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Ultraviolet-B radiation, water deficit and abscisic acid: a review of independent and interactive effects on grapevines

**Rodrigo Alonso · Federico J. Berli ·
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Abstract Viticulture is present around the word in a large diversity of climates. The water availability in the soil and the quality of sunlight are two environmental factors that affect the fruit characteristics for winemaking. Ultraviolet (UV)-B radiation comprises a small fraction of sunlight that reaches the Earth's surface, but has enough energy to cause large photobiological effects on higher plants. High UV-B increases metabolites with antioxidant properties as phenolic and volatile organic compounds in berries that improve oenological quality although affecting growth and fruit yield. Water restriction is a common cultural practice used in many wine regions to increase berry quality for winemaking and it is well documented that main effects are mediated by abscisic acid (ABA). Generally, ABA is a phytohormone that, besides to control stomatal aperture, regulates many physiological and biochemical processes of acclimation to adverse environmental conditions; and also controls grape berry maturation. Stress conditions and/or environmental signals generally increase ABA, and a promotive effect by UV-B has been found in grapevines. This review provides an overview of existing literature on the effects of UV-B radiation, moderate water deficit practices and sprayed ABA on grapevines (*Vitis vinifera* L.). The focus is on the physiological and biochemical aspects affecting growth, yield and quality for winemaking.

Keywords ABA · Drought · Secondary metabolism · UV-B · *Vitis vinifera* L

Abbreviations
ABA	Abscisic acid
ORAC	Oxygen radical absorbanse capacity
PAR	Photosynthetic active radiation
UV	Ultraviolet
UVAC	UV-absorbing compounds
+UV-B	Full UV-B treatment
−UV-B	Filtered UV-B treatment
VOCs	Volatile organic compounds
Ψ_s	Stem water potential

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1 Introduction

Viticulture is an activity of major importance worldwide, present in at least 40 countries, with a large diversity of climates. The water availability in the soil and the quality of sunlight are two environmental factors that affect the quality of the fruit for

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winemaking (Koyama et al. 2012; Chaves et al. 2007). Some grape-growing regions like California (USA) although receive ample winter rainfall, have seasonal drought on summer and must be irrigated to achieve optimum fruit yield and quality. Others regions like Mendoza (Argentina) have an arid temperate continental climate with scarce rainfall (annually 200–300 mm), which also makes irrigation necessary for the normal growth and development of the vines. Regarding the quality of sunlight naturally perceived (i.e., the characteristic solar electromagnetic radiation) many viticultural areas located in southern hemisphere receive high levels of ultraviolet (UV)-B radiation (McKenzie et al. 2006; Gregan et al. 2012). For example, the Uco Valley, one of the highest growing areas of Mendoza, has vineyards drip irrigated and located at 1500 m asl, that receive high levels of UV-B during summer, with irradiances up to 0.40 W m^{-2} at noon hours (Berli et al. 2011). The UV-B levels increase with altitude and vineyards at higher elevations are increasing their surface (Berli et al. 2015). Additionally, within a context of global warming, the search for new areas with lower temperatures may cause the establishment of vineyards each time at higher altitudes (Hannah et al. 2013).

Solar UV-B radiation and water deficit represents environmental factors/signals that modulate physiological characteristics of vines including the accumulation of secondary metabolites in ripening berries (Berli and Bottini 2013; Chaves et al. 2010).

2 Phenolic and volatile compounds

Phenolics are products of secondary metabolism of plants (and microorganisms) that can be defined as molecules containing at least one phenolic ring attached to a hydroxyl group or other substituents. Derived from the phenylpropanoid and flavonoid biosynthetic pathways, they are represented by non-flavonoids as phenolic acids (hydroxycinnamic and hydroxybenzoic acids) and stilbenes like resveratrol; and by flavonoids classified as anthocyanins, flavanonols, flavonols and flavanols. Phenolics accumulate in the cell vacuoles of different plant tissues, so providing protection to different environmental stressful conditions since they absorb UV (filtering harmful radiation) and possess antioxidant properties (Dixon

and Paiva 1995). While many compounds serve as attractants for pollinators and seed dispersers, others act as defense compounds against herbivores and pathogens (Reyes and Cisneros-Zevallos 2003; Petroni and Tonelli 2011). There are also compounds which have more than one function. For example, anthocyanins, the major red, purple, violet and blue pigments in many flowers and fruits, attract pollinators and seed dispersers, but also defend plants against abiotic and biotic stresses (Solovchenko and Schmitz-Eiberger 2003). In addition to their biological function, phenols play a significant role in winemaking since they determine wine quality. Organoleptic characteristics such as wine color, astringency and bitterness are highly dependent of phenolics profile. Several authors have shown the nutraceutical properties of phenolics to human health by acting as antimicrobials, anticancer and antioxidant agents (Vaquero et al. 2007; Guilford and Pezzuto 2011).

Volatile organic compounds (VOCs) are emitted by plants as crucial signaling molecules that interact with the biotic surrounding environment (Dudareva et al. 2006). They are secondary metabolites mostly derived from fatty acids and terpenes (Pichersky and Gershenzon 2002), and function attracting pollinators and seed dispersers, in plant to plant signaling, as well protecting plants from pathogens, parasites and herbivores (Gershenzon and Dudareva 2007; Clavijo McCormick et al. 2012; Dudareva et al. 2013). It has also been demonstrated that VOCs protect against different abiotic stressful factors, mainly through reduction of oxidative damage since antioxidant actions were observed in essential oils based on their radical-scavenging activities and inhibition of the lipid oxidation cycle (Wei and Shibamoto 2007).

The aroma, one of the main factors that determine the quality of wines, derives from VOCs present in berries and from compounds produced during alcoholic and malolactic fermentations and aging with precursors such as amino acids and conjugated soluble compounds (Bartowsky and Pretorius 2009; Garde-Cerdán et al. 2010). Gas chromatography coupled to mass spectrometry has resulted in the identification of many aroma compounds in different foods, including wine (Robinson et al. 2014). The relative importance of VOCs to wine varietal aroma character varies with the type of grapevine cultivar, growing conditions and management practices (Ou et al. 2010). There are aroma compounds which are always present; i.e. C$_6$-

compounds, higher alcohols, fatty acids, esters, monoterpenes, norisoprenoids and thiols (Robinson et al. 2014, and references cited therein). Others are characteristics of some cultivars, i.e. present in relatively greater proportions, like rotundone in Shiraz (Siebert et al. 2008) and methoxypyrazines in Cabernet Sauvignon, Sauvignon Blanc, Cabernet Franc and Merlot (Sidhu et al. 2015).

3 UV-B

Solar radiation reaching the Earth's surface includes infrared radiation (wavelengths higher than 700 nm), photosynthetically active radiation (PAR, 400–700 nm), UV-A (315–400 nm) and UV-B (280–315 nm). UV-B represents only 0.5 % of the total solar energy passing through the atmosphere (mostly absorbed by the ozone layer in the stratosphere and by atmospheric gases), but entertains enough energy to cause large photobiological effects on plants (Jansen 2002; Kakani et al. 2003). Solar angle, elevation of the sun over the zenith, altitude and local weather conditions such as cloud cover, surface reflection and atmospheric pollution are factors that greatly affects the amounts of UV-B (McKenzie et al. 2007). Solar angle determines the trajectory of light through the atmospheric barrier so defining the air mass thickness and interception by gases, which makes UV-B levels greater in the tropics than in higher latitudes. Elevation of the sun above the zenith changes during the day and with the seasons, thus UV-B levels are higher at midday and in summertime (in middle and high latitudes). The effect of altitude is related to the atmospheric column mass (gases, water vapor, water droplets and aerosols) that solar rays must traverse; i.e. at high altitudes there is less air masses and hence greater solar UV-B levels (Piazena 1996).

High fluence rates and short wavelength radiations are generally feared because in the scientific literature there are many references of their detrimental effects. For example, it is mentioned that high UV-B damages proteins and DNA (affecting DNA replication and transcription), peroxidates membrane lipids (reducing membrane integrity), and destroys chloroplast pigments, as well as inhibits Rubisco activity (less photosynthetic activity and growth; Jenkins 2009; McKenzie et al. 2007). However, those experimental results may exaggerate the UV-B damaging potential in nature because of the use of inadequate experimental systems; that is, excessive fluence rates and inappropriate PAR/UV-B ratios. In general, experiments performed in growth chambers with reduced PAR levels exaggerate the effects of UV-B, presumably because environmental PAR induces protective and repairing mechanisms of acclimation that reduce UV-B damages (Kolb et al. 2001). Rather, when plants are submitted to contrasting UV-B situations, moderate effects are observed under field trials than in more strictly controlled environmental conditions (Caldwell et al. 2003).

3.1 Effects on growth and leaf tissues

Some detrimental effects of solar UV-B on plants have been reported in field experiments, including impairments of vegetative growth (shoot length and leaf area) and diminution of gas exchange in grapevines grown at high altitude (Berli et al. 2013). Morphological changes have also been reported in various species as a plant acclimation to UV-B, mainly to reduce the UV-B interception by the canopy (Jansen 2002). Hectors et al. (2012) have postulated that the lower leaf expansion observed in *Arabidopsis* plants exposed to UV-B was due to lower content of indole acetic acid (IAA), key in the leaf expansion process (Keller et al. 2004).

Berli et al. (2013) observed that the defense mechanisms triggered by solar UV-B signal reduced lipid peroxidation (measured as malondialdehyde), although they were insufficient to protect photosynthetic pigments (chlorophylls and carotenoids). The effects however are evident only when results are expressed on tissue weight basis, but the differences disappear when pigments are expressed as per leaf area basis due to full UV-B (+UV-B) treatment also increase the thickness of the leaves. Therefore, the thicker leaves obtained in the +UV-B treatment and the concentration effect (plants with lower leaf area) may be masking the direct deleterious effect of UV-B on the photosynthetic pigments accumulation. Berli et al. (2010) found in field-grown potted grapevines cv. Malbec that UV-B did not affect photosynthetic pigments, but even increased carotenoids when the results were expressed on leaf area basis. Núñez-Olivera et al. (2006) observed decreases in chlorophyll content due to UV-B, even expressed by leaf area, but

only in the cv. Tempranillo and not in cv. Viura. That is, effects of UV-B on photosynthetic pigments seem to be also cultivar dependent in grapevine.

High UV-B levels increased markedly UV-absorbing compounds (UVAC), photoprotective pigments (mainly flavonols like kaempferol and quercetin and anthocyanins), in leaves of grapevines cv. Malbec (Berli et al. 2010). UVAC can play as sunscreens filtering high-energy radiation (which therefore cannot reach mesophyll cells), and also act as antioxidant molecules (Bilger et al. 2001). Consistent with the antioxidant function mentioned, Majer and Hideg (2012) and Berli et al. (2013) have reported increases in oxygen radical absorbance capacity (ORAC) in leaves exposed to UV-B. It was proposed that UV-B also modulates VOCs metabolism as an acclimation and protective response against high UV-B. Grapevine leaves grown in vitro and exposed to high UV-B increased the content of α-pinene, 3-carene, terpinolene and nerolidol, all VOCs with strong antioxidant properties (Gil et al. 2012).

Increases in the amino acid proline causes an osmotic adjustment that allows the plant to incorporate water through roots especially when the water in the soil is scarce (reduced soil water potential conditions; Pollard and Wyn Jones 1979). Saradhi et al. (1995) have reported increases of proline in different species exposed to UV radiation lamp (including UV-C), suggesting that this amino acid would act as an antioxidant by reducing lipid peroxidation. Berli et al. (2013) have obtained increments of proline in grapevine leaves exposed specifically to UV-B (field experiment).

UV-B radiation effects on the leaf transcriptome of grapevine was studied by Pontin et al. (2010) treating in vitro Malbec plants with the same dose of biologically effective UV-B radiation (4.75 kJ m^{-2} d^{-1}), but administered at two different irradiations (16 h at $\cong 8.25$ μW cm^{-2}, 4 h at $\cong 33$ μW cm^{-2}). They found a general protective response activation under both UV-B treatments as well as transcripts specifically regulated in an UV-B intensity dependent way. While high fluence rate UV-B had regulatory effects mainly on defense or general multiple-stress responses pathways, low fluence rate UV-B promoted the expression of genes that could be involved in UV-B protection or the amelioration of the UV-B induced damage.

3.2 Effects on flower and berries

Berli et al. (2008) reported that high solar UV-B increased total phenolic compounds (including flavonoids and non-flavonoids), anthocyanins and the stilbene resveratrol in berry skins of the cv. Malbec. These results were obtained in a field experiment with grapevines exposed to contrasting solar UV-B levels, i.e. under sunlight with +UV-B or −UV-B during grape berry ripening, in three different locations of Mendoza at 500, 1000, and 1500 m asl (where altitude accounted for solar UV-B differences in the +UV-B treatment). It has been documented that solar UV-B improves grape berry skin phenols (mainly flavonols, flavanonols and flavanols), which are protective for plant tissues, increasing the quality for red winemaking, but at the expense of berry growth and fruit yield (Berli et al. 2011). As well, Berli et al. (2015) found that treatment with high UV-B during all the season increased the ORAC of skin extracts.

In berries (Gil et al. 2013) and flowers (Gil et al. 2014), both from high altitude field experiments with cv. Malbec grapevines, solar UV-B effects on the production of VOCs were studied. In berries, UV-B markedly increased monoterpenes at pre-harvest, and also augmented levels of some aldehydes, alcohols and ketones (Gil et al. 2013). The total amount of VOCs in flowers did not change irrespective to UV-B treatments, suggesting that the total amount of those compounds is constitutive of the flowers, although UV-B differentially increased the proportion of valencene, β-farnesene, α-panasinsene and hepatriacontanedione (Gil et al. 2014).

A specific UV-B photoreceptor, UV resistance locus 8 (UVR8) was identified in *Arabidopsis* by Rizzini et al. (2011). Liu et al. (2014) working with grapevine berries, found that genes involved in the low fluence UV-B pathway are more central in determining flavonol biosynthesis in response to UV-B radiation. Additionally, Carbonell-Bejerano et al. (2014) suggest that the photoreceptor homolog, VvUVR8, might mediate the UV-B induced accumulation of flavonols in the grape skin by up-regulating secondary metabolism-related transcripts.

In summary, UV-B radiation affect grapevine plants directly through impairment of vegetative growth, diminution of gas exchange and activation of secondary metabolite pathways (mainly, phenolics and VOCs). In the recent years discovery of UVR8

was an important advance to understand the response mechanisms.

4 Water restriction

The restriction of water supply to the vines is a cultural practice commonly used in many wine regions of the world, especially in red cultivars. It consists of providing only part of water loss by evapotranspiration during a certain growth stage (Intrigliolo and Castel 2009). In grapevine, high-quality yield is generally achieved under suboptimal crop conditions (stressful conditions). Therefore, water restriction has become a management target to secure high fruit quality and improve sustainability of water use by rewarding crop quality over quantity (Medrano et al. 2015). Figure 1 shows that the quantity of experiments that evaluated the effects of water restriction on grapevine is much higher respect to those in which the effects of UV-B radiation were assessed.

Vines are adapted to grow and develop in moderate stressful water conditions, possibly due to a broad and deep root system, an efficient mechanism of stomatal control, and the ability to perform and osmotic adjustment (Rodrigues et al. 1993; Chaves et al. 2007; Blum 2009). In red cultivars, the effects of water stress have been extensively studied (Kennedy et al. 2002; Lovisolo et al. 2010). In general, grapevines respond to water restrictions by closing stomata to reduce water losses, so affecting diffusion of CO_2 and

Fig. 1 Published papers (by November 2015, using the Scopus database) of grapevine in which independent and interactive effect of water deficit and UV-B radiation were evaluated. Bars with oblique lines represent papers in which the participation of ABA was also evaluated

photosynthesis (Chaves et al. 2003). Effects of water deficit on grapevine physiology depend on the phenologic stage, the severity of the stress and also the cultivar studied (Ojeda et al. 2002; Chaves et al. 2010).

The period of berries growth known as veraison is characterized by the initiation of sugar accumulation and also the pigmentation of berry skins by anthocyanins in red cultivars. Stem water potential (Ψs) represents whole vine water status during the day hours, and it is a particularly useful tool for irrigation management (Choné 2001). Leeuwen et al. (2009) proposed Ψs ca. -1 MPa, a moderate water deficit, after veraison as a management strategy to improve berry quality for red winemaking because enhances fruit ripening and phenolic synthesis in berries.

Berry size is sensitive to water stress, especially when it occurs in the early stages of development, i.e. prior to veraison (Ojeda et al. 2001, 2002). It has been suggested that there is a differential sensitivity to water deficit amongst the different grape cultivars due to, at least in part, alterations in hormonal status of berries at the time of water stress (Niculcea et al. 2014). In red cultivars such as Cabernet Sauvignon, Syrah, Tempranillo and even Malbec, several authors have reported a reduction in the size of the berries due to the water restriction (Castellarin et al. 2007; Santesteban et al. 2011; Song et al. 2012; Shellie and Bowen 2014). Ojeda et al. (2002) subjected cv. Syrah vines to moderate water deficit after veraison, observing a reduction of the sugar content per berry but not in the concentration of sugars (°Brix, dependent of berry size). Additionally, Ojeda et al. (2002) and Castellarin et al. (2007) found that moderate water restriction produced an increase of polyphenols in cv. Syrah and Cabernet Sauvignon musts, not only because it reduces the size of the berry (increasing the pulp/skin ratio), but also because there is an increase in the synthesis of these compounds and in the expression of anthocyanin related genes in the skin.

Deluc et al. (2011) investigated the impact of water deficit on stilbene biosynthesis in berries. They found that water deficit increased the accumulation of trans-piceid (the glycosylated form of resveratrol) by 5-fold in Cabernet Sauvignon berries but not in Chardonnay, suggesting cultivar specificity for resveratrol biosynthesis in grapes.

Water deficit also increases the abundance of transcripts of enzymes involved in the production of VOCs in Cabernet Sauvignon and Chardonnay berries
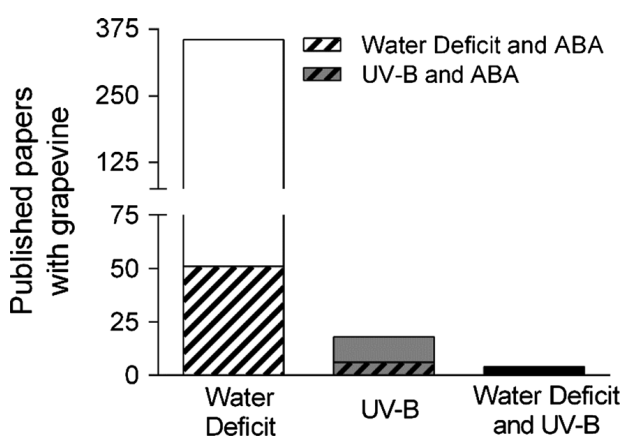
(Deluc et al. 2009). That is, the improved quality through moderate water deficit between veraison and maturity can be given as an indirect effect due to reduced berry size (concentration effect), and at the same time as a direct effect since there is an increase in the metabolic pathways affecting important flavor and quality traits in grape berries.

Moderate water restriction is an efficient strategy to allow an optimal grape maturity, increasing the oenological quality through indirect effect (increase pulp/skin ratio) and direct effect (increase phenolic and VOCs).

5 ABA

The plant hormone abscisic acid (ABA) is a sesquiterpene (15 carbons), and its naturally occurring active form is S-*cis* ABA (Fig. 2). ABA regulates many physiological and biochemical acclimation processes, some of them common to different stress conditions (Creelman 1989; Seki et al. 2002). That is, stressful conditions and/or environmental signals (abiotic and biotic factors) generally stimulate the increase of ABA levels (biosynthesis and accumulation), which is responsible for controlling plant responses (Lim et al. 2015; Zhu 2002). ABA biosynthesis in grapevine is induced by water deficit in leaves (Iacono et al. 1998) and berries (Deluc et al. 2009), but also by high UV-B (mainly in leaves; Berli et al. 2010; Gil et al. 2012). While it has been shown in grapevine that ABA participates in certain antioxidant responses toward UV-B (Berli et al. 2010), also it has been demonstrated that +ABA treatment did not produce the same effect as the +UV-B treatment, which indicates not only that the UV-B signal is mediated by ABA (Berli et al. 2011). In barley seedlings, Fedina et al. (2009) suggest that the hormone jasmonic acid could acts as a mediator in plant defense responses to UV-B
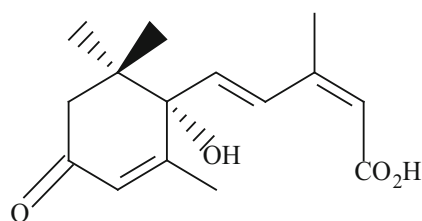
Fig. 2 Chemical structure of S-*cis* abscisic acid (ABA), the naturally occurring active form

irradiation by enhancing the activity of antioxidant system and free radical scavenging capability of plant cells.

Sansberro et al. (2004) showed that ABA promoted vegetative growth in *Ilex paraguariensis*, which was positively correlated with a decrease in stomatal aperture and increases in the relative water content in leaves. Therefore, ABA promoted higher cell turgor required for cellular expansion (Acevedo et al. 1971).

In Carvalho et al. (2015), grapevine of cultivars Touriga Nacional and Trincadeira were subjected to drought, heat and high light (individually and in combination). Regarding ABA concentration in leaves, they observed differential responses between cultivars and among the kind of abiotic stresses imposed. They suggested that ABA may be implicated in grapevine osmotic responses since it is correlated with tolerance parameters, especially in combined stresses involving drought, although they also suggest that other chemical signals (cytokinins or ethylene) might be involved.

While it is known that ABA is involved in maturation of grape berries, the mechanisms of action are not fully understood (Davies and Böttcher 2009). It has been demonstrated that grapevine berry skin ABA levels increases markedly during veraison reaching the maximum after two weeks, and subsequently decline to be low at harvest (Wheeler et al. 2009; Berli et al. 2011).

5.1 Effects of ABA applications

The effects of sprayed ABA depend on the growth stage in which is applied, dose and frequency of application. In general, ABA administered at a physiological dose has no direct effect on visible growth in several plant species (Travaglia et al. 2007; Travaglia et al. 2009; Cohen et al. 2009). Quiroga et al. (2009) found that weekly applications of ABA in Cabernet Sauvignon starting in the sprouting, tended to reduce plant growth at harvest, while Moreno et al. (2011) working with cv. Malbec plants in pots, did not found growth differences, although the measurements were made at veraison.

The accumulation of phenolic compounds in the skin is one of the most studied effects of ABA application in grape berries (Balint and Reynolds 2013). Peppi et al. (2008), Koyama et al. (2010) and Lacampagne et al. (2010) found out that ABA applied to bunches enhanced expression of skin genes

involved in the biosynthesis of anthocyanins. Additionally, applications of ABA have been shown to increase the anthocyanin content of grape skin, improving the color of table grapes like Flame Seedless and Redglobe (Peppi et al. 2006, 2007). Some time ago, the cost of producing ABA was too high to justify its commercial use, but recently ABA production methods have been improved and its application in table grape viticulture is being considered (Ferrara et al. 2013).

ABA applications increased sugar accumulation in berries (Moreno et al. 2011), enhancing the flow of carbohydrates to the fruit, being the effect noticeable at veraison (Moreno et al. 2011), but then the differences reduced at harvest (Wheeler et al. 2009; Berli et al. 2011). Accumulation of glucose and fructose in berries was hastened in ABA-treated plants at the stage of full veraison, which was correlated with enhancement of gene expression involved in sugar transport and the increase of phloem area and sucrose content in leaves (Murcia et al. 2015).

Regarding the effect of exogenous ABA on leaf physiology, there are few reports. Foliar ABA application advanced bud dormancy in grapevines of cultivar Chambourcin, also decreased bud water content, and eventually increased freezing tolerance (Zhang and Dami 2012). Berli et al. (2010) found that weekly applications of ABA from bud-break to harvest improved grape leaf tolerance to elevated solar UV-B (reducing oxidative damage), mainly through the increment of antioxidant enzymes activities, accumulation of membrane-sterols that participate in structural defense, and accumulation of UVAC in epidermal cells. Alonso et al. (2015) suggested that only two application of ABA on leaves, at veraison and 15 days after, seems to be enough to activate compounds with antioxidant and antifungal properties, suggesting that it may increase the plant defensive mechanism against environmental signals, both biotic and abiotic.

Summarizing, ABA participates in the maturation of grapes and mediates some common responses to UV-B and water deficit. ABA application can be an interesting tool for vineyard management.

6 UV-B, water restriction and ABA interactions

Plant response to the simultaneous action of various stressors is different than the response to the same

factors when acting separately (Alexieva et al. 2003). Some plant defense mechanisms against high levels of UV-B can mitigate the detrimental effects produced by a subsequent occurrence of a water deficit (Bandurska et al. 2013). Drilias et al. (1997) found that pretreatments with high levels of UV-B on *Nerium oleander* leaves reduced the subsequent incidence of water deficit increasing the cuticle thickness and reducing transpiration rates. While the effects of water deficit in grapevines have been widely studied (Chaves et al. 2010), there are only limited reports in relation to water deficit and UV-B interactions and most of them have been conducted in growth chambers and greenhouses with unrealistic UV-B/PAR ratios (Bandurska et al. 2013). In grapevine, only few papers have evaluated the effects of water deficit and UV-B interactions (Doupis et al. 2011; Martínez-Lüscher et al. 2014, 2015; Alonso et al. 2015), finding that some mechanisms of response are common while others are specific to the stressor/signal.

6.1 Effects of interaction on gas exchange and vegetative growth

Doupis et al. (2011) combined drought and UV-B treatments in cv Sultanina and found significant interactions between factors decreasing shoot growth rate and leaf dry weights. They also found independent effecs, i.e. that the activities of antioxidant enzymes and the production of UVAC were increased by enhancement of UV-B radiation, while proline was increased by drought. Martínez-Lüscher et al. (2014, 2015) worked with pot-grown plants of cv. Tempranillo under greenhouse conditions treated with drought and three levels of UV-B applied after fruit set. When the physiological response was studied, little interactive effects between UV-B and drought on photosynthesis performance was found (the impact of UV-B was over shadowed by the effects of water deficit). UV-B induced a transient decrease in net photosynthesis, actual and maximum potential efficiency of photosystem II, particularly on well-watered plants. UVAC concentration and superoxide dismutase activity increased only with UV-B. Water deficit decrease net photosynthesis and stomatal conductance, and did not change non-photochemical quenching and the de-epoxidation state of xanthophyll, dark respiration and photorespiration, which are alternative ways to dissipate the excess of energy. Significant

interactions between UV-B and water availability were observed for carotene, lutein, neoxanthin and zeaxanthin.

In contrast with the works of Doupis et al. (2011) and Martínez-Lüscher et al. (2014, 2015), Alonso et al. (2015) performed a field experiments in a commercial vineyard in which high levels of solar UV-B were filtered with a plastic film, water restriction was applied after veraison, and plants received ABA applications. Berli et al. (2013) found that grapevine vegetative growth (shoot length, number of leaves and leaf area) was reduced by exposure to high UV-B mainly through limitation in gas exchange (photosynthesis and stomatal conductance), while the maximum quantum efficiency of PSII photochemistry (F_v/F_m) was not affected. Then, Alonso et al. (2015) found increments in the impairment of gas exchange and photosynthesis (significant interaction effects) by combining high UV-B with water deficit. That is, gas exchange and photosynthesis were reduced by water deficit and highly impaired in the UV-B and water deficit combined treatment. In addition, applications of ABA in well-watered treatments did not impair photosynthesis. The latter may suggest that ABA has additional indirect effects on photosynthesis via stimulation of carbohydrate transport as it has been shown in wheat (Travaglia et al. 2007) and even in grape (Moreno et al. 2011; Murcia et al. 2015).

UVAC accumulation in cv. Malbec leaves was significantly increased by high UV-B and was not responsive to water restriction and ABA applications (Alonso et al. 2015). Regarding the VOC contents, interaction effects were observed on monoterpenes content, in which α-pinene, 3-carene and terpinolene, the sesquiterpene nerolidol, the triterpene squalene and the diterpene phytol were augmented by UV-B, water deficit or sprayed ABA. The increase of some terpenes seems to be a common response of the leaves against UV-B and water deficit, and signalized by ABA (significant interactions). Linolenic acid in grapevine leaves was reduced when high UV-B, water restriction and applications of ABA were combined (Alonso et al. 2015). It is the major polyunsaturated fatty acid of membrane lipids, and the degree of fatty acid unsaturation is an important factor for membrane fluidity related to adaptation to adverse environmental conditions (Upchurch 2008). In concordance with Alonso et al. (2015) it has also been reported that water deficit and UV-B reduce the degree of fatty acids unsaturation (Bettaieb et al. 2009; Hamrouni et al. 2001).

6.2 Effects of interaction on berries

ABA application at vineyards can be an interesting tool to enhance the biological quality of grape, although it is important to consider the interaction with the environment signals. High UV-B and ABA applications increase total phenols in grape berries, especially those with higher antioxidant capacity (i.e. dihydroxylated anthocyanidins and flavonols like quercetin; Berli et al. 2011). The quality of grape berries for winemaking integrates various aspects, but for red wines, it has a high correlation with accumulation of phenolics stimulated by UV-B and ABA. Berli et al. (2011) did not found significant interactions between UV-B and ABA (effects of UV-B and ABA applications on phenolic compounds were additively increased). However, Berli et al. (2015), evaluating the effects during three growing seasons, found that UV-B x ABA interact significantly for berry skin anthocyanins and total polyphenols. These treatments also hasten berry sugar and phenol accumulation, but reduce berry growth and sugar per berry at harvest, and therefore decrease yield (Berli et al. 2011, 2015).

Martínez-Lüscher et al. (2014) found that UV-B upregulated in berries two key genes of flavonol and anthocyanin biosynthesis. Significant interactions between UV-B and water deficit were also observed in flavonol profiles as a result of the competition of flavonol synthase, flavonoid 3′5′ hydroxylase and flavonoid 3′ hydroxylase for the same flavonol substrates. Authors suggested that deficits of irrigation did not modify the adaptive response of grapevine to UV-B.

While, further investigations are necessary to understand the response of grapevine under UV-B and water deficit, current knowledge suggests that the adaptive response to UV-B radiation is not modified by water deficit. Terpenes, phenolics and the activities of antioxidant enzymes are the main mechanisms studied. Also, it is important to increase the knowledge about the involvement of ABA in mechanisms responsible for interacting.

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