addition, compared with the control, UV-B interaction with water deficit increased the contents of skin anthocyanin and skin tannin in the glasshouse trials. Similar results were found by MARTÍNEZ-LÜSCHER *et al.* (2014a) in 'Tempranillo' berries of glasshouse trials.

In the glasshouse, UV-B caused increases in skin anthocyanins and skin total phenolics during ripening, compared to the control (Fig. 2a/b), which were consistent with the vineyard results and previous findings (GONZÁLEZ *et al.* 2015, DEL-CASTILLO-ALONSO *et al.* 2016, SUN *et al.* 2017). Flavonols are the main component of skin total phenolics and can act as UV screening to protect grapes from UV-B damage (GREGAN *et al.* 2012). In other aspects, FLS was activated by UV-B radiation in grapes, resulting in the accumulation of flavonols, as reported in previous research (MARTÍNEZ-LÜSCHER *et al.* 2014a, LIU *et al.* 2015). This is because the VvMYB1 transcription factor was a flavonol biosynthesis-specific regulator in grapevine interception by the UV-B photoreceptor, UVR8. VvMYBF1 has a high specificity for FLS to stimulate flavonol biosynthesis (YIN *et al.* 2015, LIU *et al.* 2015). Therefore, the increases in skin total phenolics are constituted by the increase in skin anthocyanins and the accumulation of flavonols. Moreover, in the vineyard, the increases in skin total phenolics were induced by WL/DL in comparison with WP/DP and WS/DS, which can be attributed to the increases in skin anthocyanins and flavonols. Noticeably, the skin total phenolics were increased much less by the combination of UV-B and water deficit than UV-B alone in the glasshouse. In the vineyard, skin total phenolics were increased by UV treatment. Thus, less change in skin total phenolics in the glasshouse and vineyard showed water deficit may make no additional response to UV-B.

UV-B or water deficit can induce the accumulation of ROS, and anthocyanins in grape skins can play a role as antioxidants to scavenge ROS (BERLI *et al.* 2011), resulting in the accumulation of skin anthocyanins. The increase in skin anthocyanins is also induced by the up-regulation of FLS1, UFGT and F3H through UV-B, and up-regulation of F3H and OMT2 through water deficit (BERLI *et al.* 2011, MARTÍNEZ-LÜSCHER *et al.* 2014a, COOK *et al.* 2015, MARTÍNEZ-LÜSCHER *et al.* 2019). In this study, there were increases in the skin anthocyanins under UV-B in the glasshouse and vineyard or water deficit in the glasshouse. Thus, both of UV-B and water deficit could enhance the skin anthocyanin contents. Furthermore, as described previously, studies have shown that skin anthocyanins were increased by UV-B exposure, while shaded or no UV-B fruit had lower contents (FALGINELLA *et al.* 2012, MARTÍNEZ-LÜSCHER *et al.* 2014a). Our results in this study further determined that UV-B was the major component of radiation that induced anthocyanins in grape berries, and this is supported by previous UV-B exclusion experiments (NÚÑEZ-OLIVERA *et al.* 2006). Skin anthocyanins, however, were not accumulated to a greater extent under the combination of UV-B and water deficit, so the combined treatment did not increase the response compared to either individual stress.

In the vineyard, different fruit temperatures could induce changes in skin anthocyanins. Higher temperatures of about 30-35 ℃ can cause the degradation of skin anthocyanins (DE OLIVEIRA and NIEDDU 2016, CARBONELL-BEJERANO *et al.* 2014). GREGAN *et al.* (2012), who used the same screening system and vineyard as used in this research, reported that daily temperatures around the fruiting area were slightly raised with leaf removal and PETG covers (0.2/0.6 ℃, respectively). The increases in temperature were found at solar noon and there were no differences in temperature during the morning and evening. In our study, the skin anthocyanins in the UV-B exposure treatment (leaf removal) were higher than in the PETG treatment at harvest, but temperature in the leaf removal treatment was lower than in the PETG treatment. Given the magnitude of air temperature change around the fruit in this research, it seems likely that temperature did not significantly affect the skin anthocyanins.

Skin tannin contents in +UV-W were higher than -UV+W (the control) and lower than +UV+W and -UV-W in the glasshouse trials. In the vineyard, skin tannin contents frequently changed in all treatments during ripening, but there were no consistent significant differences of skin tannins between treatments. The fluctuation of skin tannins during ripening may relate to the polymeric flavan-3-ols. Polymerization is dramatically influenced by environmental factors, such as UV-B and water deficit, and changed at different stages of berry development (KENNEDY *et al.* 2002, DOWNEY *et al.* 2003, CORTELL and KENNEDY 2006). Skin tannins are synthesised via a branch in the anthocyanin-forming pathway by LAR that is affected by UV and water deficit (BINDON *et al.* 2011, DEL-CASTILLO-ALONSO *et al.* 2016). The accumulation of flavonoids in skins increases free-radical scavenger activity, which can protect berries from the damage of UV-B and water deficit (DOWNEY *et al.* 2006). In addition, the berries collected at veraison had significantly higher levels of skin tannins than at harvest in the glasshouse and vineyard. Skin tannins during ripening can be bound to the insoluble matrix of berries, consisting of cell wall pectins and glycans (KENNEDY *et al.* 2001).

Compared to the glasshouse, in the vineyard, skin tannin contents frequently changed in all treatments during ripening, but there were no consistent significant differences of skin tannins between treatments, which may be an effect of other environmental conditions on the evolution of skin tannins, such as air temperature (BLANCQUAERT *et al.* 2019), light intensity and seasons (NICHOLAS *et al.* 2011). These environmental conditions also had a potential impact on tannins accumulation in the skin during the berry development (PASTORE *et al.* 2017). The different fruit exposure and water treatments resulted in changes in the temperature and relative humidity around the fruiting zone. Previous studies have reported that the increase in temperature increased the biosynthesis of proanthocyanidins and a greater of degree of proanthocyanidin polymerization to tannins in berry skins (KENNEDY *et al.* 2012, COHEN *et al.* 2008).

Conclusions

This research reports increased contents of skin anthocyanin and skin total phenolics in fruit under an individual or a combined UV-B and water deficit. In the glasshouse, the combination of UV-B treatment and water deficit showed a greater accumulation of skin anthocyanins than the control but not than UV-B or water deficit treatments (Fig. 2), so the combined treatments did not increase responses compared to the individual stress. In the vineyard, when berries were shaded (SC) or exposed to UV-B (LR) and protected from UV-B (PETG), combined with water deficit, the most statistically significant increases in phenolic composition were detected on skin anthocyanins and skin total phenolics during ripening (Fig. 3). The interaction of leaf removal with water deficit (DL) increased skin anthocyanins and skin total phenolics by around 40 % and 17 %, respectively, compared to the shading and well-watered treatments (WS) at harvest. Moreover, DP increased skin anthocyanins by around 13 % and skin total phenolics by less than 10 %. This demonstrated that the exposure can increase the accumulation of anthocyanin and total phenolics in berry skins under water deficit, and the key component of radiation was UV-B to increase the levels of phenolics. It is essential that the consequences of a changing environment be considered along with multiple environmental parameters. Consequently, it is critical to understand the mechanisms of formation studied here response to viticulture.

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