The stilbene profile in edible berries

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Abstract Edible berries are becoming increasingly popular to consume in fresh, dried, frozen or processed forms due to their high content and wide diversity of bioactive compounds with considerable health benefits. Among the wide variety of phytochemicals found in berries are stilbenes, which demonstrate a broad range of biological and pharmacological activities. Their content depends on many factors, including the cultivar, ripening stage, climatic conditions, agromonomic management, storage conditions and postharvest management. However, the application of various abiotic and biotic external stimuli could be a strategy for increasing the production of stilbenes in edible berries. To date, several different elicitors, as inducers of plant secondary metabolite stilbenes, have been applied in different studies. This review focuses on the isolation and identification of stilbenes from edible berries and presents the influence of different external stimuli on their profile in grapes.

Keywords Stilbenes · Edible berries · External stimuli

Introduction

In recent years, edible berries have attracted much interest due to their high content and wide diversity of bioactive compounds with potential health benefits (Zhao 2007; Seeram 2012; Jimenez-Garcia et al. 2013; Nile and Park 2014). Berry fruits are widely consumed in fresh, dried, frozen forms or as processed products, including canned fruits, beverages, jams and yogurts. The most consumed berries are red raspberries (*Rubus idaeus*), strawberries (*Fragaria x ananassa*), blackberries (*Rubus* spp.), blueberries (*Vaccinium corymbosum*), black currants (*Ribes nigrum*), red currants (*Ribes rubrum*), chokeberries (*Aronia melanocarpa*), cranberries (*Vaccinium macrocarpon*), grapevines (*Vitis vinifera* L. and other *Vitis* species), bilberries (*Vaccinium myrtillus* L.), deerberries (*Vaccinium stamineum* L.), cowberries (*Vaccinium vitis-idaea* L.), passion fruits (*Passiflora edulis*) and tomatoes (*Lycopersicon esculentum* Mill.).

Among the wide variety of phytochemicals found in berries are stilbenes. These molecules occur within a limited group of plant families, which have the gene encoding the enzyme stilbene synthase (*STS*, EC 2.3.1.95). Biosynthesis occurs via the phenylalanine pathway, where phenylalanine ammonia lyase (*PAL*), cinnamate-4-hydroxylase (*C4H*), coumaroyl-CoA ligase (*4CL*) and *STS* play a core role in the synthesis. (Fig. 1) A transcriptional factor, *Myb14*, has been found to regulate the expression of *STS* (Holl et al.

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Fig. 1 Early stages of stilbene biosynthesis. *PAL* phenylalanine ammonia lyase, *C4H* cinnamate-4-hydroxylase, *4CL* coumaroyl-CoA ligase, *CHS* chalcone synthase, *STS* stilbene synthase

2013). Chalcone isomerase (*CHI*) is responsible for the conversion of chalcone to flavanones. On the other hand, resveratrol O-methyltransferase (*ROMT*) is involved in the methylation of resveratrol. Stilbenes are biosynthesized and accumulate into lipid vesicles in the cytoplasm. Their content can be determined by many factors, including the cultivar, ripening stage, climatic conditions, soil type, agronomic management, storage conditions and postharvest management (Dixon and Paiva 1995; Castrejon et al. 2008). Due to the potential health benefits, stilbenes in edible fruits are of high interest. These compounds have demonstrated a wide range of biological and pharmacological activities, including anti-tumoural (Bai et al. 2010; Tsai et al. 2017), anti-viral (Nguyen et al. 2011), anti-inflammatory (Zhang et al. 2010), anti-atherogenic (Ramprasath and Jones 2010), anti-aging (Kasiotis et al. 2013) and neuroprotective (Lin and Yao 2006) effects.

This review focuses on stilbenes as a specific class of non-flavonoid phenolic compounds present in edible berries. The aim of this review is to summarize the isolation and identification methods applied for stilbenes present in edible berries as well as the influence of external stimuli on the quantitative and qualitative composition of stilbenes in edible berries.

Molecular structures of stilbenes found in berry fruits

The stilbene structure is characterized by two aromatic rings linked by a double bond, of which the *E* isomer is the most common configuration. They can be found in berry fruits as monomers, dimers and more complex oligomers (Figs. 2, 3, 4, 5, 6, 7). According to a current paper, the most widely found monomeric stilbenes in berry fruits are *E*-resveratrol (1) and *E*-piceid (3)

- 1** $R_1, R_3, R_5 = H, R_2, R_4, R_6 = OH$
2 $R_1, R_3, R_5 = H, R_2, R_4 = OCH_3, R_6 = OH$
3 $R_1, R_3, R_5 = H, R_2, R_6 = OH, R_4 = OGlc$
4 $R_1, R_3 = H, R_2, R_4, R_5, R_6 = OH$
5 $R_1, R_3 = H, R_4, R_5, R_6 = OH, R_2 = OGlc$
6 $R_1, R_3 = H, R_4, R_6 = OH, R_5 = OCH_3, R_2 = OGlc$

Fig. 2 Molecular structures of *E*-stilbene monomers isolated from edible berries: **1**: *E*-resveratrol (3,4',5-trihydroxy-*E*-stilbene), **2**: 3,5-O-dimethyl-*E*-resveratrol (*E*-pterostilbene), **3**: *E*-resveratrol-3-O- β -D-glucopyranoside (*E*-piceid), **4**: 3,3',4,5-tetrahydroxy-*E*-stilbene (*E*-piceatannol), **5**: *E*-piceatannol-3-O- β -D-glucopyranoside (*E*-astringin), **6**: isorhapontin

- 7** $R_1, R_3, R_5 = H, R_2, R_4, R_6 = OH$
8 $R_1, R_4 = H, R_2, R_5 = OH, R_3 = OGlc$
9 $R_1 = H, R_3, R_4, R_5 = OH, R_2 = OGlc$

Fig. 3 Molecular structures of *Z*-stilbene monomers isolated from edible berries: **7**: *Z*-resveratrol, **8**: *Z*-resveratrol-3-O- β -D-glucopyranoside (*Z*-piceid), **9**: *Z*-piceatannol-3-O- β -D-glucopyranoside (*Z*-astringin)

(Fig. 2). Their *Z*- and *E*-isomers mainly accumulate in the berry skin during all stages of development (Jeandet et al. 1991). *E*-isomer plant stilbenes may undergo several types of modifications, such as isomerisation, glycosylation, methoxylation, and oligomerization (Chong et al. 2009). Due to these modifications, different derivatives of stilbenes are formed in edible berries from dimers to hexamers (Figs. 2, 3, 4, 5, 6, 7). In plants, these metabolites generally accumulate in both free and glycosylated forms. Glycosylation of stilbenes could be involved in their storage, transport from the cytoplasm to the

apoplasm and protection from peroxidative degradation (Morales et al. 1998). The oligomeric stilbenes are formed due to the oxidative coupling of *E*-resveratrol (**1**) or other monomeric stilbenes catalysed by peroxidase isoenzymes localized in the vacuole, cell wall and apoplast of grapevine cells (Ros Barcelo et al. 2003).

Isolation and identification of stilbenes in edible berries

The isolation and identification of stilbenes in edible berry extracts constitutes a complex procedure due to complex composition of the matrices in which they occur, their low concentration and structural complexity. Several strategies have been applied for the isolation and identification of stilbenes in edible berries. An overview of the preparation conditions, analytical methods and stilbene concentrations in accordance with the research objectives are presented in Table 1. In general, the extraction techniques applied in stilbene extraction are classified into two categories: conventional and green techniques. The conventional techniques involve soaking in solvent, which relies on the solubility of stilbenes from edible berries in the solvent at room or elevated temperature. These techniques consume a large volume of solvents and are usually time consuming. In contrast, the green extraction technique applies minimal volumes of solvent and requires a shorter time. It has been used as preparation procedure by Ehala et al. (2005) to isolate *E*-resveratrol from bilberry via microwave-assisted extraction. In conventional extraction techniques of stilbenes from edible berries solid–liquid extraction of lyophilized, air-dried, frozen or fresh samples with different solvents is applied (see Table 1). Unfortunately, there are no studies in which the influence of matrices (lyophilized, air-dried, frozen, fresh) on the presence of stilbenes was examined. From a quantitative point of view, the results obtained by different extraction solvents cannot be compared because solvents of different natures have different extractabilities. Basing on the analysed works (Table 1), the most often used solvent for the extraction process is methanol or the mixtures of methanol with other solvents. In the research conducted by Sun et al. (2006) and Romero et al. (2001) the influence of extraction solvents on the amount of

Fig. 4 Molecular structures of stilbene dimers isolated from edible berries: **10**: *E*- and *Z*- ϵ -viniferin, **11**: *E*- and *Z*- δ -viniferin, **12**: *E*- and *Z*- ω -viniferin, **13**: scirpusin B, **14**: parthenocissin A,

15: pallidol, **16**: pallidol-3-O-glucoside, **17**: ampelopsin D, **18**: caraphenol B, **19**: ampelopsin B

extracted stilbenes was examined. Based on Sun et al. work (Table 1, entry no. 15), methanol acidified with 0.1% HCl was the best solvent to extract specific stilbenes from grape skins and seeds. In the research conducted by Romero et al. (2001) the influence of temperature and time of extraction on stilbenes content was examined. The highest extraction of *E*-resveratrol and piceid isomers was observed at 60 °C for 30 min with 80% ethanol. *Z*-Resveratrol was not detected in any conditions assayed. The longer time of extraction at 60 °C, the lower stilbenes content was measured, probably due to their degradation. It is only known that resveratrol and its glycon piceid are stable at 40 °C in the presence of ambient air (Prokop et al. 2006). However *E*-isomer is unstable in solution when exposed to light and readily isomerizes to the *Z*-form and other degradants (Jensen et al. 2010).

Therefore, the preparation procedure of stilbenes isolation should be carried out in the dark due to the light sensitivity of double bond in stilbenes.

Few studies have dealt with the influence of ultrasound on the resveratrol extraction efficiency from grapes (Burin et al. 2014; Babazadeh et al. 2017). The ultrasonication-assisted extraction of resveratrol showed more efficiency than the conventional solvent extraction with 80% ethanol at 60 °C for 30 min. The recovery of resveratrol increased by 24–30% compared with the conventional solvent extraction (Cho et al. 2006).

To decrease background noise in analytical techniques and improve the identification of stilbenes, the purification stage in the preparation procedure is very often applied. Typically, this purification utilizes an additional extraction with other solvent, often EtOAc

Fig. 5 Molecular structures of stilbene trimers isolated from edible berries: **20**: amurensin B, **21**: gnetin H, **22**: vitisin E, **23**: α -viniferin, **24**: miyabenol C, **25**: dividol A, **26**: amurensin G, **27**: ampelopsin G (wilsonol B), **28**: wilsonol A

(He et al. 2009a, b; Sun et al. 2006; Jiang et al. 2012), silica gel (Jiang et al. 2012) or C18 solid-phase extraction (Kiselev et al. 2017).

Many analytical methods with various detection techniques are reported for the separation and identification of individual stilbenes in edible berries, such as liquid chromatography-tandem mass spectrometry (LC-MS/MS) (Vrhovsek et al. 2012), liquid chromatography-mass spectrometry (LC-MS) (Može et al. 2011), liquid chromatography with dual detection by a photodiode array and quadrupole time-of-flight mass spectrometry (LC-PDA-QTOF/MS) (Samoticha et al. 2017), high-pressure liquid chromatography-mass spectrometry (HPLC-MS) (Bavaresco et al. 2002; Jiang et al. 2012; Kiselev et al. 2017), high-pressure liquid chromatography with diode array detection (HPLC-DAD) (Bavaresco et al. 2002; Sun et al. 2006; Vilanova et al. 2015; Guerrero et al. 2010a, 2016), high-pressure liquid chromatography with UV detection (HPLC-UV) (Vincenzi et al. 2013; Kawakami et al. 2014; He et al. 2009a), ultra-high-pressure liquid chromatography quadrupole time-of-flight mass spectrometry (UHPLC/QTOF/MS) (Flamini et al. 2016; De Rosso et al. 2016), ultra-performance liquid chromatography with dual detection by a photodiode array and fluorescence detectors (UPLC/DAD/FL) (Samoticha et al. 2017), ultra-performance liquid chromatography with dual detection by a diode array and tandem quadrupole mass spectrometry (UPLC/

DAD/TQD) (Guerrero et al. 2010a), gas chromatography-mass spectrometry (GC-MS) (Ragab et al. 2006; Viñas et al. 2009, 2011), gas chromatography-mass spectrometry with selected ion monitoring (GC-MS SIM) (Rimando and Cody 2005), gas-liquid chromatography with flame ionization detection (GLC-FID) (Moriarty et al. 2001), capillary electrophoresis (CE) (Ehala et al. 2005) and high-speed counter-current chromatography (HSCC) (He et al. 2009b). Various methods are used for analyses of stilbenes contents in the edible berries are different which could also contribute to the observed variability in the published results. However, the most commonly used methods for stilbenes analysis in different edible berries is normal- and reverse-phase liquid chromatography connected to a diode array detector (DAD) or mass spectrometry (MS). To improve the identification of stilbenes the ultra-performance LC (UPLC) technique coupled with QTOF-MS has been used due to higher resolution and sensitivity of analysis (Flamini et al. 2016) (Table 1, entry no. 24, 26, 27).

Gas chromatography coupled with mass spectrometry (GC-MS) has also been applied for the analyses of stilbenes (Ragab et al. 2006; Rimando and Cody 2005; Viñas et al. 2009, 2011). Prior to GC-MS, the derivatization of hydroxy groups in stilbenes was performed in order to reduce polarity and increase volatility, and simultaneously, thermal stability of

Fig. 6 Molecular structures of stilbene tetramers isolated from edible berries: **28**: vitisin A, **29**: vitisin B, **30**: vitisin C, **31**: hopeaphenol, **32**: isohopeaphenol, **33**: vaticanol C, **34**: wilsonol C, **35**: heyneanol A, **36**: diviniferin B

metabolites. Stilbenes derivatization was based on silylation reactions by means of *N,O*-bis(trimethylsilyl)trifluoroacetamide (BSTFA) or *N*-methyl-*N*-(trimethylsilyl)-trifluoroacetamide (MSTFA) (Rimando and Cody 2005; Ragab et al. 2006; Viñas et al. 2009, 2011). However, due to the lower detectability of this technique only mono-stilbenes were determined such as *E*- and *Z*-resveratrol, *E*- and *Z*-piceid, pterostilbene and piceatannol.

Two strategies have been applied to identify stilbenes. In the case of known compounds, the identification was based on comparison of their retention times and MS or MS/MS data with those of standards. For unknown stilbenes, the characterization

was performed by IR, MS, UV–Vis and NMR methods.

It is well known that the highest concentrations of stilbenes are in berries seeds and skins (Sun et al. 2006; Babazadeh et al. 2017). The amount of *E*-resveratrol in grape skin is approximately three times higher than in pulp (Babazadeh et al. 2017). Among the analysed edible berries, the highest concentration of stilbenes was found in the seeds of passion fruit (*Passiflora edulis*) (Kawakami et al. 2014) by applying 80% EtOH as the solvent for extraction. However, the highest concentration of *E*-resveratrol in the skin has been found in table grapes (*Vitis vinifera* L.) (Ragab et al. 2006) by using extraction with ethyl acetate at 70 °C.

Fig. 7 Molecular structure of stilbene hexamer isolated from edible berries: **37**: chunganenol

Influence of external stimuli on the presence of stilbenes in grapes

Because stilbenes are secondary metabolites in edible berries, their quantitative and qualitative composition depends on many factors, including the cultivar, genotype, type of soil, climatic conditions, developmental stage, agronomic management, storage conditions (time, temperature) and postharvest treatments. In addition, there are other external stimuli (stress factors) that activate defence mechanisms in fruits responsible for the accumulation of stilbene as phytoalexins. The defence mechanism may be induced by abiotic elicitors such as UV irradiation, ozone, ultrasonication, methyl jasmonate, chitosan and visible light or biotic elicitors such as *Aspergillus carbonarius* and *Botrytis cinerea*. Recent review has discussed the influence of external stimuli on resveratrol synthesis in grapes (Hasan and Bae 2017). Various abiotic and biotic stress conditions have significant influence on the quantitative and qualitative composition of stilbenes in grapes, which are presented in Table 2.

Abiotic preharvest treatments of grape

Preharvest UV-C treatment of the Crimson seedless variety was applied daily for 3 days before harvest

(Table 2, no. 1) and resulted in an increased concentration of stilbenes (Guerrero et al. 2016). The maximum content of *E*-resveratrol and *E*-piceatannol was achieved 24 h after each daily treatment. However, the ϵ -viniferin concentration was maximal at 48 and 72 h. In the case of *E*-piceid, *Z*-piceid and ω -viniferin, the maximum concentration was achieved at 72 h. The maximal contents of *E*-resveratrol, *Z*-piceid, *E*-piceid, *E*-piceatannol, ϵ -viniferin, ω -viniferin, isohopeaphenol and stilbenoids were 12-, 9-, 5-, 4-, 7-, 4-, 3- and 4-fold increased over those in the control sample. After daily periodic preharvest treatment of berries, the *E*-resveratrol content increased 83-fold in comparison with 18-fold growth for a single UV-C irradiation over the initial concentration. The first and the second treatments significantly increased the stilbene content, but the third daily treatment might have been important for maintaining their concentration. First, the biosynthesis of *E*-resveratrol is induced, and then the compound is glycosylated to *E*-piceid, which, under UV-C irradiation from the daily preharvest treatment, is transformed into *Z*-piceid.

The maximum *E*-resveratrol concentration detected in grape after UV-C treatment depends on its initial concentration, which correlates with the developmental stage of berries (Guerrero et al. 2010a, b). In another work (Table 2, no. 2), UV-C light preharvest treatment was applied on different days before grape ripeness to establish the optimum application day to reach the maximum *E*-resveratrol concentration. Due to UV-C irradiation, the highest *E*-resveratrol concentration in Red Globe grapes was achieved 3 days before harvest and was 46-fold higher than that observed in the non-treated control sample. However, at harvest, the *E*-resveratrol content was only 8.8 times higher than that in the control sample. UV-C treatment of berries 1 day before harvest resulted in 26 times higher *E*-resveratrol concentrations (Table 2, no. 2). The maximum *E*-resveratrol and ϵ -viniferin content was achieved when the UV-C dose was approximately 10,000 J/m². Both the dose and the application method, in terms of output power and exposure time, are key factors determining the final stilbene content. Treatment with an output power and exposure time of 1040 W and 5 min, respectively, was selected as the most suitable condition for the UV-C treatment.

According to the literature, UV-C irradiation of edible berries effectively induces stilbene biosynthesis (Liu et al. 2010; Wang et al. 2010; Crupi et al. 2013).

Table 1 Preparation conditions and analytical methods for stilbene separation and identification from edible berries

No.	Sample	Preparation conditions	Analytical method	Stilbenes: concentration (µg/g)	References
1	Bilberry (<i>Vaccinium myrtillus</i> L.)	1. Material: frozen fruits 2. Solvent: MeOH 3. Conditions: room temperature	LC–MS	<i>E</i> -resveratrol: 2 µg/g fw	Može et al. (2011)
2	Bilberry (<i>Vaccinium myrtillus</i> L.) Cultivar: wild	<i>Method used for berries from US location</i> 1. Material: lyophilized berries 2. Solvent: MeOH/acetone/H ₂ O/ CH ₃ COOH (40:40:20:0.1) 3. Conditions: 40 °C, 1000 psi 4. Purification: extraction with EtOAc 5. Derivatization: MSTFA/DFA/MeOH (3.5:1:0.5) <i>Method used for berries from Canada</i> 1. Material: frozen berries 2. Solvent: MeOH/acetone/H ₂ O/ HCOOH (40:40:20:0.1) 1. Conditions: room temperature 2. Purification: C18 solid-phase extraction 3. Derivatization: MSTFA/DFA/MeOH (3.5:1:0.5)	GC–MS SIM	Resveratrol: 0.768 µg/g dw	Rimando and Cody (2005)
3	Bilberry (<i>Vaccinium myrtillus</i> L.)	<i>Method I: The microwave-assisted extraction</i> 1. Material: frozen berries 2. Solvent: EtOH/H ₂ O (7:3) 3. Conditions: 180 W 4. Purification: C18 solid-phase extraction <i>Method II: The ultrasonic extraction</i> 1. Material: frozen berries 2. Solvent: MeOH/H ₂ O (1:1), MeOH/ H ₂ O (7:3), and EtOH/H ₂ O (7:3) 3. Conditions: room temperature in ultrasonic bath 4. Purification: C18 solid-phase extraction	CE	<i>E</i> -resveratrol: 6.78 µg/g fw	Ehala et al. (2005)
4	Blueberries (<i>Vaccinium corymbosum</i> L.)	1. Material: frozen fruits 2. Solvent: MeOH 3. Conditions: room temperature	LC–MS	<i>E</i> -resveratrol: 4 µg/g fw	Može et al. (2011)

Table 1 continued

No.	Sample	Preparation conditions	Analytical method	Stilbenes: concentration (µg/g)	References
5	Highbush blueberry (<i>Vaccinium corymbosum</i> L.) Cultivars: Bluecrop wild	<i>Method used for berries from US location</i>	GC–MS SIM	<i>Bluecrop from conventional farming</i>	Rimando and Cody (2005)
		1. Material: lyophilized berries		Resveratrol: 0.853 µg/g dw	
		2. Solvent: MeOH/acetone/H ₂ O/ CH ₃ COOH (40:40:20:0.1)		Piceatannol: 0.422 µg/g dw	
		3. Conditions: 40 °C, 1000 psi		<i>Bluecrop from sustainable farming</i>	
		4. Purification: extraction with EtOAc		Resveratrol: 0.327 µg/g dw	
		5. Derivatization: MSTFA/DFA/ MeOH (3.5:1:0.5)		Piceatannol: 0.186 µg/g dw	
		<i>Method used for berries from Canada</i>		<i>Wild</i>	
		1. Material: frozen berries		Resveratrol: 1.074 µg/g dw	
		2. Solvent: MeOH/acetone/H ₂ O/ HCOOH (40:40:20:0.1)			
		3. Conditions: room temperature			
6	Rabbiteye blueberry (<i>Vaccinium ashei</i> Reade) Cultivars: Tifblue Climax Premier	<i>Method used for berries from US location</i>	GC–MS SIM	<i>Tifblue</i>	Rimando and Cody (2005)
		1. Material: lyophilized berries		Resveratrol: 0.106 µg/g dw	
		2. Solvent: MeOH/acetone/H ₂ O/ CH ₃ COOH (40:40:20:0.1)		Pterostilbene: 0.151 µg/g dw	
		3. Conditions: 40 °C, 1000 psi		<i>Climax</i>	
		4. Purification: extraction with EtOAc		Resveratrol: 0.390 µg/g dw	
		5. Derivatization: MSTFA/DFA/ MeOH (3.5:1:0.5)		Pterostilbene: 0.099 µg/g dw	
		<i>Method used for berries from Canada</i>		<i>Premier</i>	
		1. Material: frozen berries		Resveratrol: 0.007 µg/g dw	
		2. Solvent: MeOH/acetone/H ₂ O/ HCOOH (40:40:20:0.1)			
		3. Conditions: room temperature			
		4. Purification: C18 solid-phase extraction			
		5. Derivatization: MSTFA/DFA/ MeOH (3.5:1:0.5)			

Table 1 continued

No.	Sample	Preparation conditions	Analytical method	Stilbenes: concentration (µg/g)	References
7	Cowberry (<i>Vaccinium Vitis-idaea</i> L.)	<i>Method I: The microwave-assisted extraction</i> 1. Material: frozen berries 2. Solvent: EtOH/H ₂ O (7:3) 3. Conditions: 180 W 4. Purification: C18 solid-phase extraction <i>Method II: The ultrasonic extraction</i> 1. Material: frozen berries 2. Solvent: MeOH/H ₂ O (1:1), MeOH/H ₂ O (7:3), and EtOH/H ₂ O (7:3) 3. Conditions: room temperature in ultrasonic bath 4. Purification: C18 solid-phase extraction	CE	<i>E-resveratrol</i> : 30 µg/g fw	Ehala et al. (2005)
8	Cranberry (<i>Vaccinium oxycoccos</i>)	<i>Method I: the microwave-assisted extraction</i> 1. Material: frozen berries 2. Solvent: EtOH/H ₂ O (7:3) 3. Conditions: 180 W 4. Purification: C18 solid-phase extraction <i>Method II: the ultrasonic extraction</i> 1. Material: frozen berries 2. Solvent: MeOH/H ₂ O (1:1), MeOH/H ₂ O (7:3), and EtOH/H ₂ O (7:3) 3. Conditions: room temperature in ultrasonic bath 4. Purification: C18 solid-phase extraction	CE	<i>E-resveratrol</i> : 19.29 µg/g fw	Ehala et al. (2005)
9	Red currant (<i>Ribes rubrum</i> L.) Black currant (<i>Ribes nigrum</i> L.)	<i>Method I: the microwave-assisted extraction</i> 1. Material: frozen berries 2. Solvent: EtOH/H ₂ O (7:3) 3. Conditions: 180 W 4. Purification: C18 solid-phase extraction <i>Method II: The ultrasonic extraction</i> 1. Material: frozen berries 2. Solvent: MeOH/H ₂ O (1:1), MeOH/H ₂ O (7:3), and EtOH/H ₂ O (7:3) 3. Conditions: room temperature in ultrasonic bath 4. Purification: C18 solid-phase extraction	CE	<i>Red currant</i> <i>E-resveratrol</i> : 15.72 µg/g fw <i>Black currant</i> <i>E-resveratrol</i> : nd	Ehala et al. (2005)

Table 1 continued

No.	Sample	Preparation conditions	Analytical method	Stilbenes: concentration (µg/g)	References
10	Deerberry (<i>Vaccinium stamineum</i> L.) Cultivars: wild SHF3A-2-108 B-76	<i>Method used for berries from US location</i> 1. Material: lyophilized berries 2. Solvent: MeOH/acetone/H ₂ O/ CH ₃ COOH (40:40:20:0.1) 3. Conditions: 40 °C, 1000 psi 4. Purification: extraction with EtOAc 5. Derivatization: MSTFA/DFA/MeOH (3.5:1:0.5) <i>Method used for berries from Canada</i> 1. Material: frozen berries 2. Solvent: MeOH/acetone/H ₂ O/HCOOH (40:40:20:0.1) 3. Conditions: room temperature 4. Purification: C18 solid-phase extraction 5. Derivatization: MSTFA/DFA/MeOH (3.5:1:0.5)	GC–MS SIM	<i>Wild</i> Resveratrol: 0.204 µg/g dw <i>SHF3A-2-108</i> Resveratrol: 0.115 µg/g dw Pterostilbene: 0.520 µg/g dw <i>B-76</i> Resveratrol: 0.503 µg/g dw Piceatannol: 0.195 µg/g dw	Rimando and Cody (2005)
11	Table grapes (<i>Vitis vinifera</i> L.) Californian cultivars: Black Corinth Flame Seedless skin	1. Material: fresh skin 2. Solvent: MeOH/0.1% HCl 3. Conditions: room temperature 4. Purification: extraction with EtOAc	GLC-FID	Resveratrol <i>Black Corinth cultivar</i> Non-irradiated fruits: 0–25.1 µg/g fw Irradiated fruits: 0.9–33.2 µg/g fw <i>Flame Seedless cultivar</i> Non-irradiated fruits: 1–13.2 µg/g fw Irradiated fruits: 1.8–57.3 µg/g fw	Moriarty et al. (2001)
12	Grapes (<i>Vitis vinifera</i> L.) Cultivar: Cabernet sauvignon	1. Material: fresh berries (without seeds) 2. Solvent: 95% MeOH 3. Conditions: room temperature 4. Purification: EtOAc/5% NaHCO ₃ (1:1)	HPLC– DAD HPLC–MS	<i>E</i> -resveratrol: 0.297 µg/g fw <i>E</i> -piceid: 0.097 µg/g fw Piceatannol: 0.052 µg/g fw <i>Z</i> -resveratrol: nd <i>Z</i> -piceid: nd	Bavaresco et al. (2002)
13	Grapes (<i>Vitis vinifera</i> L.) Cultivars: Cabernet Pinot Noir Merlot Table grapes	<i>Method used for berries from US location</i> 1. Material: lyophilized berries 2. Solvent: MeOH/acetone/H ₂ O/ CH ₃ COOH (40:40:20:0.1) 3. Conditions: 40 °C, 1000 psi 4. Purification: extraction with EtOAc 5. Derivatization: MSTFA/DFA/MeOH (3.5:1:0.5) <i>Method used for berries from Canada</i> 1. Material: frozen berries 2. Solvent: MeOH/acetone/H ₂ O/HCOOH (40:40:20:0.1) 3. Conditions: room temperature 4. Purification: C18 solid-phase extraction 5. Derivatization: MSTFA/DFA/MeOH (3.5:1:0.5)	GC–MS SIM	<i>Cabernet</i> Resveratrol: 2.475 µg/g dw <i>Pinot Noir</i> Resveratrol: 5.746 µg/g dw <i>Merlot</i> Resveratrol: 6.356 µg/g dw <i>Table grapes</i> Resveratrol: 6.471 µg/g dw	Rimando and Cody (2005)

Table 1 continued

No.	Sample	Preparation conditions	Analytical method	Stilbenes: concentration (µg/g)	References
14	Table grapes (<i>Vitis vinifera</i> L.) seedless red	1. Material: lyophilized tomato or grape skin 2. Solvent: EtOAc 3. Conditions: 70 °C 4. Derivatization: MSTFA/pyridine	GS-MS	Z-resveratrol: 20 µg/g dw E-resveratrol: 2680 µg/g dw Z-piceid: 30 µg/g dw E-piceid: 50 µg/g dw	Ragab et al. (2006)
15	Grapes (<i>Vitis vinifera</i> L.) Cultivars: Castelao Syrah Tinta Roriz seeds skin	<i>Method I</i> 1. Material: lyophilized grape skin 2. Solvent: MeOH, 80% MeOH/H ₂ O, 50% MeOH/H ₂ O, 75% acetone/H ₂ O 3. Conditions: room temperature 4. Purification: extraction with EtOAc <i>Method II</i> 1. Material: lyophilized grape skin 2. Solvent: EtOAc 3. Conditions: room temperature <i>Method III</i> 1. Material: lyophilized grape skin 2. Solvent: MeOH 3. Conditions: room temperature 4. Purification: extraction with EtOAc <i>Method IV</i> 1. Material: lyophilized grape skin 2. Solvent: MeOH/0.1% HCl 3. Conditions: room temperature 4. Purification: extraction with EtOAc <i>Method V</i> 1. Material: lyophilized grape skin 2. Solvent: 75% acetone/H ₂ O 3. Conditions: room temperature 4. Purification: extraction with EtOAc <i>Method VI</i> 1. Material: lyophilized grape skin 2. Solvent: model wine solution (12% of EtOH, 5 gL ⁻¹ of l-tartaric acid, pH 3.2) 3. Conditions: room temperature 4. Purification: extraction with EtOAc	HPLC–DAD	<i>Method I</i> E-resveratrol: ~ 40 µg/g fw E-piceid: ~ 70 µg/g fw Z-piceid: ~ 130 µg/g fw <i>Method II</i> E-resveratrol: ~ 40 µg/g fw E-piceid: ~ 10 µg/g fw Z-piceid: ~ 20 µg/g fw <i>Method III</i> E-resveratrol: ~ 80 µg/g fw E-piceid: ~ 120 µg/g fw Z-piceid: ~ 170 µg/g fw <i>Method IV</i> E-resveratrol: ~ 100 µg/g fw E-piceid: ~ 140 µg/g fw Z-piceid: ~ 200 µg/g fw <i>Method V</i> E-resveratrol: ~ 30 µg/g fw E-piceid: ~ 20 µg/g fw Z-piceid: ~ 130 µg/g fw <i>Method VI</i> E-resveratrol: ~ 10 µg/g fw E-piceid: ~ 10 µg/g fw Z-piceid: ~ 30 µg/g fw <i>Method IV</i> <i>Seed</i> Total resveratrol: 4.76 ± 0.25 µg/g dw Total piceid: nd <i>Skin</i> Total resveratrol: 208.50 ± 51.97 µg/g dw Total piceid: 762.47 ± 164.16 µg/g dw	Sun et al. (2006)

Table 1 continued

No.	Sample	Preparation conditions	Analytical method	Stilbenes: concentration (µg/g)	References
16	Southeast China grape (<i>Vitis chunganensis</i>)	1. Material: fresh grape 2. Solvent: MeOH 3. Conditions: room temperature 4. Purification: EtOAc and silica gel/EtOAc/light petroleum	HPLC–UV	Chunganenol: 8.57 µg/g fw Amurensin B: 242.86 µg/g fw Gnetin H: 131.43 µg/g fw ε-viniferin: 154.29 µg/g fw Amurensin G: 262.86 µg/g fw Vitisin A: 191.43 µg/g fw Hopeaphenol: 88.57 µg/g fw Resveratrol: 48.57 µg/g fw	He et al. (2009a)
17	Southeast China grape (<i>Vitis chunganensis</i>)	1. Material: dried fruits 2. Solvent: MeOH 3. Conditions: room temperature 4. Purification: extraction with EtOAc	HSCCC	Hopeaphenol: 84.4 µg/g dw Amurensin G: 148.8 µg/g dw Vitisin A: 382.4 µg/g dw	He et al. (2009b)
18	Grapes (<i>Vitis vinifera</i> L.) red and white	1. Material: fresh grapes 2. Solvent: EtOH 3. Conditions: sonication at room temperature 4. Derivatization: BSTFA	GC–MS	<i>Red grapes</i> <i>E</i> -resveratrol: 0.029 µg/g fw <i>Z</i> -resveratrol: 0.0028 µg/g fw Piceatannol: 0.024 µg/g fw <i>White grapes</i> <i>E</i> -resveratrol: 0.0056 µg/g fw <i>Z</i> -resveratrol: nd Piceatannol: 0.0012 µg/g fw	Viñas et al. (2009)
19	Grapes (3 <i>Vitis vinifera</i> <i>sylvestris</i> , 7 <i>Vitis vinifera sativa</i> , 2 Hybrid Direct Producers)	1. Material: frozen grapes 2. Solvent: Et ₂ O 3. Conditions: room temperature	UPLC–DAD–TQD identification HPLC–DAD determination	<i>Merlot: non-UV, UV-C treatment</i> (µg/g fw) <i>E</i> -resveratrol: 2.82, 9.75 Piceatannol: 0.48, 2.55 Viniferins: 0.29, 2.39 <i>Syrah: non-UV, UV-C treatment</i> (µg/g fw) <i>E</i> -resveratrol: 3.56, 19.56 Piceatannol: 0.46, 0.31 Viniferins: nd, 1.49 <i>Tempranillo: non-UV, UV-C treatment</i> (µg/g fw) <i>E</i> -resveratrol: 0.31, 3.78 Piceatannol: nd, 1.10 Viniferins: 0.14, 1.19	Guerrero et al. (2010a)
20	Grapes (<i>Vitis vinifera</i> L.) red and white	1. Material: fresh fruits 2. Solvent: undecanone 3. Conditions: 30 °C 4. Derivatization: BSTFA	GC–MS	<i>Red grapes</i> <i>E</i> -resveratrol: 1.639 µg/g fw <i>Z</i> -resveratrol: 0.405 µg/g fw Piceatannol: 0.374 µg/g fw <i>White grapes</i> <i>E</i> -resveratrol: 0.239 µg/g fw <i>Z</i> -resveratrol: 0.082 µg/g fw Piceatannol: 0.043 µg/g fw	Viñas et al. (2011)

Table 1 continued

No.	Sample	Preparation conditions	Analytical method	Stilbenes: concentration (µg/g)	References
21	Grapes (<i>Vitis vinifera</i> L.)	1. Material: fresh fruits 2. Solvent: H ₂ O/MeOH/CHCl ₃ (20:40:40) 3. Conditions: room temperature 4. Purification: extraction with H ₂ O/MeOH (1:2)	LC–MS/MS	Piceatannol: 0.08 µg/g fw <i>E</i> -piceid: 0.27 µg/g fw <i>Z</i> -piceid: 0.02 µg/g fw Astringin: 0.69 µg/g fw Isorhapontin: 0.08 µg/g fw <i>E</i> - ϵ -viniferin: 0.32 µg/g fw Pallidol: 0.04 µg/g fw Isohopeaphenol: 0.19 µg/g fw	Vrhovsek et al. (2012)
22	Wild grape (<i>Vitis wilsonae</i>)	1. Material: air-dried grapes 2. Solvent: MeOH 3. Conditions: room temperature 4. Purification: extraction with EtOAc and silica gel/EtOAc/petroleum ether	HPLC–MS	Wilsonol A: 1.87 µg/g dw Wilsonol B: 0.72 µg/g dw Wilsonol C: 1.13 µg/g dw Diviniferin B: 3.03 µg/g dw Pallidol: 0.75 µg/g dw ϵ -viniferin: 0.23 µg/g dw Ampelopsin B: 1.13 µg/g dw Ampelopsin D: 0.32 µg/g dw Miyabenol C: 3.75 µg/g dw Dividol A: 1.9 µg/g dw Hopeaphenol: 6.13 µg/g dw Gnetin H: 11.67 µg/g dw Heyneanol A: 4.3 µg/g dw Ampelopsin G: 1.87 µg/g dw Amurensin G: 2.78 µg/g dw Visitin E: 4.02 µg/g dw	Jiang et al. (2012)
23	Grapes (<i>Vitis vinifera</i> L.) 21 red cultivars, skin	1. Material: skin of frozen berries 2. Solvent: MeOH/HCl (40 mL/50 µL) 3. Conditions: room temperature 4. Purification: extraction with EtOAc and then MeOH/HCOOH	HPLC–UV	<i>E</i> -resveratrol: detected in all 21 cultivars, 19–508 µg/g fw; <i>E</i> -piceid: detected in 19 cultivars, from n.d. to 551 µg/g fw; <i>Z</i> -piceid: detected in 20 cultivars, from n.d. to 1 196 µg/g fw; <i>E</i> -piceatannol: detected in 7 cultivars, from n.d. to 72.1 µg/g fw; <i>Z</i> -resveratrol: detected in the berry skins at very low concentrations.	Vincenzi et al. (2013)

Table 1 continued

No.	Sample	Preparation conditions	Analytical method	Stilbenes: concentration (µg/g)	References
24	Red grapes (<i>Vitis vinifera</i>) Cultivars: Raboso Piave Primitivo	1. Material: fresh berries 2. Solvent: MeOH 3. Conditions: room temperature	UHPLC-QTOF-MS	<i>Primitivo</i> (µg/g fw) <i>E</i> -astringin: 0.8842 ± 0.0034 <i>E</i> -piceid: 2.3321 ± 0.0489 <i>Z</i> -astringin: 0.1214 ± 0.0010 piceatannol: 0.1815 ± 0.0102 <i>Z</i> -piceid: 1.7762 ± 0.0474 Pallidol: 0.3562 ± 0.0026 Pallidol-3-O-glucoside: 0.1875 ± 0.0016 Parthenocissin A: 0.1310 ± 0.0011 <i>E</i> -resveratrol: 1.1364 ± 0.0536 Caraphenol B: 0.1042 ± 0.0014 Hopheapenol: 0.1010 ± 0.0023 Ampelopsin H/vaticanol C/isohopheapenol: 0.5366 ± 0.0129 <i>Z</i> -ε-viniferin: 0.380 ± 0.0070 <i>E</i> -ε-viniferin: 0.7021 ± 0.0074 <i>Z</i> -miyabenol C: 0.2362 ± 0.0078 <i>E</i> -miyabenol C: 1.3578 ± 0.0119 δ-viniferins: 0.0679 ± 0.0011	Flamini et al. (2013)
25	Commercial Grapes (<i>Vitis vinifera</i>) Cultivar: Mencía	1. Material: lyophilised skin 2. Solvent: MeOH/HCl (99:1 and 95:5) 3. Conditions: room temperature	HPLC-DAD	<i>E</i> -resveratrol: 2.10–3.28 µg/g dw	Vilanova et al. (2015)
26	Grapes (<i>Vitis vinifera</i>) Cultivar: Negro Amaro	1. Material: fresh berries 2. Solvent: MeOH 3. Conditions: room temperature	UHPLC-QTOF-MS	<i>Non-infected, infected grapes</i> (µg/g fw) <i>E</i> -resveratrol: $1.83 \pm 0.15, 3.89 \pm 0.92$ Piceatannol: $0.65 \pm 0.08, 0.78 \pm 0.30$ <i>Z</i> -piceid: $0.78 \pm 0.57, 0.71 \pm 0.27$ <i>E</i> -piceid: $1.71 \pm 0.23, 0.92 \pm 0.23$ <i>E</i> -astringin: $1.08 \pm 0.01, 0.50 \pm 0.09$ <i>Z</i> -astringin: $0.05 \pm 0.01, 0.05 \pm 0.01$ Pallidol: $0.70 \pm 0.09, 0.59 \pm 0.25$ <i>Z</i> -ε-viniferin: $0.29 \pm 0.05, 0.25 \pm 0.02$ ω-viniferin: $0.88 \pm 0.23, 1.99 \pm 0.21$ <i>Z</i> -miyabenol C: $0.04 \pm 0.00, 0.05 \pm 0.02$ <i>E</i> -miyabenol C: $0.66 \pm 0.07, 1.46 \pm 0.60$ Ampelopsin H/vaticanol C/hopeaphenol/isohopeaphenol/vitisin A/B/C: $0.21 \pm 0.02, 0.57 \pm 0.02$	Flamini et al. (2016)

Table 1 continued

No.	Sample	Preparation conditions	Analytical method	Stilbenes: concentration (µg/g)	References
27	Grapes (<i>Vitis vinifera</i>) Cultivars: Corvina Raboso Piave	1. Material: fresh berries 2. Solvent: MeOH 3. Conditions: room temperature	UHPLC-QTOF-MS	<i>Raboso Piave: fresh, dried</i> (µg/g) α -viniferin: 0.79 ± 0.20 , 1.05 ± 0.27 Z-piceid: 4.00 ± 1.32 , 5.34 ± 1.76 <i>E</i> -astringin: 1.44 ± 0.30 , 1.91 ± 0.39 Pallidol-3-O-glucoside: 0.91 ± 0.26 , 1.21 ± 0.34 Piceatannol: 1.95 ± 0.14 , 2.59 ± 0.19 Pallidol: 1.02 ± 0.15 , 1.36 ± 0.21 Parthenocissin A: $0.56.0 \pm 0.05$, 0.57 ± 0.07 Z- ϵ -viniferin: 1.55 ± 0.22 , 2.07 ± 0.30 <i>E</i> - ϵ -viniferin: 5.80 ± 1.88 , 7.73 ± 2.50 δ -viniferins: 0.81 ± 0.30 , 1.08 ± 0.40 Z-miyabenol C: 0.61 ± 0.19 , 0.82 ± 0.25 <i>E</i> -miyabenol C: 5.51 ± 0.87 , 7.35 ± 1.16 <i>E</i> -piceid: 3.84 ± 1.00 , 5.13 ± 1.33 <i>E</i> -resveratrol: 4.93 ± 0.36 , 6.58 ± 0.48 Z-astringin: 0.13 ± 0.03 , 0.17 ± 0.04	De Rosso et al. (2016)
28	Grapes (<i>Vitis vinifera</i> L.) Cultivar: Crimson Seedless	1. Material: freeze-dried fresh grape skins 2. Solvent: Et ₂ O 3. Conditions: room temperature	HPLC-DAD	<i>After UV-C treatment</i> (µg/g fw) <i>E</i> -resveratrol: 121.62 Z-piceid: 61.22 <i>E</i> -piceid: 15.81 <i>E</i> -piceatannol: 14.7 ϵ -viniferin: 11.25 ω -viniferin: 5.8 Isohopeaphenol: 4.27 Stilbenoid: 234.67	Guerrero et al. (2016)

Table 1 continued

No.	Sample	Preparation conditions	Analytical method	Stilbenes: concentration (µg/g)	References
29	Grapes (<i>Vitis vinifera</i> L.) 28 grape interspecific hybrids 2 <i>Vitis vinifera</i>	1. Material: freeze-dried berries 2. Solvent: 80% MeOH/1% HCl 3. Conditions: room temperature	LC-PDA-QTOF-MS identification UPLC-PDA-FL determination	<i>E</i> -piceid: Rielsing: 71 µg/g dw Hibernal: 25 µg/g dw Muscat Odeski: 26 µg/g dw Biona: 19 µg/g dw	Samoticha et al. (2017)
30	Wild-type plants of <i>Vitis amurensis</i> Rupr.	1. Material: oven-dried fruits 2. Solvent: 96% EtOH 3. Conditions: 60 °C 4. Purification: C18 solid-phase extraction	HPLC-MS	<i>E</i> -piceid: 55 ± 12 µg/g dw <i>Z</i> -piceid: 127 ± 41 µg/g dw <i>E</i> -resveratrol: 14 ± 2 µg/g dw <i>Z</i> -ε-viniferin: 7 ± 5 µg/g dw <i>E</i> -ε-viniferin: 46 ± 5 µg/g dw <i>E</i> -δ-viniferin: nd	Kiselev et al. (2017)
31	Lingonberry (<i>Vaccinium vitis-idaea</i> L.) Cultivar: wild	<i>Method used for berries from US location</i> 1. Material: lyophilized berries 2. Solvent: MeOH/acetone/H ₂ O/CH ₃ COOH (40:40:20:0.1) 3. Conditions: 40 °C, 1000 psi 4. Purification: extraction with EtOAc 5. Derivatization: MSTFA/DFA/MeOH (3.5:1:0.5) <i>Method used for berries from Canada</i> 1. Material: frozen berries 2. Solvent: MeOH/acetone/H ₂ O/HCOOH (40:40:20:0.1) 3. Conditions: room temperature 4. Purification: C18 solid-phase extraction 5. Derivatization: MSTFA/DFA/MeOH (3.5:1:0.5)	GC-MS SIM	Resveratrol: 5.884 µg/g dw	Rimando and Cody (2005)
32	Passion fruit (<i>Passiflora edulis</i>) seeds	1. Material: freeze-dried fruit seeds 2. Solvent: 80% EtOH 3. Conditions: room temperature	HPLC-UV	Piceatannol: 85 400 µg/g dw Scirpusin B: 54 700 µg/g dw	Kawakami et al. (2014)

Table 1 continued

No.	Sample	Preparation conditions	Analytical method	Stilbenes: concentration (µg/g)	References
33	Tomato (<i>Lycopersicon esculentum</i> Mill.) Cultivars: MicroTom Beafsteak UglyRipe Heirloom PlumTom	1. Material: lyophilized tomato or grape skin 2. Solvent: EtOAc 3. Conditions: 70 °C 4. Derivatization: MSTFA/ pyridine	GC–MS	<i>MicroTom</i> Z-resveratrol: 2.71 µg/g dw <i>E</i> -resveratrol: 15.30 µg/g dw Z-piceid: 0.26 µg/g dw <i>E</i> -piceid: 0.10 µg/g dw <i>Beafsteak</i> nd <i>UglyRipe</i> <i>E</i> -resveratrol: 0.38 µg/g dw <i>Heirloom</i> Z-resveratrol: 0.11 µg/g dw <i>E</i> -resveratrol: 1.75 µg/g dw <i>PlumTom</i> <i>E</i> -resveratrol: 0.34 µg/g dw	Ragab et al. (2006)

nd not detected, fw fresh weight, dw dry weight

However, these studies only focused on berries at veraison and ripening. It is known that the biosynthesis and accumulation of stilbenes in berries after UV-C treatment depends on the developmental stages of fruits. From genomic analyses, it has been deduced that there are two main stages during grape development that are sensitive to UV-C irradiation (Pilati et al. 2007), namely, before and after veraison. “Before veraison” constitutes the restructuring phase of cell metabolism, characterized by an up-regulation of genes associated with hormone signalling and transcription. “After veraison” is characteristic of fruit ripening, whereas ‘veraison’ is characterized by an oxidative burst and antioxidant regulation. Therefore, it has been speculated that ‘veraison’ may be the most sensitive stage in which to apply UV-C treatment.

Under natural conditions, before veraison, the *E*-resveratrol content was very low in ‘Beihong’ (*V. vinifera* × *V. amurensis*) berries (Wang et al. 2015). From veraison to maturity, the *E*- and Z-piceid contents increased. UV-C treatment significantly stimulated the biosynthesis of *E*-resveratrol and *E*-piceid. The response of berries to UV-C irradiation

was also related to berry development. Among the six developmental stages, the stage at 55 DAA (days after anthesis, 2 weeks before veraison) was the most sensitive to UV-C treatment. The contents of *E*-resveratrol and *E*-piceid increased 292- and 11-fold, respectively (Table 2, no. 3). Along with developmental factors, the sensitivity of resveratrol synthesis to UV-C irradiation gradually declined, which may be associated with the regulation of *STS* by the *Myb14* promoter. *STS* expression was the highest when the berries were exposed to UV-C irradiation at 55 DAA, which may explain why resveratrol accumulated during this developmental stage. The expression of the *Myb14* promoter reached maximum levels 12 h before *STS*. These results suggest that *Myb14* expression may play an important role in the transcriptional regulation of resveratrol biosynthesis induced by UV-C irradiation.

Table 2 Influence of abiotic and biotic external stimuli on the presence of stilbenes in grapes

No	Sample	External stimuli	Conditions	Induction of stilbenes content by fold increase (↑) /decrease (↓) content	Ref.
Abiotic preharvest treatments of grape					
1	Crimson seedless table grapes (<i>Vitis vinifera</i> L.)	UV-C treatment	Light intensity: 31.1 W/m ² Dose: 9330 J/m ² Time: 5 min 3 days before harvest	<i>E</i> -resveratrol: 12 ↑ <i>Z</i> -piceid: 9 ↑ <i>E</i> -piceid: 5 ↑ <i>E</i> -piceatannol: 4 ↑ <i>ε</i> -viniferin: 7 ↑ <i>ω</i> -viniferin: 4 ↑ isohopeaphenol: 3 ↑ stilbenoids: 4 ↑	(Guerrero et al. 2016)
2	Redglobe table grapes (<i>Vitis vinifera</i> L.)	UV-C treatment	Treatment 5 day before harvest Treatment 3 day before harvest Treatment 1 day before harvest Power: 1040 W, time: 1 min Power: 1040 W, time: 5 min Power: 1040 W, time: 10 min Postharvest storage: 3 days, at 20°C, 80% RH Postharvest storage: 3 days, at 4°C, 60% RH	<i>E</i> -resveratrol: 22 ↑ <i>E</i> -resveratrol: 46 ↑ <i>E</i> -resveratrol: 26 ↑ <i>ε</i> -viniferin: 10 ↑ <i>ε</i> -viniferin: 30 ↑ <i>ε</i> -viniferin: 20 ↑ <i>E</i> -resveratrol: 14.4 ↑ <i>ε</i> -viniferin: 3.4 ↑ <i>E</i> -resveratrol: 4 ↑ <i>ε</i> -viniferin: 0.3 ↑	(Guerrero et al. 2015)
3	Beihong grapes (<i>Vitis vinifera</i> × <i>Vitis amurensis</i>)	UV-C treatment at different development stages (days after anthesis – DAA)	55 DAA 126 DAA Illumination power: 6 W/m ² Distance: 15 cm Time: 10 min Temperature: 25°C in the dark Storage conditions: at 25°C in the dark, time: 0–72 h	<i>E</i> -resveratrol: 292 ↑ <i>E</i> -piceid: 11 ↑ <i>E</i> -resveratrol: 6.9 ↑ <i>E</i> -piceid: nd ↑	(Wang et al. 2015)
Abiotic postharvest treatments of grape					
4	Grape varieties: 3 <i>Vitis vinifera</i> sylvestris, 7 <i>Vitis vinifera</i> sativa, 2 Hybrid Direct Producers	UV-C treatment	Power: 500 W Distance: 42 cm Time: 60 s Light intensity: 14.72 mW/cm ² <u>Storage conditions:</u> at 18°C, 75% RH for 7 days	<u>Merlot:</u> <i>E</i> -resveratrol: 2.5 ↑ piceatannol: 4.3 ↑ viniferins: 7.2 ↑ <u>Syrah:</u> <i>E</i> -resveratrol: 4.5 ↑ piceatannol: 0.5 ↓ viniferins: nd ↑ <u>Tempranillo:</u> <i>E</i> -resveratrol: 11.2 ↑ piceatannol: nd ↑ viniferins: 7.5 ↑	(Guerrero et al. 2010a)
5	White/black grapes (<i>Vitis vinifera</i> L.)	UV-C treatment	Time: 10 min Dose: 0.36 J/cm Storage time: 48 h	<u>Gamay:</u> <i>E</i> -piceid: 0.3 ↓ <i>Z</i> -piceid: 0.1 ↑ <i>E</i> -resveratrol: 19 ↑ <i>ε</i> -viniferin: 2.6 ↑ pterostilbene: 0.5 ↑ <u>Chardonnay:</u> <i>E</i> -piceid: 0.1 ↓ <i>Z</i> -piceid: 0.4 ↓ <i>E</i> -resveratrol: 1.2 ↑ <i>ε</i> -viniferin: 4.1 ↑ pterostilbene: 100 ↑	(Adrian et al. 2000)
6	Napoleon table grapes (<i>Vitis vinifera</i> L.)	UV-C treatment	Distance: 20–60 cm Temperature: 25°C Treatment time and power: 5 s, 30 W 5 s, 90 W 5 s, 240 W 5 s, 510 W 30 s, 30 W 30 s, 90 W 30 s, 240 W 60 s, 510 W 60 s, 30 W	Resveratrol: 0.2 ↑ 1.5 ↑ 3.5 ↑ 8.4 ↑ 0.6 ↑ 8 ↑ 9.2 ↑ 10.5 ↑ 3.4 ↑ 9.4 ↑	(Cantos et al. 2001)

Table 2 continued

			60 s, 90 W 60 s, 240 W 60 s, 510 W 300 s, 30 W 300 s, 90 W 300 s, 240 W 300 s, 510 W	10 ↑ 10.5 ↑ 5 ↑ 9.4 ↑ 8 ↑ 6.5 ↑	
7	Redglobe table grape (<i>Vitis vinifera</i> L.)	UV-C treatment	Dose: 0.8, 2.4, 4.1 kJ/m ² Distance: 40 cm Treatment time: 3 min, storage time: 48 h at 4°C Treatment time: 3 min, storage time: 48 h at 25°C	<i>E</i> -piceid: 1.2 ↑ <i>Z</i> -piceid: 2.6 ↑ <i>E</i> -piceid: 0.1 ↑ <i>Z</i> -piceid: 0.5 ↑	(Crupi et al. 2013)
8	Red grapes (<i>Vitis vinifera</i> L.): Syrah, Merlot, Cabernet sauvignon, Pinot noir	UV-C treatment	Power: 1020 W Distance: 42 cm Time: 60 s <u>Storage conditions:</u> at 20°C for 7 days, 80% RH	<u>Syrah, terroir Jerez:</u> resveratrol: 2.7 ↑ piceatannol: 6.1 ↑ viniferin: 1.6 ↑ total stilbenes: 3.1 ↑ <u>Syrah, terroir Cabra:</u> resveratrol: 1.1 ↑ piceatannol: 3.5 ↑ viniferin: 2 ↑ total stilbenes: 1.5 ↑	(Fernández-Marin et al. 2013)
9	Pinot Noir (<i>Vitis vinifera</i> L.)	UV-C treatment	Distance: 50 cm Light intensity: 0.25 μW/cm ² Time: 1 h <u>Storage conditions:</u> 23 h in the dark at 25°C	<i>E</i> -resveratrol: 355 ↑ <i>ε</i> -viniferin: 4.8 ↑ piceid: 2.4 ↑ <i>Z</i> -resveratrol: 0.7 ↑	(Suzuki et al. 2015)
10	Red Globe grapes (<i>Vitis vinifera</i> L.)	UV treatment 302.1 nm resonant wavelength (R) 300.0 nm non-resonant wavelength (NR)	<u>Storage conditions:</u> 4°C during 4 weeks Treatment time: 30 min: R Treatment time: 30 min: NR Treatment time: 45 min: R Treatment time: 45 min: NR Treatment time: 60 min: R Treatment time: 60 min: NR	<i>E</i> -resveratrol: 0.8 ↑ 0.3 ↓ 6.2 ↑ 0.1 ↑ 0.4 ↓ =	(Jiménez Sánchez et al. 2007)
11	Crimson red table grapes (<i>Vitis labrusca</i>)	UV-C treatment and 0.5%/1% chitosan coating (CHT)	Light intensity: 2.82 mW/cm ² Distance: 60 cm Temperature: 10°C Treatment with UV-C: Treatment with UV-C and storage 20°C/24 h: Treatment with CHT 0.5%: Treatment with UV-C, CHT 0.5%, storage 5 days: Treatment with UV-C, CHT 0.5%, storage 20°C/24 h, 5 days: Treatment with UV-C, CHT 0.5%, storage 8 days: Treatment with UV-C, CHT 0.5%, storage 20°C/24 h, 8 days:	<i>E</i> -resveratrol: 0.4 ↑ 3 ↑ = 2 ↑ 4.9 ↑ 2.9 ↑ 3.7 ↑	(Freitas et al. 2015)
12	Beihong (<i>Vitis vinifera</i> × <i>V. amurensis</i>) Hongbaladuo	Treatment with UV and CaCl ₂	Light intensity: 6 W/m ² Distance: 15 cm Time: 10 min <u>Storage conditions:</u> at 25°C in the dark for 24 h, then at -1°C for 27 days, RH 95% Treatment with CaCl ₂ : Treatment with UV-C: Treatment with UV-C and CaCl ₂ :	<i>E</i> -resveratrol: 0.5 ↑ <i>E</i> -piceid: = <i>Z</i> -piceid: 0.2 ↓ <i>E</i> -resveratrol: 11 ↑ <i>E</i> -piceid: 0.8 ↑ <i>Z</i> -piceid: 0.6 ↓ <i>E</i> -resveratrol: 16.7 ↑ <i>E</i> -piceid: 0.6 ↑ <i>Z</i> -piceid: 1.4 ↓	(Wang et al. 2013)
13	Campbell Early grapes (<i>Vitis labrusca</i> × <i>V. vinifera</i>)	Ultrasonication treatment (40 kHz)	Temperature storage: 25°C Treatment time 5 min: Treatment time 10 min: Treatment time 15 min: Treatment time 5 min, 6 h storage: Treatment time 10 min, 6 h storage: Treatment time 15 min, 6 h storage: Treatment time 5 min, 12 h storage:	<i>E</i> -resveratrol: 1.3 ↑ 1.3 ↑ 0.8 ↑ 6.7 ↑ 0.3 ↑ = =	(Hasan and Baek 2013)

Table 2 continued

			Treatment time 10 min, 12 h storage: Treatment time 15 min, 12 h storage:	2 ↑ 0.2 ↑ 0.3 ↑	
14	Superior Seedless (<i>Vitis vinifera</i> L.) Regina Victoria (<i>Vitis vinifera</i> L.) Cardinal CL80° (<i>Vitis vinifera</i> L.)	Ozone treatment	<u>Storage conditions:</u> 5°C for 0, 15, 30, 56, 72 days Air, continuous 2 ppm O ₃ : Air, intermittent 2 ppm O ₃ , 12 h/day: Air, continuous 2 ppm O ₃ : Air, intermittent 2 ppm O ₃ , 12 h/day: Air, continuous 2 ppm O ₃ : Air, intermittent 2 ppm O ₃ , 12 h/day:	Resveratrol: <u>Superior Seedless</u> 0.3 ↓ 0.2 ↑ <u>Cardinal CL80</u> = 0.5 ↑ <u>Regina Victoria</u> 1 ↓ 0.6 ↑	(Cayuela et al. 2010)
15	Table grape Napoleon (<i>Vitis vinifera</i> L.)	Ozone treatment	8 ppm O ₃ , storage 38 days at 0°C: 8 ppm O ₃ , storage 6 days at 15°C:	<u>E-piceid</u> : 11 ↑ <u>E-resveratrol</u> : 2.5 ↑ <u>stilbenoids</u> : 0.6 ↑ <u>E-piceid</u> : 4.5 ↑ <u>E-resveratrol</u> : 3.1 ↑ <u>stilbenoids</u> : 3.6 ↑	(Artés-Hernández et al. 2003)
16	Campbell Early (<i>Vitis labrusca</i>) Kyoho grapes (<i>Vitis labruscana</i> Bailey)	Treatments with: white fluorescent light (FL) 380 nm purple LED 440 nm blue LED 660 nm red LED	Time: 48 h, at 25°C Storage conditions: 0–24 h at 25°C Treatment with FL: Treatment with 380 nm: Treatment with 440 nm: Treatment with 660 nm:	<u>Campbell Early</u> <u>E-resveratrol</u> : 1.8 ↑ <u>Z-resveratrol</u> : = <u>piceatannol</u> : 0.6 ↑ <u>E-piceid</u> : 0.1 ↑ <u>Z-piceid</u> : = <u>E-resveratrol</u> : 2.8 ↑ <u>Z-resveratrol</u> : = <u>piceatannol</u> : 0.4 ↑ <u>E-piceid</u> : 0.4 ↑ <u>Z-piceid</u> : = <u>E-resveratrol</u> : 7.4 ↑ <u>Z-resveratrol</u> : = <u>Piceatannol</u> : 4.6 ↑ <u>E-piceid</u> : 1.1 ↑ <u>Z-piceid</u> : 3 ↑ <u>E-resveratrol</u> : 6.2 ↑ <u>Z-resveratrol</u> : = <u>piceatannol</u> : 3 ↑ <u>E-piceid</u> : 0.5 ↑ <u>Z-piceid</u> : =	(Ahn et al. 2015)
17	White grapes (<i>Vitis vinifera</i>) Aledo variety	Dry nitrogen treatment	Time: 24 h	<u>E-resveratrol</u> : 2 ↑	(Jiménez et al. 2007)
18	Corvina grapes (<i>Vitis vinifera</i> L.) Raboso Piave (<i>Vitis vinifera</i> L.)	Withering process (dehydration process)	18°C, 40% RH, 30 days and 60 days	<u>Raboso Piave</u> : <u>α-viniferin</u> : 0.7 ↑ <u>Z-piceid</u> : 0.7 ↑ <u>E-astringin</u> : 0.7 ↑ <u>pallidol-3-O-glucoside</u> : 0.7 ↑ <u>piceatannol</u> : 0.7 ↑ <u>pallidol</u> : 0.7 ↑ <u>Z-ε-viniferin</u> : 0.7 ↑ <u>E-ε-viniferin</u> : 0.7 ↑ <u>δ-viniferins</u> : 0.7 ↑ <u>Z-miyabenol C</u> : 0.7 ↑ <u>E-miyabenol C</u> : 0.7 ↑ <u>E-piceid</u> : 0.7 ↑ <u>E-resveratrol</u> : 0.7 ↑ <u>Z-astringin</u> : 0.6 ↑	(De Rosso et al. 2016)
Combined abiotic pre- and postharvest treatments of grape					
19	Syrah red grapes (<i>Vitis vinifera</i> L.)	1) Preharvest methyl jasmonate (MEJA) treatment, 2) Postharvest UV-C treatment, 3) Preharvest methyl jasmonate/postharvest UV-C treatment (MEJA-UV-C)	Power: 1020 W Distance: 42 cm Time: 60 s Storage conditions: at 20°C for 4 days, 80% RH 1) Preharvest treatment with MEJA:	<u>2 days after treatment</u> : <u>E-resveratrol</u> : 0.5 ↑ <u>piceatannol</u> : 0.4 ↑ <u>isorhapontigenin</u> : nd ↑	(Fernández-Marín et al. 2014)

Table 2 continued

			<p>2) Postharvest treatment with UV-C:</p> <p>3) Treatment with MEJA (preharvest) and UV-C (postharvest):</p>	<p><i>ε</i>-viniferin: nd <u>4 days after treatment:</u> <i>E</i>-resveratrol: 0.5 ↑ piceatannol: 0.8 ↑ isorphapontigenin: 0.5 ↑ <i>ε</i>-viniferin: 1 ↑ <u>at harvest:</u> <i>E</i>-resveratrol: 1 ↑ piceatannol: nd ↑ isorphapontigenin: nd <i>ε</i>-viniferin: nd</p> <p><u>2 days after treatment:</u> <i>E</i>-resveratrol: = piceatannol: = isorphapontigenin: nd <i>ε</i>-viniferin: nd</p> <p><u>4 days after treatment:</u> <i>E</i>-resveratrol: 0.5 ↑ piceatannol: 0.4 ↑ isorphapontigenin: 0.7 ↑ <i>ε</i>-viniferin: 0.4 ↑</p> <p><u>2 days after treatment:</u> <i>E</i>-resveratrol: 0.6 ↑ piceatannol: 0.3 ↑ isorphapontigenin: nd ↑ <i>ε</i>-viniferin: nd</p> <p><u>4 days after treatment:</u> <i>E</i>-resveratrol: 2 ↑ piceatannol: 1.7 ↑ isorphapontigenin: 1.8 ↑ <i>ε</i>-viniferin: 1.7 ↑</p>	
20	Autumn Black grapes (<i>Vitis vinifera</i> L.) B36-55 (<i>Vitis vinifera</i> L.)	1) Preharvest treatment with chitosan 2) Postharvest treatment with UV-C 3) Postharvest treatment with UV-C/chitosan	Dose: 0.36 J/cm ² Time: 10 min Distance: 10 cm Storage conditions: 48 h at 20°C, RH 95-98% Preharvest treatment with chitosan Postharvest treatment with UV-C Postharvest treatment with UV-C/chitosan	<i>E</i> -resveratrol in B36-55: = 8.8 ↑ 11 ↑	(Romanazzi et al. 2006)
Biotic postharvest treatments of grape					
21	Palomino fino grapes (<i>Vitis vinifera</i> L.)	Infection with <i>Botrytis cinerea</i>	Infection degree 50%: Infection degree 75%: Infection degree 100%:	resveratrol: 1.3 ↓ piceid: 1.3 ↑ resveratrol: 0.2 ↑ piceid: 2.6 ↑ resveratrol: 0.4 ↑ piceid: 3.5 ↑	(Roldán et al. 2003)
22	Negro Amaro grapes (<i>Vitis vinifera</i> L.)	Infection with <i>A. carbonarius</i>	at 20 °C for 5 days	<i>E</i> -resveratrol: 1.1 ↑ piceatannol: 0.2 ↑ Z-piceid: 0.1 ↓ <i>E</i> -piceid: 0.9 ↓ <i>E</i> -astringin: 1.2 ↓ Z-astringin: = pallidol: 0.2 ↓ Z- <i>ε</i> -viniferin: 0.2 ↓ ω-viniferin: 1.3 ↑ <i>E</i> - <i>ε</i> -viniferin: 1.7 ↑ δ-viniferin: 1 ↑ caraphenol: 0.9 ↑ pallaidol glucoside: 0.3 ↑ α-viniferin: 1.5 ↑ Z-miyabenol C: 0.3 ↑ <i>E</i> -miyabenol C: 1.2 ↑ ampelopsin H/vaticanol C/hopeaphenol/isohopeaphenol l/vitisin A/B/C: 1.7 ↑	(Flamini et al. 2016)
Combined abiotic and biotic postharvest treatments of grape					
23	Napoleon table grape (<i>Vitis vinifera</i> L.)	UV-C treatment and fungal infection with ochratoxigenic <i>Aspergillus</i>	Illumination power: 50 W/m ² Distance: 40 cm Time: 60 s Temperature: 15°C Storage condition: at 22°C Undamaged grape:		(Selma et al. 2008)

Table 2 continued

			treatment with UV-C, infection, storage 5 days:	<i>E</i> -resveratrol: 6 ↑ <i>E</i> -piceid: 1 ↓	
			treatment with infection, UV-C, storage 5 days:	<i>E</i> -resveratrol: 7 ↑ <i>E</i> -piceid: =	
			<u>Damaged grape:</u> treatment with UV-C, infection, storage 5 days:	<i>E</i> -resveratrol: 6 ↑ <i>E</i> -piceid: 1 ↑	
			treatment with infection, UV-C, storage 5 days:	<i>E</i> -resveratrol: 4 ↑ <i>E</i> -piceid: 0.5 ↑	

nd: not detected

= no changes, ↑ increase, ↓ decrease

Abiotic postharvest treatments of grape

Postharvest treatment with UV-C light has been proposed as a valuable method to increase the stilbenes content in the grape berries (Langcake and Pryce 1977; Douillet-Breuil et al. 1999; Versari et al. 2001; Petit et al. 2009; Yin et al. 2016).

Postharvest treatment of grape varieties with UV-C resulted in higher concentrations of stilbenes, such as *E*-resveratrol, piceatannol, viniferins and pterostilbene (Table 2, no. 4, 5) (Adrian et al. 2000; Guerrero et al. 2010a). Differences in concentration after UV-C irradiation depended on the variety and campaign, but not on the grape subspecies. Each variety seemed to be influenced to a different degree by the climate. Thus, the same variety behaved in a different way in each campaign, and climate could determine the final concentration of stilbenes.

The highest accumulation of resveratrol (tenfold) in irradiated Napoleon grapes was achieved using the following combination of parameters: irradiation power, 510 W; irradiation time, 30 or 60 s; irradiation distance, 40 cm; and elapsed days, 3 (Table 2, no. 6). Therefore, controlled UV irradiation parameters are useful as a simple postharvest treatment to increase the resveratrol concentration in Napoleon grapes (Cantos et al. 2001).

To achieve the highest possible stilbene accumulation, the interactive effects of storage time, temperature and UV-C irradiation on the stilbene content in postharvest Red globe table grapes were investigated (Table 2, no. 7) (Crupi et al. 2013). During storage, both cold storage and UV-C doses of 3 min raised the contents of *Z*- and *E*-piceid, achieving 90 and 34 µg/g

in skin, respectively, which was approximately three-fold higher than those in control berry samples. Similar results were found in Napoleon table grapes (Cantos et al. 2001). Cold storage in combination with UV irradiation increased the piceid concentration more than cold storage alone. Also Cho et al. (2012) reported that it is possible to enrich resveratrol content in harvested grapes by modulating cell metabolism with UV treatment and storage conditions. Storage temperature had an effect on time-delayed resveratrol biosynthesis after removal of the UV irradiation. A larger amount of resveratrol was formed when UV-treated grapes were stored at higher temperature.

After UV-C postharvest irradiation, all of the red grape varieties in each terroir increased their resveratrol, piceatannol and viniferin contents (Table 2, no. 8) (Fernández-Marín et al. 2013). The stilbene content was different depending on the variety and the terroir. Cabra was the terroir where the varieties achieved the highest induction capacity (2.02 µg/g per day after UV-C irradiation), especially the Syrah variety. This is in agreement with previous research in which Syrah increased its stilbene content more than the other thirteen varieties studied (Guerrero et al. 2010a). However, the highest increase in the resveratrol and piceatannol contents in the Syrah variety was from the Jerez terroir, which amounted to 2.7 and 6.1 times, respectively, in comparison to those in the untreated berries.

With regard to piceatannol and viniferins, higher concentrations were found in varieties that achieved higher resveratrol levels because resveratrol has been proposed as the precursor of the other stilbenes (Coutos-Thévenot et al. 2001). Thus, it could be

concluded that resveratrol determines the tendency for the synthesis of other stilbenes and the amount of total stilbenes.

Moreover, varieties reached the highest level of resveratrol induction in different periods of time depending on the terroir. The day of maximum concentration (dm) was constant for Cabernet sauvignon (dm = 7). Pinot noir showed the same dm in all terroirs (dm = 6), except for Cadiar, where it was delayed 1 day (dm = 7). However, in Syrah and Merlot varieties, the dm changed depending on the terroir, ranging from 4 to 7 days.

Treatment of the postharvested Pinot Noir grape berries with UV-C irradiation increased the *E*-resveratrol, ϵ -viniferin, piceid and *Z*-resveratrol contents 355, 4.8, 2.4 and 0.7 times, respectively, in comparison with those in the control sample (Table 2, no. 9) (Suzuki et al. 2015). Transcriptome analysis revealed that 238 genes were up-regulated more than fivefold in grape berry skin by UV-C treatment. Enrichment analysis of the gene ontology terms showed that genes encoding stilbene synthase were enriched in the up-regulated genes.

Two different wavelengths were used for the UV treatment of red grapes: 302.1 nm for the resonant wavelength and 300.0 nm for the non-resonant wavelength (Table 2, no. 10) (Jiménez Sánchez et al. 2007). Four sets of irradiation times were selected for each of the two different wavelengths: 15, 30, 45 and 60 min. The use of photons of resonant energy to produce absorption through the real electronic states of the molecule significantly increased the absorption yield, producing an important effect on the photoinduced *E*-resveratrol level in the grapes. The enhancement was optimal for 45 min of irradiation at 302.1 nm. The samples were prepared for analysis immediately after irradiation to detect the direct effect of resonant elicitation.

The combination of UV-C treatment with a chitosan coating and incubation was investigated (Table 2, no. 11) (Freitas et al. 2015). The concentration of *E*-resveratrol in red table grapes with a 0.5% chitosan coating treated with UV-C irradiation, incubated at 20 °C and then stored for 5 days under refrigeration was approximately 5 and 2.5 times higher than that in control and UV-C treated grapes with a 0.5% chitosan coating, respectively. After 8 days of storage at 4 °C, treated berries also showed a 2.9 times

higher content of *E*-resveratrol and lower susceptibility to fungal decay than control grapes.

The individual and combined effects of CaCl₂ and ultraviolet light on the biosynthesis of resveratrol in berry skins were investigated (Table 2, no. 12) (Wang et al. 2013). CaCl₂ application had no effect on the *E*-piceid content and little influence on the *Z*-piceid content, but it resulted in a 0.5 times higher content of *E*-resveratrol compared with that in the control sample. UV-C and UV-C irradiation with CaCl₂ treatment increased *E*-resveratrol and *E*-piceid biosynthesis and accumulation in berry skins. This accumulation continued until 13 days after cold storage. Then, the *E*-resveratrol content slightly decreased but still remained at high levels at the end of storage, while the *E*-piceid content increased continuously until the end of storage. In contrast, the *Z*-piceid content after UV-C and UV-C/CaCl₂ treatments decreased by 0.6 and 1.4 times, respectively, compared with that in the control sample.

UV-C and UV-C/CaCl₂ treatments significantly stimulated the expression of *PAL*, *C4H*, *4CL* and *STS*, which are related to the biosynthesis of *E*-resveratrol. Moreover, the expression levels of these genes in the UV-C/CaCl₂ combination treatment were higher than those in the UV-C irradiation treatment. The expression of *PAL*, *C4H*, *4CL*, and *STS* in both treatments reached a maximal content at 12 h after initiating the treatment and then declined rapidly to approach the control level at the end of the experiment. CaCl₂ treatment alone did not modify the expression of any of these genes (Wang et al. 2013).

Increased accumulation of *E*-resveratrol in grape skin by ultrasonication treatment has also been investigated (Table 2, no. 13) (Hasan and Baek 2013). A significantly higher amount of *E*-resveratrol over that in the control sample was observed following ultrasonication treatment. Ultrasonic treatment for 5 min followed by 6 h of incubation induced the highest levels of *E*-resveratrol, with amounted to a level that was 6.7 times higher than that in the control sample. However, the treatment did not lead to an increase in the maintenance of the level of *E*-resveratrol. When the amount of *E*-resveratrol was measured again in fruits incubated for another 6 h, it had decreased drastically to the level in samples treated by 5 min of ultrasonication without any incubation.

In grape skin, the expression levels of resveratrol synthase increased directly in response to 5 min of ultrasonication treatment and were then maintained during 12 h of incubation. This suggests that the accumulation of *E*-resveratrol in grape in response to ultrasonication occurs in a time-dependent manner based on the induction of the resveratrol synthase gene.

Ozone was also found to stimulate the synthesis of stilbenes in grape berries (Sarig et al. 1996; Palou et al. 2002). Continued and intermittent ozone treatments (2 ppm) were applied during the storage of 3 varieties of table grapes at 5 °C for 72 days (Table 2, no. 14) (Cayuela et al. 2010). The continuous presence of ozone in the storage atmosphere inhibited the biosynthesis of resveratrol, whereas intermittent treatment with O₃ stimulated its biosynthesis. It was found that the treatment consisting of intermittent shocks of 8 ppm O₃ had the strongest influence on table grapes (Artés-Hernández et al. 2003). It was also found that the grapes stored in an atmosphere containing 0.1 ppm O₃ exhibited higher concentrations of resveratrol than those kept in air. Mild ozone treatments, such as those using ozonized water, which are effective in the control of microbial growth, did not induce stilbenoid accumulation in grapes (Gonzalez Ureña et al. 2003). Continuous exposure of the berries to a high concentration of O₃ could reduce the content of antioxidant compounds such as resveratrol produced by the plant as a defensive metabolite against oxidative stress.

The influence of the combination of ozone and UV-treatment on stilbenes content was also investigated (González-Barrio et al. 2006). The results showed that UV-C was generally much more efficient (shorter treatment time) in inducing resveratrol content than ozone. However, with regard to total stilbenoids accumulated in the grape skin, the ozone treatment with the highest concentration and the longest time led to higher stilbenoid content than the UV-C irradiation. Also the viniferin content accumulated was threefold higher than that induced by the UV-C treatment. However, UV-C light treatment resulted in less damage to grape tissues than ozone gas.

Different gaseous treatments have been applied because of their efficacy in ensuring the quality of Napoleon table grapes (Table 2, no. 15) (Artés-Hernández et al. 2003). The *E*-resveratrol content increased up to threefold its value sampled at harvest in O₃ shock-treated clusters and up to twofold for other

treatments, probably because these treatments induced a faster biosynthesis of this compound. The increases were more marked when clusters were stored at 15 °C, which is in agreement with previous reports, where control and UV-treated cv. Napoleon table grapes increased their resveratrol content after the grapes were transferred to 15 °C (Cantos et al. 2000). However, O₃-treated clusters that underwent shock treatment increased their *E*-piceid content by 11 and 4.5 times compared to that sampled at harvest.

The accumulation of stilbenes and the expression of genes related to their synthesis in ‘Campbell Early’ and ‘Kyoho’ grapes were investigated by irradiating the harvested grapes with four different light sources for 48 h (Table 2, no. 16) (Ahn et al. 2015). The total concentrations of five stilbene derivatives at 24 h after irradiation differed in response to different light sources and cultivars. The accumulation of stilbenes in the skins of two grape cultivars and the expression of *PAL* and *STS1* genes were induced under mainly red and blue LED light. The amount of stilbenes tended to be higher in blue and red light-treated grapes than in the grape berries treated with white fluorescent or purple light. Among the stilbenes tested, *E*-resveratrol was present in ‘Campbell Early’ berries treated with blue, red, purple and fluorescent light at levels 7.4-, 6.2-, 2.8- and 1.8-fold higher than the levels in the control sample, respectively. The expression of *PAL*, *CHS*, *CHI*, *STS1*, *STS12* and *ROMT* genes was differently induced in response to irradiation with different light sources in both grape cultivars. The mRNA levels of *PAL* and *STS1* were higher than those of *CHS*, *CHI*, *STS12* and *ROMT* in the two grape berries. The results indicated that red and blue LEDs induced the accumulation of stilbenes and the expression of genes related to their syntheses in grape berries.

Accumulation of *E*-resveratrol in post-harvested grapes by dry nitrogen treatment was also investigated (Table 2, no. 17) (Jiménez et al. 2007). *E*-resveratrol content in the grape berries increased with the duration of the dry nitrogen treatment up to 24 h (twofold). For longer treatment, only a slight enhancement was observed. However, shorter treatments kept higher content of *E*-resveratrol during several days with no appreciable damage of the grape berries regarding to their organoleptic quality.

It was also observed that storage conditions influence the stilbene concentration (Table 2, no. 18).

Grapes stored under mild conditions (20 °C) favoured *E*-resveratrol synthesis, whereas cold storage (4 °C) decreased its concentration. Cold storage apparently inhibited *E*-resveratrol synthesis after harvest, and its concentration slowly decreased. This may be explained by the action of peroxidase enzymes and the subsequent formation of ϵ -viniferin. In non-UV-C irradiated grapes, the *E*-resveratrol content increased by nearly 14 times when after 3 days of storage at low temperature, the grapes were stored under mild storage conditions.

After 60 days of withering, Raboso Piave and Corvina grape samples showed an evident increase in the content of most stilbenes (Table 2, no. 18) (De Rosso et al. 2016). Raboso Piave had a statistically significant increase in *E*-resveratrol, pallidol, and *E*- ϵ -viniferin. In Corvina grape, *E*-resveratrol, piceatannol, *E*-astringin, *E*-piceid, pallidol, pallidol glucoside, *E*-miyabenol C, and ϵ -viniferin increased significantly. In general, these findings are in agreement with those reported in a study of Aleatico grape withering (Mencarelli et al. 2010).

Combined abiotic pre- and postharvest treatments of grape

Preharvest red grapes (Syrah *Vitis vinifera* L.) treated with methyl jasmonate (MEJA) showed a significant increase in *E*-resveratrol and piceatannol contents compared to those in the control sample (piceatannol not detected) (Table 2, no. 19) (Fernández-Marín et al. 2014). The highest concentrations of piceatannol and *E*-resveratrol were found at harvest. Larronde et al. (2003) described an *E*-resveratrol increase (ninefold) in Cabernet sauvignon berries when treated with MEJA vapours 15 days after veraison. However, berries rapidly lose the capacity to respond to MEJA with ripening. Vezzulli et al. (2007) found that MEJA treatment of the Barbera grape variety improved the *E*-resveratrol and ϵ -viniferin contents in an accumulative manner. Thus, it seems that there is an effect of MEJA on the stilbene concentration in grapes.

Harvested red grapes were treated with UV-C irradiation and stored for 4 days (Table 2, no. 19) (Fernández-Marín et al. 2014). On the 4th day, control red grapes showed a significantly lower *E*-resveratrol content than grapes treated with UV-C, and UV-C samples a lower *E*-resveratrol content than MEJA

samples, whereas MEJA-UV-C achieved the highest *E*-resveratrol content. In fact, UV-C irradiation has been described as a stronger stress than MEJA, causing higher *E*-resveratrol induction in grape, but a longer grape storage period was required (Fernández-Marín et al. 2012).

The accumulation of piceatannol, isorhapontigenin, and ϵ -viniferin were also induced (Table 2, no. 19). At harvest, piceatannol was found in MEJA grapes, but it was absent in control samples. After 2 days of storage, piceatannol was found in every batch, and isorhapontigenin was found in the MEJA and MEJA-UV-C batches in concentrations that were not significantly different. The trend of these stilbenes was similar to that of *E*-resveratrol. The control batch showed the lowest concentration, in contrast to MEJA-UV-C, which showed the highest concentration after 4 days of storage.

The effectiveness of the chitosan treatment of table grapes (Autumn Black and B36-55 variety) in combination with UV-C irradiation to determine the *E*-resveratrol concentration in grape berry skins was investigated (Table 2, no. 20) (Romanazzi et al. 2006). Grape berries were sprayed in the vineyard with 1% chitosan and then harvested daily for 5 days. Immediately after harvest, they were inoculated with *B. cinerea*. In cv. Autumn Black and selection B36-55, *E*-resveratrol was not detected in control berries or berries with a chitosan coating. In berries exposed to UV-C irradiation alone and in berries treated with 1% chitosan coating and later exposed UV-C, *E*-resveratrol was found. The berries treated with the combination of chitosan and UV-C irradiation contained approximately 11 times more *E*-resveratrol than the control grapes and 0.2 times more than those only irradiated with UV-C. Z-Resveratrol, *E*-piceid, and Z-piceid were not detected in any of the samples.

Biotic postharvest treatments of grape

Infection of the postharvested *Palomino fino* grapes with *Botrytis cinerea* led to a domination of piceid over resveratrol (Table 2, no. 21) (Roldán et al. 2003). At the early stage of fungal development, the content of piceid increased more than onefold in fruits over that in the control sample, while the level of resveratrol decreased more than onefold. At more advanced infection stages, the piceid and resveratrol contents

increased 3.5-fold and 0.4-fold, respectively. According to the literature, resveratrol synthesis occurs in the skin of edible berries (Sotheeswaran and Pasupathy 1993). Thus, an accumulation of resveratrol in the skin after infection by *B. cinerea* could be expected. However, the results showed that even at the early stage of pathogen development, a sharp decrease in the resveratrol content occurred. This could be because before pathogen exposure, resveratrol synthesis is stimulated. The resveratrol already present in the skin is used by the fruit as part of its defence mechanism. This phytoalexin would become a building block of stilbenes such as ϵ - and δ -viniferins, which are more toxic to the pathogen. For this reason, the piceid and resveratrol contents decreased. In the second stage of pathogen development, an accumulation of resveratrol occurred until a certain level was reached, and it was maintained during external stress. These results are in accordance with the literature, which showed that in grape berry skins infected by powdery mildew, the resveratrol and piceid isomers were considerably increased and the degree of infection was positively related to their stilbene content (Romero et al. 2001).

Infection with *Aspergillus carbonarius* at ripening induced in the grapes an approximately onefold increase in *E*-resveratrol and resveratrol dimers, such as ω -viniferin, *E*- ϵ -viniferin, caraphenol and δ -viniferin, and resveratrol trimers, such as α -viniferin and *E*-miyabenol C (Table 2, no. 22) (Flamini et al. 2016). However, infection with this pathogen decreased the *E*-piceid and *E*-astringin concentrations by approximately onefold in grapes. The total stilbene content in grapes infected with *A. carbonarius* increased 60% over that in uninfected berries. Glycosylation of stilbenes is involved in storage, transport from the cytoplasm to the apoplasm and protection from peroxidative degradation. Subsequent storage in vacuoles may protect plant cells from potentially their toxic effects. In susceptible cultivars, such as Gamay, Gamaret, Pinot Noir and Chasselas, resveratrol was found to be either glycosylated or present in very low concentrations (Pezet et al. 2004). Studies of grapevine varieties resistant to *P. viticola* reported that *E*-resveratrol is probably rapidly oxidized into toxic stilbenes, such as ϵ - and δ -viniferins, while in susceptible cultivars, it is rapidly glycosylated into less toxic piceid (Pezet et al. 2004). In the case of infected Negro Amaro grape, the content of *E*-resveratrol increased, but the content of glycosylated

stilbenes decreased, which confirms the low susceptibility of this cultivar against *A. carbonarius* infection.

In the research conducted by Bavaresco et al. (2003) the influence of fungal infection with *A. japonicus*, *A. ochraceus*, *A. fumigatus* and *A. carbonarius* on the stilbenes content in the grape berries was examined. All tested fungi, except *A. fumigatus*, significantly increased *E*-resveratrol concentration over the control sample, while *E*-piceid content was not affected. Among tested fungi, only *A. ochraceus* significantly elicited the grape berries to synthesize piceatannol.

Combined abiotic and biotic postharvest treatments of grape

In another study, phenyl propanoid metabolism induction by abiotic (UV-C) and biotic elicitors (fungal infection—ochratoxigenic *Aspergillus*) in undamaged and damaged Napoleon table grapes was investigated (Table 2, no. 23) (Selma et al. 2008). In addition, the effect of the sequence of elicitors on the content of stilbenes and storage time was analysed. The contents of *E*-resveratrol in non-inoculated and inoculated grapes were similar and maintained at the same level during 5 days of storage. Treatment of undamaged or damaged grapes with UV-C and fungal infection increased the content of *E*-resveratrol 6 times (7 or 4 times for undamaged and damaged berries, respectively, in the case of infection and subsequent UV-C treatment) compared with that in non-inoculated samples, after 5 days of storage. In addition, the *E*-resveratrol content did not increase in damaged grapes compared to that in undamaged grapes either at day 0 or after storage. These results suggest that *E*-resveratrol was not elicited by ochratoxigenic *Aspergillus*. However, in another study, it has been shown that *E*-resveratrol accumulates in *A. carbonarius* inoculated grapes at veraison time but not during ripening (Bavaresco et al. 2003). Moreover, *E*-resveratrol formation decreases from veraison to ripening in berries, and this formation is elicited by biotic (ochratoxigenic *Aspergillus*) and abiotic (UV-C) factors (Jeandet et al. 1991). However, the induction capacity for *E*-resveratrol was sevenfold, which is higher than the value of 4.4-fold obtained in another study (Cantos et al. 2002). The accumulation of *E*-

resveratrol was significantly enhanced by increasing the storage time and by UV-C treatment, as well as by the combination of both treatments.

Inoculation with ochratoxigenic *Aspergillus* did not specifically elicit the accumulation of *E*-piceid (Table 2, no. 23). However, there was a significant increase in the induction of *E*-piceid during storage, and this induction was particularly faster in damaged berries than in undamaged grapes. Therefore, *E*-piceid induction in UV-C untreated grapes could be a consequence of the total microbial contamination rather than a specific response to ochratoxigenic *Aspergillus*. On the other hand, in undamaged berries, the *E*-piceid content increase in response to microbial infection was faster in UV-C treated berries than in untreated berries. The *E*-piceid content in damaged grapes after treatment with UV-C and fungal infection increased onefold.

UV-C treatment induced the biosynthesis of *E*-resveratrol as a result of an increased transcription of genes encoding stilbene synthase. Fungal infection induced not only the transcription of stilbene synthase but also the transcription of genes encoding glycosyltransferases, which transform *E*-resveratrol to *E*-piceid.

Conclusions

Edible berries are a rich source of nutritive and bioactive compounds, including stilbenes, among which *E*-resveratrol, piceatannol, *Z/E*-piceid and viniferin are the most common. The extraction techniques applied in stilbene isolation can be classified into two categories: green techniques and conventional techniques. Conventional techniques use a large volume of solvent, especially methanol or ethanol and their aqueous mixtures or mixtures with other solvents. Green techniques are not as common as conventional techniques but allow minimalization of solvent usage.

Among the analysed edible berries, the highest concentration of stilbenes has been found in passion fruit (*Passiflora edulis*). However, the highest concentration of *E*-resveratrol in the skin has been found in table grapes (*Vitis vinifera* L.). The quantitative and qualitative composition of stilbenes in edible berries depends on many environmental factors. However, the application of various abiotic and biotic external

stimuli may increase the production of stilbenes in grapes. Several different elicitors, as inducers of secondary metabolite stilbenes, were analysed: UV irradiation, visible light, ultrasonication, signalling compounds and fungicides. Among them, UV treatment was the most effective method to enhance stilbene derivative production. The enhancement of the stilbene content depended on the UV wavelength, UV intensity, duration of irradiation and developmental stage of the berry fruit. The *STS* expression responsible for stilbene production was the highest when the berries were exposed to UV-C irradiation at 2 weeks before veraison. In general, the effect of biotic stressors, such as *Aspergillus carbonarius* and *Botrytis cinerea*, was found to be not as efficient as the effect of abiotic elicitors.

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