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Role of the Physical Elicitors in Enhancing Postharvest Antioxidant Capacity of Table Grape *cv* Redglobe (*Vitis vinifera* L.)

Pasquale Crupi[1], Arianna Pichierri[1], Rosa Anna Milella[1], Rocco Perniola[1] & Donato Antonacci[1]

[1] CRA - Consiglio per la Ricerca e la sperimentazione in Agricoltura - Unità di ricerca per l'uva da tavola e la vitivinicoltura in ambiente mediterraneo, Italy

Correspondence: Donato Antonacci, CRA - Consiglio per la Ricerca e la sperimentazione in Agricoltura - Unità di ricerca per l'uva da tavola e la vitivinicoltura in ambiente mediterraneo, Italy. Tel: 39-080-891-5711. E-mail: donato.antonacci@entecra.it

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Abstract

Polyphenols, such as anthocyanins, are secondary metabolites produced in plants which can play an important health-promoting role considering their strong correlation with antioxidant capacity. The biosynthesis of these compounds generally increases as a response to biotic or abiotic stress, therefore, in order to achieve as high phenolic accumulation as possible, the interactive effects of storage conditions (temperature and time) and postharvest ultraviolet irradiation (UV-C) on total polyphenols (TPP) and total anthocyanins (TA) content, as well as oxygen radical antioxidant capacity (ORAC), in postharvest "Redglobe" table grape variety were investigated in 2011 vintage. Gathered findings showed that UV-C exposure ranging from 1 to 3 min (0.8-2.4 KJ m^{-2}) positively influence the TA level (with an increase almost twice higher than the control) during a storage time longer than 48 h, independently from the storage temperature; while, with regard to TPP and ORAC, a progressive increment of their values (roughly from 2 to 4 folds higher than the control) up to 120 h of storage was observed, in particular in Redglobe grapes irradiated for 1 min and stored at 4 °C. Responding to the rising consumers needs to have foods that support and promote health, this research demonstrated that the postharvest simultaneous application of physical elicitors can lead to grapes with enhanced antioxidant properties, within normal conditions of market commercialization. The practical relevance of this finding is evident considering that grapes are economically the most important fruit species in the world and approximately 30% of its production is used as fresh fruit.

Keywords: physical elicitors, UV-C, polyphenols, anthocyanins, ORAC

1. Introduction

The grape consumption has been associated with multiple beneficial health effects mainly due to the polyphenol content in this fruit (Cook & Samman, 1996; Teissendre et al., 1996). Phenolics are secondary metabolites that are widely distributed in the plant kingdom. Typically in *Vitis vinifera* they are present as flavonoids, comprising flavanols, anthocyanins and flavan-3-ols, and non-flavonoids, comprising hydroxybenzoic acids, hydroxycinnamic acids and stilbenes (Glories, 1998). Numerous studies have established that total anthocyanins as well as phenolic concentrations are positively related to the total antioxidant activity (Wang, Cao, & Prior, 1997; Meyers, Watkins, Pritts, & Liu, 2003; Sun, Chu, Wu, & Liu, 2002).

Recently, due to health awareness campaigns, consumers have become more and more interested in foods that support and promote health which are characterized by high health-promoting compound content rather than having superior external quality attributes, as was previously the case. Therefore, to meet this shift in consumer needs the use of postharvest elicitors, that can promote the levels of phytochemicals in postharvest crops, has become an area of key interest (Goldmann, Kader, & Heintz, 1999; Huyskens-Keil & Schreiner, 2004).

It is known that quantitative and qualitative pattern of polyphenols depends on the developing stage of a plant, which means that by selecting the harvest time it is possible to obtain products with different flavonoid profiles. Generally, in order to improve the elicitor's effect on the accumulation of phenols during the postharvest stage, fruit and vegetables should be harvested at optimum maturity (Schreiner & Huyskens-Keil, 2006; Terry & Joyce, 2004). The storage process can modify the content of phenolic acids and flavonoids in the plant material, leading to an increase or decrease which depend on the storage conditions, such as temperature and time, but also

phytochemical stability, and quality of the analyzed food. Generally, a decrease in the polyphenol content with high temperature was shown, but, in other cases, fruit stored at higher temperature has shown higher anthocyanin and flavonoid concentrations and higher antioxidant activity than at lower temperature (Amarowicz et al., 2009; Kalt, Forney, Martin, & Prior, 1999; Shin, Liu, Nock, Holliday, & Watkins, 2007).

Ultraviolet irradiation (UV-C) acts as an abiotic physical elicitor of resistance mechanisms, and thus leads to a rapid increment of stress-response compounds such as phenols, flavonoids, and phytoalexins, due to the increased activity of phenylalanine ammonia-lyase and other enzymes involved in flavonoid synthesis (Tomas-Barberan & Espin, 2001). This effect was found in several fruits, such as citrus (Oufedjikh, Mahrouz, Amiot, & Lacroix, 2000), apples (Dong, Mitra, Kootstra, Lister, & Lancaster, 1995), peas (Plustoka, Michalczyk, & Gorecki, 2005), and grapes (Takayanagi, Okuda, Mine, & Yokotsuka, 2004). UV-C of fruit and vegetables as a postharvest treatment has been shown to improve quality throughout storage, e.g. by increasing anthocyanin levels in strawberries; moreover, a recent study has also demonstrated that postharvest application of UV-C is effective in stimulating the antioxidant capacity of some fruit (Wang, Cao, & Prior, 2009; Alothman, Bhat, & Karim, 2009).

However, to the best of our knowledge, few researchers have studied the simultaneous influence of physical postharvest treatments on antioxidant activity in grapes (Li et al., 2009); therefore, the aim of this work was to evaluate the interactive effects of UV-C and storage conditions (time and temperature) on the antioxidant capacity, expressed as total polyphenols (TPP) and ORAC values, together with total anthocyanins (TA) concentration in Redglobe table grape variety from 2011 vintage, in order to monitor its health and nutritional aspects during current conditions of market commercialization (short term and cold storage).

2. Materials and Methods

2.1 Plant Material and Growth Conditions

The experiment was conducted in 2011 on the table grape variety "Redglobe" (*Vitis vinifera* L.) grown in Apulian region. The vineyard was located in a trial site on a hilly area (in Turi, Southern Italy, long. 40.56° E, lat. 17.12° N) at about 250 m on the sea level and planted in a sandy-clay soil composed of 50% sand, 12% slit and 38% clay, with a root zone depth of 1 m. All vines were established in 2004 on *140 Ruggeri (Vitis berlandieri x Vitis rupestris*) rootstocks, with a planting density of 1600 vines ha^{-1}, and a vine spacing of 2.5 m between rows and 2.5 m within a row. They were trained to a "double tendon" trellis system, widely used in Apulian region, and were cane pruned (two canes every 12-15 buds per vines) with free-standing shoots (complete overhead canopy separated from fruit). Improving the canopy management, the "double tendon" assured optimal microclimate conditions for bunches and avoided the leaves to rub them, during very windily days. Grape samples (10 bunches by taking a bunch for each vine, in the middle of the fruit cane) were harvested at commercial maturity on the basis of total soluble solids (TSS), measured as °Brix using a portable refractometer (Atago PR32, Norfolk, Virginia, USA), and titratable acidity which was determined in the juice by titration with 0.1 N of NaOH (J.T. Baker, Deventer, Holland) to a pH 7 end point, and was expressed as gram of tartaric acid per liter.

2.2 Experimental Design of the Postharvest Treatments

Berries of set weight (10 ± 1 g) were detached from bunches and mixed to obtain a homogeneous and representative sample. Three replicates of 10 berries samples were weighted and treated with a full factorial experimental design, as described in Table S1 (Supporting Information), with a sample size of 2 x 4 x 4 = 32 unique runs, given by the product among the levels of the factors,. Germicidal UV-C lamp (SANKYO DENKI G30T8 – Levanchimica s.r.l. Bari - Italy) has been used as UV-C source with peak emission at 254 nm and 893 x 25.5 mm dimensions. The UV-C light intensity was kept constant (13.4 W) and the applied doses (0.8, 2.4, and 4.1 KJ m^{-2}, respectively) varied by altering the exposure time (1, 3, and 5 min) at the fixed distance of 40 cm (López-Rubira, Conesa, Allende, & Artés, 2005) from the berries. The 10 berries have been irradiated only on a side.

Each sample was stored (for a time of 24, 48, and 120 h) at either room temperature (25 °C) or 4 °C in perforated plastic bags and at relative humidity of 90-95% to avoid water loss and shriveling. Finally, the treated grape samples were immediately frozen at -20 °C for later analyses.

2.3 Extraction and Analysis of Total Polyphenols and Anthocyanins

The frozen 10-berries samples were manually separated from pulp and freeze-dried skin samples were homogenized by an IKA A11 basic homogenizer (IKA Works, NC, USA). The homogenate was transferred to a volumetric flask and extracted using 25 mL of 70% ethanol (J.T. Baker, Deventer, Holland) solution, containing

1% hydrochloric acid (J.T. Baker, Deventer, Holland). The mixture was sonicated for 5 min at 20 °C and then centrifuged (4000 rpm; 3 min). This procedure was repeated three times and the effectiveness of repetitive extraction was tested by measuring the absorbance at 520 nm. The third extraction represented less than 1% of the compounds that were extracted. Then three supernatants were combined and filtered through a 0.45 μm syringe cellulose filter (VWR International, USA), after which the absorbance of the extract as such, and of diluted extract (1:50) using Folin-Ciocalteau method (as fully described in Milella et al., 2012), was determined at 520 nm and 750 nm, respectively, by means of a FLUOstar OPTIMA (BMG LABTECH, Offenburg, Germany) plate reader. From these values, total anthocyanins (TA) and total polyphenols (TPP) were calculated by using calibration curves of malvidin-3O-glucoside (at concentrations 0.1-50 mg L^{-1}; $R^2 = 0.9908$) and catechin (at concentrations 1-100 mg L^{-1}; $R^2 = 0.9912$), respectively (Extrasynthese – Genay, France). Finally, they were expressed in mg equivalents per Kg of berry fresh weight (fw).

2.4 Oxygen Radical Absorbance Capacity Assay (ORAC)

This fluorimetric procedure is based on a previously reported method (Ou, Hampsch-Woodill, & Prior, 2001) with slight modifications. Briefly, 25 μL of diluted sample (1: 500), blank, or Trolox calibration solution (6.25-100 μM) were mixed with 150 μL of fluorescein (7.7 μM) and incubated for 15 min at 37 °C before injection of 25 μL AAPH (2,2'-azobis[2-methylpropionamide]dihydrochloride, Sigma-Aldrich, Milano, Italy) solution (221.3 mM). The fluorescence was measured at $\lambda_{exc} = 485$ nm and $\lambda_{ems} = 535$ nm every 90 sec for 60 min, using a FLUOstar OPTIMA (BMG LABTECH, Offenburg, Germany) plate reader. All samples were analyzed in duplicate. The final ORAC values were calculated using the differences of the area under the fluorescence decay curve (AUC) between the blank and the sample, and were expressed as μmol of Trolox Equivalents (TE) per Kg of berry fresh weight (fw).

2.5 Statistical Analyses

The data were statistically analyzed by means of STATISTICA 8.0 software package (StatSoft Inc., Tulxa, OK), using the General Regression Model (GRM) module in order to analyze an ANOVA design with categorical predictor variables. Three factorial analysis of variance (ANOVA) were applied to TPP, TA, and ORAC data of 2011 samples, and the significance of single factors and interactions of them were determined at $P < 0.05$, $P < 0.01$, or $P < 0.001$; moreover, the optimizazion of the experimental conditions was evaluated using a response surface methodology (RSM). The proposed model to which the experimental data were fitted was a second-order polynomial model. The following equation was used:

$$Y = a_0 + a_1X_1 + a_2X_2 + a_3X_3 + a_{12}X_1X_2 + a_{13}X_1X_3 + a_{23}X_2X_3 + a_{11}X_1^2 + a_{22}X_2^2 + a_{33}X_2^2$$

where Y is the amount (mg) of extracted compounds per Kg of fresh weight of grapes and is normalized to control samples, a_i are the regression coefficients, and X_1, X_2, and X_3 are the experimental factors.

3. Results and Discussion

According to previously reported data for Redglobe variety (Morelli et al., 2008), berries of uniform size and weight were chosen in order to prevent their dimension variability could affect the experimental results. Moreover, on the basis of TSS and titratable acidity values (15 °Brix and 4.13 g L^{-1}, 17.2 °Brix and 4.65 g L^{-1}, measured in 2011 and 2012 vintages, respectively) the optimal harvest time was chosen to allow postharvest physical elicitors to get the best activity on the phytochemicals improvement. Indeed, color development during postharvest ripening is significantly affected by the initial pigment content and even fruits harvested at commercial maturity may exhibit increases in the anthocyanin content throughout cold-temperature storage (Schreiner & Huyskens-Keil, 2006; Nunes, Brecht, Morais, & Sargent, 2006).

Table 1 lists the values of postharvest TPP and TA content, together with ORAC values in the skin extracts of Reglobe grapes (*Vitis vinifera* L.) harvested in 2011 vintage, as affected by storage conditions and UV-C treatment. Highly significant interaction among storage temperature and time, and UV-C treatment were found, a general increment with dose irradiation and storage conditions was observed, in particular higher values of TPP and ORAC were obtained at 4 °C, after 120 h (roughly 400 mg Kg^{-1} and 27000 μmol TE Kg^{-1} of fw, respectively) and 1 min of UV-C exposure, whilst for TA the better increase (up to 126 mg Kg^{-1} of fw) was detected after 48 h and between 1 and 3 min of UV-C irradiation. Moreover, it is worth noting that any irradiated samples did not improve their anthocyans level compared to control after storing for less than 48 h both at room temperature or 4 °C; conversely, they needed at least 120 h of storage to significantly increase their polyphenolic content as well as ORAC values (Table 1).

The storage time factor had a very significant ($P < 0.001$) impact on each examined parameter. TPP were significantly increased just after 24 h of storage changing from an average of 265 mg Kg^{-1}, at harvest, to 319 mg

Kg^{-1} of fw with an increment of 18% compared to control sample, moreover a further increase of TPP up to an average of 374 mg Kg^{-1} was observed in Redglobe samples after 120 h of storage (Figure 1a). A similar trend was depicted by ORAC values, too: two consecutive increases after 24 and 120 h (from an average of 6500 to 10600 and 16600 µmol TE Kg^{-1}, respectively) were observed (Figure 1c). This can be ascribed to the positive relationship ($r = 0.65$, $p < 0.05$; $N = 32$) mainly between TPP and antioxidant capacity, that is in line with previously reported data (Meyers et al., 2003; Sun et al., 2002). Also TA level was positively affected by storage time, showing a large increase after 48 h with a value (106 mg Kg^{-1} of fw) almost twice higher than the harvest one; in this case, however, no further increment was observed after 120 h of storage (Figure 1b). On the contrary, temperature has no significant effect on the TA level of the stored Redglobe grapes (Table 1). Considering that higher temperatures should enhance anthocyanin biosynthesis during storage, this finding seems in disagreement with some of literature data (Goncalves, Landbo, Knudsen, & Silva, 2004). Indeed berries, such as strawberries, blueberries, and raspberries, stored at temperatures >15 °C show higher anthocyanins and phenolics contents compared to those stored at lower ones (0 to 6 °C) (Kalt et al., 1999; Cordenunsi et al., 2005). However, other studies have demonstrated that cold storage for up to 3 days leads to relatively small changes in the concentration of different antioxidants in strawberries (Olsson, Ekvall, Gustavsson, & Nilsson, 2004), and that the anthocyanin content of raspberries is not affected by 3 days freezing at 4° C (Amarowicz et al., 2009).

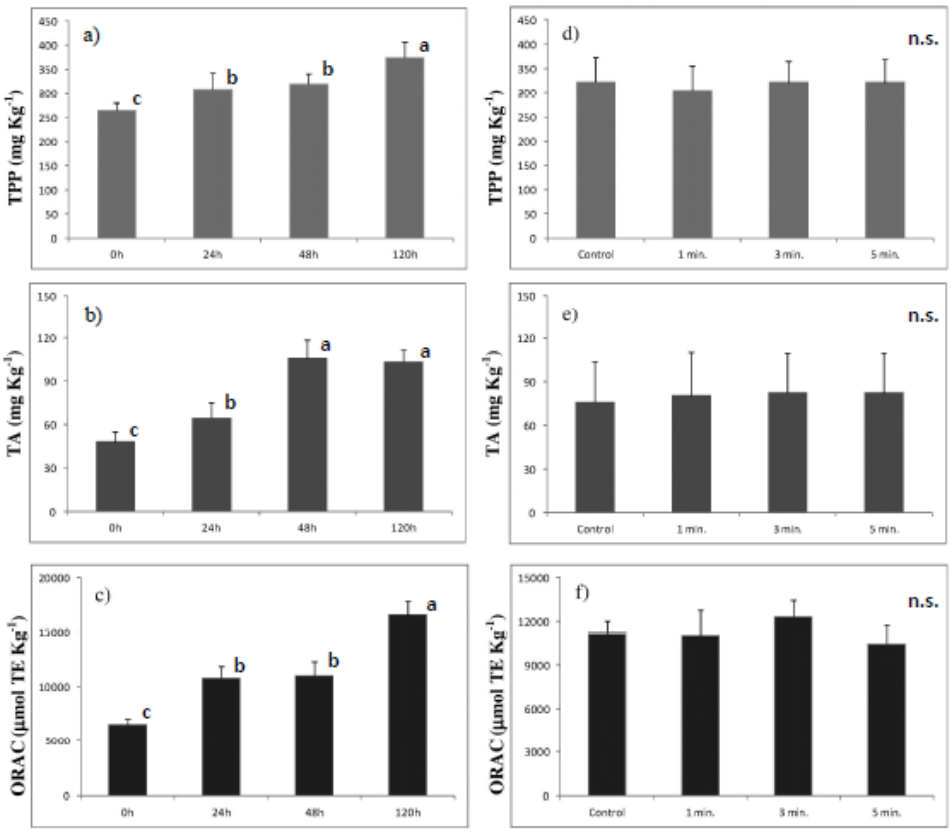

Figure 1. Effects of storage time (a-b-c) and UV-C treatment (d-e-f) on total polyphenols (TPP), anthocyanins (TA), and oxygen radical absorbance capacity (ORAC) values in the skin extracts of Redglobe (*Vitis vinifera* L.). Different letters indicate statistical significance according to Tuckey's HSD post hoc test. n.s. = not significant

Table 1. Effect of storage time, storage temperature, and UV-C treatment on the total polyphenols (TPP), total anthocyanins (TA), and oxygen radical antioxidant capacity (ORAC) postharvest values in the skin extracts of Redglobe table grape (*Vitis vinifera* L.) harvested in 2011

UV-C treatment	Storage Time	Storage Temperature	TPP (mg Kg^{-1})	TA (mg Kg^{-1})	ORAC (µmol TE Kg^{-1})
Coltrol	0h	RT[a]	272[b]	40.3	10170
		CS	278	42.9	10166
	24h	RT	282	49.4	4829
		CS	376	86.9	10238
	48h	RT	301	110.5	11813
		CS	294	78.9	9008
	120h	RT	366	106.5	11768
		CS	401	92	21134
1 min	0h	RT	243	45.7	4813
		CS	256	41	5286
	24h	RT	290	64.7	7165
		CS	290	64.5	20466
	48h	RT	339	104	3565
		CS	296	110.5	13063
	120h	RT	318	99.6	6734
		CS	405	115.6	27182
3 min	0h	RT	282	56.9	7875
		CS	284	59.2	6756
	24h	RT	316	60.7	6667
		CS	267	56.9	15549
	48h	RT	336	105.8	8568
		CS	350	126.2	20070
	120h	RT	333	93.2	13388
		CS	400	102.2	19827
5 min	0h	RT	253	49.7	3731
		CS	257	49.4	3572
	24h	RT	325	62.1	8299
		CS	321	71.4	13199
	48h	RT	308	107.2	3571
		CS	332	103	18538
	120h	RT	390	104.7	14070
		CS	378	113.1	18720
				Significance	
UV C treatment (min)			n.s.	n.s.	n.s.
Storage time (h)			***	***	***
Storage temperature (°C)			*	n.s.	***
Storage time x Storage temperature			*	n.s.	***
Storage time x UV C treatment			n.s.	**	***
Storage temperature x UV C treatment			n.s.	n.s.	***
Storage time x Storage temp. x UV C treat			**	***	***

[a] RT= room temperature, CS= cold storage (4 °C); [b]Means of three replicates. Three-way ANOVA based on F-test was performed to obtain significance of treatments and interactions; n.s. = not significant; * = P<0.05; ** = P<0.01; *** = P<0.001

The similar response of TA, irrespective to the tested temperature storage condition (room temperature and 4 °C), could be due to the typical lesser amount and non-homogeneous distribution of anthocyanin pigments on the skin of red grapes (such as Redglobe or Crimson) (Crupi et al., 2012), that would favor the further cellular biosynthesis of these compounds during postharvest storage. However more deepened molecular studies are in progress in our laboratories to support this hypothesis.

Irradiation of fruit and vegetables as a postharvest treatment has also been shown to improve antioxidant compounds throughout storage, such as in the case of citrus (Oufedjikh et al., 2000), apples (Dong et al., 1995), and peas (Plustoka et al., 2005), but in this research no significant effect was observed for UV-C dose treatment by itself (Table 1). Indeed, TA level slightly increased just after 1 min of treatment and further exposure of grapes to UV-C seem unnecessary to improve the content of these pigments (Figure 1e); conversely, TPP content, as well as ORAC values, did not change according to UV treatment if compared to control, but straight they slightly decreased after 1 min of berries exposure (Figures 1d and f).

Response surface regression analyses were employed to predict the optimal improvement conditions on TPP, TA, and ORAC levels of Redglobe grapes during postharvest. Of course, in order to generalize the 2011 results, because polyphenols of a grape variety are mainly affected by the environmental conditions (Crupi et al., 2012), the data of Table 1 were first normalized to the control sample values and then fitted by a polynomial mathematical model to generate three-dimensional response surface plots with one constant factor (storage temperature) (Figure 2).

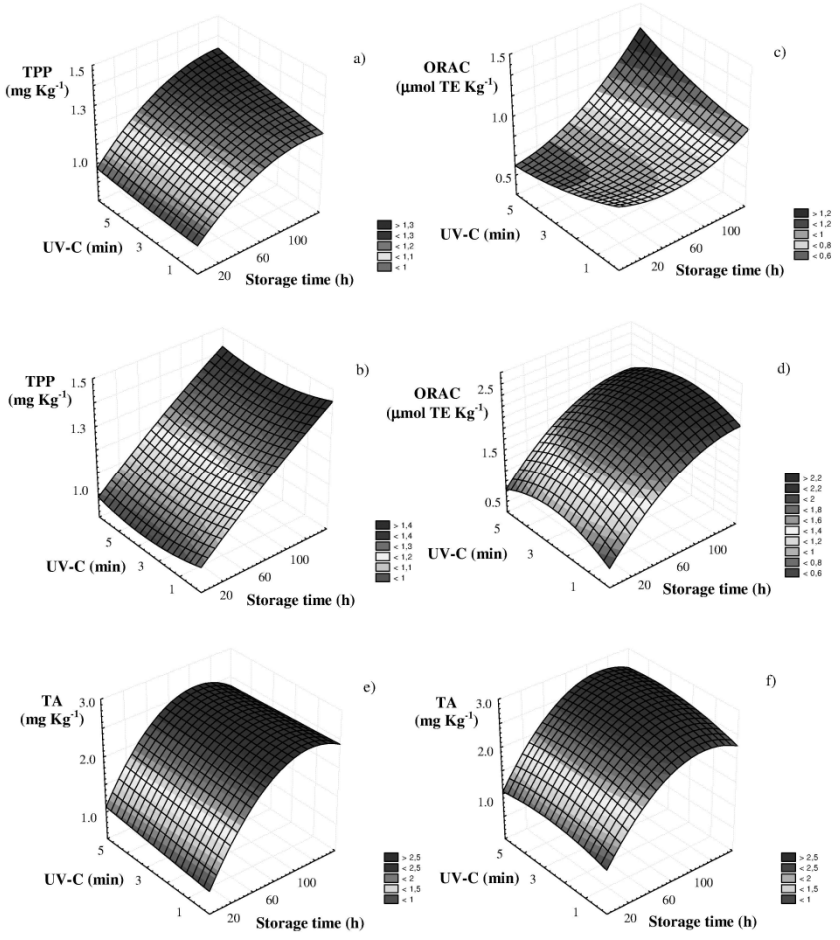

Figure 2. Response surface curves for total polyphenols (TPP), total anthocyanins (TA), and oxygen radical absorbance capacity (ORAC) variation depending on UV-C exposure and storage time effects at room temperature (a, c and e) and 4 °C (b, d and f)

With regard to polyphenols and antioxidant activity changing (Adj R^2 = 0.54 and 0.58, respectively), variation of storage time (a_2) confirmed to exert the most significant effect of all the studied predictor variables (Table S2, Supporting Information). As can be seen in Figure 2, TPP and ORAC increased with longer storage time up to 120 h. Moreover, a slight increase of total TPP level and antioxidant capacity was also observed storing samples at lower temperature (4 °C), as a consequence of positive interactions between storage time and temperature (a_{23}; see Table S2), while no significant influence of UV-C factor was noted on both parameters (a_{12} and a_{13}; see Table S2). In the case of anthocyanins (Adj R^2 = 0.72), first, the significant quadratic terms (a_{11} and a_{22}) being negative means that a maximum increment of these compounds can be found in the considered experimental domain (Table S2, Supporting Information); TA variation in Redglobe during postharvest was primarily affected by the storage time and, to a lesser extent, by the UV-C dose exposure, while no significant impact of the storage temperature, in the considered range, was observed (Figure 2e and f). More precisely, better conditions to improve anthocyanins content were represented by a storage time between 48 and 60 h and UV-C treatment of almost 1 min.

This might be ascribed to the differing effects of low and high UV-C doses on the rate of phenylalanine ammonia-lyase (PAL) expression (Pan, Vicente, Martinez, Chaves, & Civello, 2004). The biosynthesis of phenolic compounds is affected by gamma and ultraviolet irradiation due to the increased activity of PAL as well as other enzymes involved in flavonoid synthesis (Tomas-Barberan & Espin, 2001) which can promote the accumulation of phenolic compounds, such as resveratrol in grapes (Takayanagi, Okuda, Mine, & Yokotsuka, 2004) or anthocyanins in peach (Kataoka & Beppu, 2004). Moreover, considering that low temperature storage has been shown to enhance postharvest phenolic metabolism in a wide variety of plant matrices (Lattanzio, 2003), even though in our case temperature factor was not relevant for phenolic improvement in postharvest grapes, it is worth noting that an UV-C exposure of berries for 1 min would seem sufficient to stimulate the anthocyanin biosynthesis also at room temperature.

4. Conclusions

To date, the effectiveness of postharvest treatments has been assessed mainly by the quality maintenance of harvested fruit and vegetables. However, with rising consumer interest in foods that promote health, attention has shifted from quality maintenance to quality assurance with particular emphasis on the enhancement of health-promoting phytochemicals. Therefore, to obtain fruit and vegetables enriched with phytochemicals, postharvest elicitor treatments might be used either singularly or in combination to obtain the desired effect. In this research interactive effect among UV-C treatment and storage conditions (time and temperature) on phenolic compounds in postharvest Redglobe table grape variety were determined. Irrespective to storage temperature, UV-C exposure ranging from 1 to 3 min (0.8-2.4 KJ m^{-2}) positively influence TA level during a storage time longer than 48 h, while in the case of TPP and ORAC, their values progressively enhanced up to 120 h of storage, in particular when samples were irradiated for 1 min and stored at 4 °C. This means that a fresh product with enhanced quality value can be offered to consumers within the typical conditions of market commercialization.

Since polyphenol and anthocyanin profile is a varietal characteristic, further researches are in progress to extend the aforementioned findings to other cultivars for proposing such phytochemical-enriched grapes to be served as fresh products or used as raw material for functional foods and supplements and would act as a complementary or synergistic strategy to human nutrition programs and policy for enhancing the consumption of phytochemicals.

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Supporting Information

Table S1. Schematic representation of the full factorial experimental design (2 x 4 x 4 = 32 unique runs). Grape samples were exposed to UV-C irradiation during 1, 3, and 5 min (0.8, 2.4, and 4.1 KJ m^{-2}, respectively) followed by temperature (room temperature vs 4 °C) and time (0, 24, 48, and 120 h) modification. Factor A: storage temperature; Factor B: storage time; Factor C: UV-C treatment

Factor A	**Factor B**	**Factor C**			
		0	1	2	3
0	0	0 0 0	0 0 1	0 0 2	0 0 3
0	1	0 1 0	0 1 1	0 1 2	0 1 3
0	2	0 2 0	0 2 1	0 2 2	0 2 3
0	3	0 3 0	0 3 1	0 3 2	0 3 3
1	0	1 0 0	1 0 1	1 0 2	1 0 3
1	1	1 1 0	1 1 1	1 1 2	1 1 3
1	2	1 2 0	1 2 1	1 2 2	1 2 3
1	3	1 3 0	1 3 1	1 3 2	1 3 3

Table S2. Regression parameters of the equations representing the postharvest total polyphenols (TPP), anthocyans (TA), and oxygen radical antioxidant capacity (ORAC) in Redglobe (*Vitis vinifera* L.) table grape harvested in 2011[a]

	TPP	**TA**	**ORAC**
main effects			
UV-C treatment (a_1)	-0.003	0.07	0.08
Storage time (a_2)	**0.004**	**0.036**	**0.015**
Storage temperature (a_3)	**0.002**	0.00054	**-0.019**
interactions			
Storage time x UV-C treatment (a_{12})	0.000066	**-3.2E-05**	0.00043
Storage temperature x UV-C treatment (a_{13})	-0.0011	0.0013	-0.00049
Storage time x Storage temperature (a_{23})	**0.000076**	0.000021	**-0.00042**
quadratic terms			
(UV-C treatment)^2 (a_{11})	0.003	**-0.012**	-0.021
(Storage time)^2 (a_{22})	-0.000015	**-0.0002**	-0.000029
(Storage temperature)^2 (a_{33})	0.00001	-0.0002	0.000022
intercept (a_0)	**0.95**	**0.92**	**0.93**

[a]The corresponding terms in the model equations are given between brackets. Significant terms are in bold.