

REVIEW ARTICLE

Advantages and disadvantages of UV-B radiations on Grapevine (*Vitis* sp.)

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Abstract

UV radiation, as a natural component of sunlight and frequently mentioned in relation with climatic changes, has numerous regulatory effects on grapevine physiology and biochemistry. In last decades many studies gave significant advances in the understanding of the effects of UV radiation on compounds of the primary and secondary metabolism, especially those which impact grape and wine quality. Mechanisms of plant responses to solar UV-B radiation are therefore disadvantageous: such as inhibition effect on plant growth, but also advantageous such as accumulation of phenolic compounds and improved resistance to pathogenes. UV-B affects the secondary metabolism of plants and thus indicating that solar UV-B is to be regarded as an environmental challenge rather than a damage-inducing source of stress in vitiviniculture. UV irradiation might have a positive influence on grape “healthiness” or composition and consequently a positive impact on wine quality. This review provides a synopsis of the effect of UV radiation associated variables on grapevine physiology and biochemistry as potential key factor in the future of global grape production.

Key words: Climatic changes, Grape, Quality, Radiation, UV

Introduction

Vitiviniculture has developed to one of the most important agricultural sectors globally spoken, common to all continents today. According to the data by the International Organisation of Vine and Wine, nowadays 645 mio qs of grape are produced on approx. 7.6 mio ha of vineyards worldwide (OIV, 2010).

In the last decades, climatic changes have become a “daily bread”, where an increase of temperature and UV radiation, unexpected rainfalls, storms, depletion of the ozone layer etc. are all predicted and inevitable events.

UV light is an electromagnetic radiation with a wavelength shorter than that of visible light, and is commonly divided into UV-A (320-400 nm), UV-B (280-320 nm) and UV-C (<280 nm). Furthermore, much of the UV-B (~97%) and all of the UV-C are absorbed by the ozone (O₃) in the stratosphere and never reach the surface of the earth. Caldwell et al.

(1989) and McKenzie et al. (1999) reported that the depletion of stratospheric ozone causes the increase of UV-B radiation which reaches the earth’s surface, therefore influence of UV-B irradiation is gaining the interest of scientific community.

The vineyards receive a different “quantity” and intensity of UV-B radiation, what mainly depends on the position of the sun, the exposure and inclination of the vineyards, arrangement of the vineyard (terraces, plain etc.) and cloudiness.

The entire UV spectrum has some of the biological functions of ionizing radiation, in doing far more damage to many molecules in biological systems as those caused by simple heating effects (for example sunburn).

Cellular components such as proteins and nucleic acids absorb this radiation, resulting in biomass reduction, impaired photosynthesis and other chloroplast functions, decreased protein synthesis, damage to DNA. Effects of UV-B radiation include oxidative stress, and reactive oxygen species (ROS) have been shown to participate directly in the damage induced by high UV-B doses (Majer and Hideg, 2012).

Plants protect themselves from this potentially harmful radiation by altering metabolic functions and a number of studies confirmed the role of UV-B in the regulation of gene expression (Surplus et al., 1998; Brosche and Strid, 2003; Ulm and Nagy,

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2005; Jenkins, 2009). Actually UV-B is to be regarded as an environmental challenge rather than a damage-inducing source of stress (Jordan, 2002; Kolb and Pfundel, 2005).

Relevant consequences to vitivincultural are mostly altered phenolic profiles (Kolb et al., 2003), as well as susceptibility to fungal vine pathogens (Keller et al., 2003a), which tend to be more susceptible to UV-B radiation than higher plants, as well as herbivorous insects and disease vectors (Caldwell et al., 2007).

Effects on grapevine physiology

Sunlight, in the whole range of wavelengths, is recognized as the most powerful factor determining morphological and physiological variations in leaves. Many effects of UV-B radiation affect morphogenetic changes in plants (presence of leaf hairs shoot tip, young leaves (Karabourniotis et al., 1999); as well as epicuticular wax (Shepherd and Griffiths, 2006). It is a well-known fact that sun leaves display a higher leaf mass per area (LMA) and thickness (LT) than shade leaves (Groom and Lamont, 1997; Tattini et al., 2000; Evans and Poorter, 2001; Gratani et al., 2006; Temesgen and Weiskittel, 2006; Cascio et al., 2010), what was also confirmed on *Vitis vinifera* L. 'Sangiovese' (Pollastrini et al., 2011). The study confirmed that the quantity of epidermal polyphenols increased as a consequence of UV-B irradiation. Even more than the morphological effect itself it seemed an important discovery that in Mediterranean conditions the natural presence of UV is a necessary element driving morphogenetic processes that enable plants to adapt better to oxidative stresses typical of that environment (Pollastrini et al., 2011). There is also not much work to authors knowledge done on root systems: deleterious effects of UV-B radiation on mycorrhizal infection, possibly mediated by plant hormone levels, have been reported (Van de Staaij et al., 2001), but not on grapevine, and more studies on the effect of climate change associated variables on rootstocks and root systems including mycorrhiza should be conducted (Mira de Orduña, 2010).

Apart from morphogenetic changes UV irradiation plays an important role in photosynthesis. In the photosynthetic apparatus an excess of light may induce a condition of over-excitation, harmful to absorbing pigments and reaction centres (Papageorgiou and Govindjee, 2004). Unmanaged electrons lead to the formation of reactive oxygen species, thus activating mechanisms of oxidative stress (Demmig-Adams and Adams III, 2006; Cascio et al., 2010).

Photosynthetic adaptations to light excesses include absorption reduction of the apparatus and increased controlled energy dissipation from the groups of pigment molecules (antennae), as well a greater amount of photosystem I (PSI), as to speed up the reduction of the final electron acceptors (NADP, Ferredoxine) (Maxwell et al., 1999; Cascio et al., 2010).

Furthermore, impacts in a wide number of photosynthetic components have been reported, including the suppression of Chlorophyll synthesis (Chl), the inactivation of oxygen synthesis, light harvesting complex of Photosystem II (LHCII), photosystem II (PSII) reaction centres and thylakoid electron flux. Furthermore, the decrease of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) content and activity, that affects maximum rate of Rubisco carboxylation, accompanied with a large reduction in the expression and abundance of both large and small subunits of Rubisco, would contribute to a lower photosynthesis activity and yield (Lidon and Ramalho, 2011).

Kolb et al. (2001) showed that epidermal UV screening of grapevine leaves (cv. 'Silvaner') after short exposure to high natural radiation is sufficient to prevent UV-B-dependent reduction of PSII activity in the vineyard. Because UV-B effects on PSII were small and transitory when compared CO₂ assimilation, they suggest that under natural light intensities UV-B inhibition of photosynthesis is not controlled by UV-B inhibition of PSII that has also been proposed by Allen et al. (1998), Xiong and Day (2001). Two years later, Pfundel (2003) developed a model to describe, how natural radiation intensities affect PSII and thereby change leaf fluorescence, concluding that PSII inhibition by natural UV could be the main factor for UV inhibition of photosynthesis.

A strong decrease in both CO₂ uptake and stomatal conductance in all leaves has as well been observed at the grapevine variety 'Chardonnay', exposed to relatively weak UV irradiation (Majer and Hideg, 2012), while on 'Sangiovese' stomatal conductances have not been affected by different light intensities in either of the UV radiation conditions (Pollastrini et al., 2011), although the differences might be due to different experimental setup and not due to cultivar.

Among the chlorophyll fluorescence parameters the quantum yield of primary photochemistry was significantly reduced in high light conditions only in the sheltered plants (-UV) (Pollastrini et al., 2011), although authors find it conflicting with their previous work, where the

reduction of primary photochemistry has been observed in mainly irradiated leaves of *Fagus sylvatica* (Cascio et al., 2010).

Majer and Hideg (2012) have shown different reductions of effective photochemical yields on supplemental UV-B irradiation of younger leaves (-22 %) and older leaves (-44 %). But supplemental UV-B irradiation did not affect total chlorophyll contents at 'Cabernet sauvignon', 'Malbec' and 'Chardonnay' varieties (Keller et al., 2003a; Berli et al., 2010; Majer and Hideg, 2012). On the other hand, Lafontaine et al. (2005) observed that a high UV radiation caused premature loss of total chlorophyll and a decrease in the Chl a/Chl b ratio in leaves and fruits. As already suggested, the experiments cannot be compared directly, due to the differences in plant material (variety, age etc.) and photosynthetically active radiation (PAR) conditions (Kolb et al., 2001; Pollastrini et al., 2011; Majer and Hideg, 2012). Berli et al., (2010) also showed evidence for lipid peroxidation and the activation of peroxidases by UV-B, which could be a result of increased hydroxyl radical neutralizing capacities of younger leaves (Majer and Hideg, 2012).

Tevini (1996) affirmed that higher levels of UV-radiation induce an increase in the production of protective pigments - carotenoid concentration is usually higher in shaded than in exposed berries (Bureau et al., 1998) and has previously been shown to decrease as a result of UV-exposure (Schultz et al., 1998; Schultz, 2000). This forced degradation may also indicate a weakening in the photo-protecting mechanism of the xanthophyll cycle (Demmig-Adams and Adams III, 1992; Eskling et al., 1997). Steel and Keller (2000) studied the effect of UV light reduction on carotenoid contents in leaves and berries of 'Cabernet sauvignon'. Their results showed that the reduction of UV light decreased the total carotenoid content in leaves; furthermore they witnessed a decrease of β -carotene and lutein contents in berries, which may affect the biosynthesis of aromatic compounds in grape and wine.

Núñez-Olivera et al. (2006) came across some differences between red 'Tempranillo' and white 'Viura' grapevine varieties at reduced solar UV-B radiation, where at white variety a significant decrease in contents of UV-absorbing compounds were observed. The same dynamic was observed at the variety 'Tempranillo' accompanied with a reduction of the xanthophyll cycle activity and an increase in the concentration of chlorophyll and carotenoids. Pfündel (2003) report that the

carotenoid content slightly increased in the older leaves in response to UV-B radiation. Moreover, carotenoids are precursors for norisoprenoid compounds in grapes (Razungles et al., 1993), what suggested that UV-radiation may also affect grape and wine flavour. Tevini (1996) for instance reported that UV-B radiation had a positive effect on the flavour of melons.

Marais et al. (1992) found that norisoprenoid concentrations were statistically higher in sun-exposed than in shaded grape. Lee et al. (2007) reported that when leaves were removed from canopy, C13-norisoprenoid concentrations were linearly ($r > 0.90$; $p < 0.1$) and positively correlated with increasing sunlight exposure. Moreover, in contrast, in the most shaded treatments with no leaf removal there were high concentrations of norisoprenoids - β -damascenone concentrations in particular were highest when no leaves were removed. Furthermore, Hühn et al. (1999) observed UV-radiation-induced changes in indole acetic acid derivatives in grapes, which may be negative for wine quality.

Effects on grapevine biochemistry

The plants, including the grapevines, evolved a wide variety and high diversity of primary (sugar, organic acids etc.) and secondary (phenolic compounds, aromatic substances) metabolites to interact with different environmental conditions, as well as to regulate abiotic and biotic stress tolerances.

In the context of primary metabolism Tevini (1996) and Krupa et al. (1998) reported that UV radiation is likely to affect levels of the key antioxidants glutathione and ascorbate and the possible inhibition of carotenoid pigment formation and of the incorporation of nitrogen into amino acids. According to Gregan et al. (2012), UV radiation did not have a significant effect on the majority of amino acids or methoxypyrazine concentrations. The most noticeable change in amino acid and methoxypyrazine accumulation was caused by the presence of leaves over the fruiting zone, retaining these leaves maintained significantly higher concentrations in the berries at harvest.

Crippen and Morrison (1986) studied the effects of sun exposure on the compositional development of berries of the variety 'Cabernet sauvignon' and their obtained results suggested that sun-exposed berries contain significantly higher concentrations of tartrate, malate, glucose and fructose than those shaded. They also found that the

canopy-shade berries were significantly heavier than those exposed to the sun, what can be ascribed to the higher water content in the berries of shaded clusters.

On the other hand, UV radiation represents an important ecological factor that leads to a cascade of reactions that ultimately result in the formation and accumulation of secondary metabolites such as phenolic compounds (Tevini, 1996), which help plants to overcome different stresses.

Apart from stress response, secondary metabolites in grape berries determine also quality of wine (aroma, astringency, colour, stability) (Ribéreau-Gayon et al., 2006), and have health benefits, such as antioxidant, anticancer, protection on cardiovasculars (Dzhambazova et al., 2011). Owing to this, many studies have focused on how to increase the levels of phenols in grape berries.

including postharvest treatment (Cantos et al., 2000; Li et al., 2009).

Price et al. (1995) found that anthocyanin content in grape of 'Pinot noir' was not affected by sun exposure, which is conflicting with recent findings: Lafontaine et al. (2005) demonstrated that berries exposed to UV-B radiation increased both the concentration of total bound glycosidic secondary metabolites and phenolics. According to Doupis et al. (2011) the accumulation of the UV-B absorbing compounds under enhanced UV-B radiation and the increase in antioxidant enzymes activities constitute the main mechanisms of grapevine adaptation: they decrease UV-penetration through the epidermis, where colour formation may itself reduce UV-penetration (Kolb et al., 2001 and 2003).

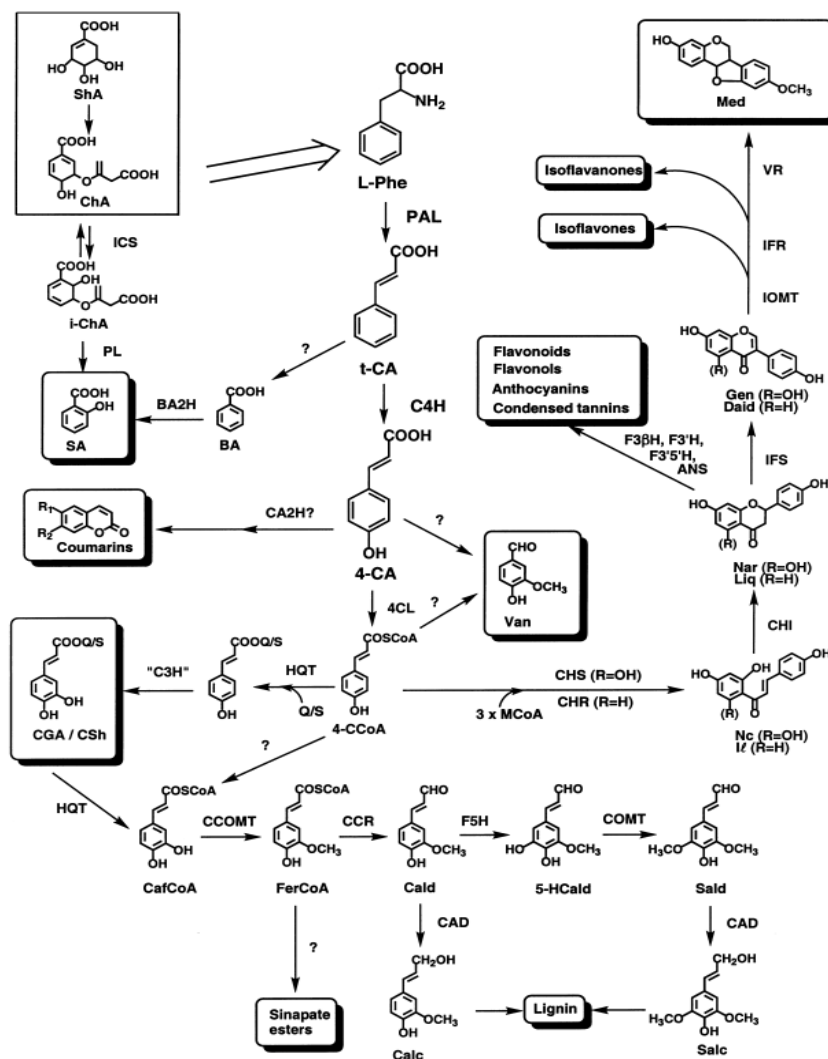


Figure 1. Phenylpropanoid pathway.
(Dixon et al. 2002)

Table 1. Main stilbenes identified in grapevines.

Stilbene	Synonym
<i>trans- / cis</i> -Resveratrol	<i>trans- / cis</i> -3,4',5-trihydroxystilbene
<i>trans</i> -Piceid	<i>trans- / cis</i> -Resveratrol-3-O- β -D- glucopyranosyde
Resveratoloside	Resveratrol-4'-O- β -D- glucopyranosyde
Pterostilbene	<i>trans</i> - 3,5-dimethoxy-4'-hydroxystilbene
Viniferins (α, \dots, δ)	
Piceatannol	<i>trans</i> -3,3',4,5'-tetrahydroxystilbene
Astringine	Piceatannol-3-O- β -D- glucopyranosyde
Pallidol	<i>trans</i> -Resveratrol dimer

According to Kolb et al. (2003), Jansen et al. (2008) and Broeckling et al. (2005) the UV light stimulates the biosynthesis of secondary metabolites, where some key enzymes involved in the phenylpropanoid pathway (Figure 1) have been showed to be regulated by UV radiation Pontin et al. (2010) demonstrated that the grapevine variety 'Malbec' responded to UV radiation in a variety of general protective responses, for example the induction of pathways regulating synthesis of UV-B absorbing compounds such as the phenylpropanoid pathway, the induction of different antioxidant defence systems and the activation of pathways commonly associated with pathogen defence and abiotic stress responses. The number of literature on secondary metabolites biosynthesis regulation is increasing fast (Matus et al., 2009; Pontin et al., 2010; Berli et al., 2011; Czemmell et al., 2012; Koyama et al., 2012; Majer and Hideg, 2012; Zhang et al., 2012).

In the last decade additional attention has been given to the effect of UV-B radiation on stilbene contents in grape berries (Adrian et al., 2000; Versari et al., 2001; Cantos et al., 2003 Belhadj et al., 2008; Bavaresco et al., 2009; Pan et al., 2009; Zhang et al., 2012), leaves (Pezet et al., 2003; Vrhovšek et al., 2012) and different callus tissues (Keller et al., 2000; Keskin and Kunter, 2009). Keller et al. (2000) found that only an actively growing callus of grapevine irradiated with UV light was capable of producing stilbenes (Table 1), including *trans*-resveratrol, one of the most beneficial compounds in wine reported (Lekli et al., 2010).

A same dynamic was observed in ripening grape berries, which gradually lose their potential for synthesizing stilbenes as they reach full-ripe maturity (Pan et al., 2009). Their profile seems to be dependent upon intensity and duration of UV-B irradiation (Gil et al., 2012).

Influence on pathogens

Pathogens and pests play a major role in determining plant performance in both agricultural and natural settings. The involvement of UV radiation in the interaction between plants and their pests is of major importance and was the subject of numerous papers (Raviv and Antignus, 2004).

Powdery mildew, caused by *Uncinula necator*

U. necator is one of the most ubiquitous pathogens in winegrowing. It can develop on all green plant parts of the grapevine. The powdery mildew fungus develops on both the upper and lower surface of leaves, but thrives in shade and often develops in the interior of dense canopies.

Willocquet et al. (1996) reported that in controlled experiments at constant leaf temperature, spore germination and mycelia growth were negatively affected by the UV-B doses, irrespective of the exposition duration. In the vineyard, radiation effects increased as the time of exposition increased, indicating that both spore germination and mycelial growth activities were slowed, but not totally stopped by the different exposures.

Also Keller et al. (2003a) reported that UV irradiation plays an important role in the natural regulation of powdery mildew under field conditions, but the increase in humidity and screening of UV caused by clouds and canopy shade may contribute to favourable conditions for *U. necator* development.

Another important factor is that for example 'Chardonnay' and 'Cabernet sauvignon' differed considerably in their susceptibility to *U. necator* (Keller et al., 2003a).

Bunch rot of grapes (grey mould), caused by *Botrytis cinerea*

Botrytis cinerea is regarded as an important organism in viticultural and oenological as well, which may be involved in noble rot and often bunch rot. The former is a prerequisite for the

production of highly priced sweet wines in specific regions (Makra et al., 2009).

The observations indicate that grapevines of the future are likely to be more prone to infections by *B. cinerea* and that both, the development of fungal pathogen and UV-B exposure lead to enhanced activities of catalase, a ubiquitous enzyme that acts to protect tissues against oxidative damage (Steel and Greer, 2005).

The high susceptibility of grape flowers to *B. cinerea* may be related not only to their poor capacity for stilbene synthesis, but also to low levels of constitutive phenolic compounds, particularly in the receptacle area (Keller et al., 2003b). Considering its importance for secondary infections and wine quality, the effect of climate change on bunch rots requires further studies (Mira de Orduña, 2010).

Downy mildew, caused by *Plasmopara viticola*

Downy mildew represents one of the most severe infections in grapevines, as it affects both the yield and the quality of wine production. The disease is usually prevented by repeated fungicide treatments of entire vineyards which cause a high economic and environmental impact.

The results of Agati et al. (2008) indicate that flavonoids can be significantly involved in the process responsible for the larger resistance to downy mildew in sun-exposed versus shaded grapevine leaves.

Conclusion

Just like other plants, *Vitis vinifera* L. is susceptible to increased UV-B irradiations, but negative influence (f.e. decreased photosynthesis) seems to be far less important than positive.

Núñez-Olivera et al. (2006) affirmed that grapevine varieties, typical of the Mediterranean climate zone are well adapted to the high solar radiation and their photosynthetic performance does not appear to be at risk from current levels of UV-B. With continuous global warming, grapes in other regions might adapt admittedly slowly as well, so minimising negative effects.

On the other hand, most important vitivinicultural relevant consequence of UV-B irradiation is an altered phenolic profile, which is advantageous for plant, and consequently for human health (increased levels of stilbenes and polyphenols in general). The effect seems to be even more important than recently reported by Jansen et al. (2008) and that there is a strong possibility that wine, in moderate consumption, is beneficial to human health (Yoo et al., 2010). With UV-induced polyphenol increase, health relevance

should even increase, causing increased wine consumption and consequently its production.

On the other hand, extracts from 'Jacquez' (*Vitis aestivalis*; Summer grape) wine grapes, are already used for in vivo protection against UV-B-induced skin erythema, tested on healthy human volunteers (Tomaino et al., 2006) indicating that efficient protection of grapes against UV-B might have also indirect health benefits for human.

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