The positive response in grape secondary metabolites under controlled stresses: a review

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Summary

Grapevine is cultivated worldwide with great economic importance. In recent years, our knowledge of the physiological and molecular basis of berry quality regulation has substantially increased. Abiotic and biotic stresses, such as deficit irrigation, low temperature, light/UV and microbes, to a certain extent, could improve grape berry quality by enhancing flavor metabolites, colorization or aroma compounds. This review summarizes recent data related to the stress of grape berry development, with special emphasis on secondary metabolism and its response to stresses. A full understanding of how grape berry metabolism responds to different stresses is important to improve the biochemical qualities of grapes and resultant products, such as wine in practice.

K e y   w o r d s : grapevine; controlled stresses; secondary metabolites; positive effect; berry quality.

Introduction

Grapevine (*Vitis vinifera* L.), is one of the most widely cultivated fruit crops worldwide. It is a non-climacteric fruit used as table fruit, dried raisins, and for producing juices, liquors and wines (Coombe and Hale 1973), with production exceeding 75 million tons per year (OIV 2020). Grapes are rich in primary and secondary metabolites, which are the quality determinants and source of health-promoting substances, such as carbohydrates, organic acids, vitamins, minerals, and polyphenols (Bender *et al.* 2020, Pintać *et al.* 2018).

The development of grape berries can be divided into three distinct phases, with a double sigmoid growth curve. Stage I and stage III (the rapid growth phases) are separated by a lag phase (stage II), which occurs 7 to 10 weeks after flowering. During Stage I, stored carbohydrates are used for seed development, cell proliferation and expansion. Organic acid accumulation in vacuoles occurs in this stage, and several phenolic compound precursors such as proanthocy-

anidins are synthesized (Coombe 1992). The transition from stage II to stage III, completed within 24 hours, is named véraison which marks the onset of ripening, characterized by softening and coloring of the berry skin and an enlarged berry size. During this time, sugars and amino acids begin to accumulate rapidly, while organic acid concentrations decrease simultaneously (Coombe 1992, Zoccatelli *et al.* 2013). The result of these changes lead to the establishment of a stabilized sugar to acid ratio, which fundamentally determines the taste of table grapes and the sensory characteristics of wines derived from them (Conde *et al.* 2007). Anthocyanins are synthesized after véraison and reach concentration peak at maturation while proanthocyanidins are synthesized before véraison (Teixeira *et al.* 2013). Towards the end of the stage III, precursors of aroma and aroma compounds (terpenoids and their derivatives, esters, aldehydes and thiols) are synthesized and stored as non-volatile precursors mainly in exocarp vacuoles (Lund and Bohlmann 2006). The exocarp (berry skin) is the main site for the synthesis of major flavor metabolites, such as flavonoids, proanthocyanidins, polyphenols (Teixeira *et al.* 2013). Subtle changes in metabolites, especially secondary metabolites, are sufficient to affect wine sensory quality. Polyphenols, such as anthocyanins, flavonols, proanthocyanidins, stilbenes, and other secondary metabolites, may endow grape organoleptic characteristics and have also been proven to play a protective role in human health (Downey *et al.* 2003, Balik *et al.* 2008, Flamini *et al.* 2013).

The physiological and biochemical compositions of grapes are mainly determined by both genetic and environmental factors (Jackson 2020, Yang *et al.* 2016). In addition to genotypes, research on how biotic and abiotic factors influence grape quality has been broadly covered. Stresses, including deficit irrigation, temperature, light, UV, pathogenic microbes and other environmental microbes, to a large degree, affect grape metabolism and subsequently the biochemical quality of grape and its resultant products. This review summarizes recent data related to the influences of stresses, mainly positive effects, on grape berry development and metabolism from an overview to detailed discussions.

Secondary metabolites in the grape berries

Plants synthesize secondary metabolites to better adapt to the environment. On the other hand, any environmental factors that influence plant growth and development will compositionally and quantitatively trigger changes in secondary metabolites in plant organs, such as grape berries, and then influence the economic value of these products. These secondary metabolites include phenolics, flavonoids, terpenoids, alkaloids and others.

Phenolic compounds: Phenolic compounds in grape berries can be structurally divided into categories of flavonoid (anthocyanins, flavonols [quercetin, kaempferol], flavan-3-ols [monomeric catechins and proanthocyanidins]) and nonflavonoid compounds (hydroxybenzoic and hydroxycinnamic acids and stilbenes [resveratrol]) (CHAVES *et al.* 2010, TEIXEIRA *et al.* 2013, ALONSO *et al.* 2016). Flavonoid and nonflavonoid compounds are synthesized from phenylalanine through the phenylpropanoid synthesis pathway (BUCHANAN *et al.* 2015). Phenylalanine, for its part, is a product of the shikimic acid pathway, which relates the metabolism of carbohydrates to the biosynthesis of aromatic amino acids and other secondary metabolites (FLAMINI *et al.* 2013, GUTIÉRREZ-GAMBOA *et al.* 2021). The total extractable phenolics in grapes are distributed with percentages of 60-70 % in seeds, 20-30 % in skins, and 10 % or lower in the pulp (SHI *et al.* 2003). Due to their close association with grape and wine color, bitter taste, astringency and others, researchers have attempted to promote their biosynthesis in grapes (HORNEDO-ORTEGA *et al.* 2020, LI and SUN 2019).

Flavonoid grape polyphenols: anthocyanins, flavonols, flavan-3-ols: Flavonoids, whose general structure is two phenyl rings and a heterocyclic ring, are grouped into several classes that differ in the oxidation state of the heterocyclic ring (ŠIKUTEN *et al.* 2020). The main classes of flavonoids are anthocyanins, flavonols and flavan-3-ols.

Anthocyanins: Structurally, anthocyanins have the typical flavonoid skeleton C6-C3-C6, which contains a heterocyclic benzopyran ring, a fused aromatic ring, and a phenyl constituent (HE *et al.* 2010). These compounds are synthesized in the cytoplasm but accumulate in vacuoles, and then adopt their distinct color (ŠIKUTEN *et al.* 2020). What produces the red, purple, and blue coloration comes down to the presence and number of hydroxyl groups, methylations, and sugar moieties. The color and stability of anthocyanins are susceptible to the action of pH, light, temperature, and the presence of enzymes, metal ions and co-pigments (BERES *et al.* 2017). Under acidic conditions, anthocyanins appear red but turn colorless at pH 4.0, and purple above pH 4.5. When the pH value increases to alkaline conditions, a blue color is produced (FONTES *et al.* 2011). The main anthocyanins in grapes are glucosides originating from 6 anthocyanins: delphinidin, cyanidin, petunidin, peonidin, malvidin, and pelargonidin (DE LORENZIS *et al.* 2016). As water-soluble pigments, anthocyanins are synthesized *via* the flavonoid pathway in the skins of red grapes during ripening and are also present in the flesh of the 'teinturier' varieties (BURNS *et al.* 2002).

Anthocyanins are responsible not only for the red color and its variations in tonality in grapes and red wines, but also for contributing to the astringency and bitterness of grapes and wines. Studies have shown that certain white grape cultivars, such as 'Sauvignon Blanc', 'Riesling' and 'Chardonnay', contain measurable traces of anthocyanins (ARAPITSAS *et al.* 2015). In addition, anthocyanins are recognized as potential pharmaceutical ingredients, as they possess antidiabetic, anticancer, anti-inflammatory, antimicrobial, anti-obesity, and neuroprotective effects, as well as contribute to the prevention of cardiovascular diseases (KHOO *et al.* 2017).

Flavonols: Flavonols, as co-pigments with anthocyanins, are responsible for stabilizing the color of wines and consequently in their by-products (BERES *et al.* 2017), and in the sensory perception of astringency and bitterness (FERRER-GALLEGO *et al.* 2016). Flavonols constitute a group of flavonoids that vary in color from white to yellow and are closely related in structure to flavones with a 3-hydroxyflavone backbone. They behave as UV- and photo-protectors as they absorb strongly at UV-A and UV-B wavelengths. Therefore, they can be mainly found in the outer epidermis of the skin of both white and red grapes in 3-*O*-glycoside forms, and no reports have shown that these compounds have been detected in the seeds or the pulp of grapes (DOWNEY *et al.* 2003, 2006). However, flavonols are also found in shoots, tendrils, inflorescences, anthers, and leaves (DOWNEY *et al.* 2003). Generally, the red cultivars are regularly richer than the white cultivars. The main representatives of flavonols in red grape berries are myricetin, quercetin and kaempferol (FRAGA 2009). In addition, other compounds, such as isorhamnetin, laricitrin, and syringetin have also been identified (CASTILLO-MUÑOZ *et al.* 2007). However, myricetin, laricitrin, and syringetin were not detected in the white grape cultivars (MATTIVI *et al.* 2006). There are two distinct periods of flavonol synthesis in grape berries, the first around flowering and the second during berry ripening, which are related to the expression of genes that encode the enzyme flavonol synthase (DOWNEY *et al.* 2003). Low temperatures and light have a synergistic effect on the expression of genes within the flavonoid biosynthesis pathway (Azuma *et al.* 2012). After exposure to sunlight, the flavonol concentration increases before the véraison stage, which is induced by the transcription factor genes of the MYB family (MATUS *et al.* 2009).

Flavan-3-ols: Flavan-3-ols, also known as flavanols, are present in grapes as monomers or polymers called proanthocyanidins (PAs) or condensed tannins. The main monomers are (+)-catechin, (−)-epicatechin, (+)-gallocatechin, (−)-epigallocatechin, and (−)-epicatechin-3-*O*-gallate (HORNEDO-ORTEGA *et al.* 2020). The favan-3-ols stabilize the color and sensory characteristics of the wines derived from the grapes due to their astringent and bitter properties (TEIXEIRA *et al.* 2014). Bitter taste perception is enhanced by epicatechin and catechin, while astringency is enhanced by PAs and galloylation. The intensity and duration of astringency can be ascribed to structural properties such as the chain length, the stereochemistry of subunits, and the bond sites between subunits (ŠIKUTEN *et al.* 2020). The monomers and the trimers of PAs contribute to the highest and the

lowest degerees of bitterness, respectively, while monomers are less astringent than dimers or trimers (Šikuten *et al.* 2020). The accumulation of flavan-3-ols in grape berries starts immediately after fruit set, reaches a maximum level around véraison and then decreases in concentration during ripening (Fujita *et al.* 2005). PAs, also known as tannins, result from the polymerization of flavan-3-ols units, and are mainly oligomeric and polymeric forms of (+)-catechin and (−)-epicatechin. Tannins are the most abundant class of soluble polyphenolics in grape berries and are found in the skins, seeds, and stalks of clusters of grapes, which may be the microbial and oak sources in wine. Several studies on the *in vitro* and *in vivo* effects of grape seed proanthocyanidins have exhibited anticancer activity. Furthermore, tannins were found to have a significant ability to scavenge peroxyl radicals in model solutions (Salehi *et al.* 2019).

Non-flavonoid grape polyphenols. Phenolic acids and stilbenes: Non-flavonoid compounds include hydroxycinnamic and hydroxybenzoic acids and stilbenes. Over the past years, these non-flavonoid compounds have attracted increasing interest because of their potential health benefits (e.g., antioxidant, antibacterial, antiviral, anti-cancerogenic, anti-inflammatory, and vasodilatory actions) (Morales-Prieto *et al.* 2020, Scalzini *et al.* 2021).

Phenolic acids: Phenolic acids are divided into two main groups, hydroxybenzoic acids (C6-C1) and hydroxycinnamic acids (C6-C3), and reach a maximum level around véraison, followed by a decrease to a constant amount as the fruit ripens (Fia *et al.* 2022). The concentrations of total hydroxybenzoic and hydroxycinnamic acids were higher in wine grapes than in table grapes. Phenolic acids, which act as co-pigments, are considered color stabilizing agents of young red wines through co-pigmentation with anthocyanins (Heras-Roger *et al.* 2016). In addition, they are also associated with the sensory characteristics of astringency and bitterness (Hornedo-Ortega *et al.* 2020). Individually, the main hydroxybenzoic acids in grapes or wines are gallic, vanillic, and syringic acids. Hydroxycinnamic acids are principally found in skins, and ferulic, caffeic, *p*-coumaric and sinapic acids are the most significant. Hydroxycinnamic acids are synthesized through the shikimate pathway from phenylalanine and tyrosine through the action of phenylalanine ammonia-lyase. In contrast, hydroxybenzoic acids are not phenylpropanoids, and they are synthesized directly from the shikimic acid pathway (Laura *et al.* 2019). Predominantly present in grapes, gallic acid is considered to be one of the most important hydroxybenzoic acids and is the precursor of hydrolyzable tannins (Boido *et al.* 2011). In addition, caffeic and *p*-coumaric acids in grapes and wines can be esterified by the glucose of the anthocyanin monoglucosides forming their acylated derivates (Hornedo-Ortega *et al.* 2020).

The stilbenes: Stilbenes (1,2-diphenylethylene), are considered as phytoalexins, produced by plants for their roles in adaptation and protection against biotic and abiotic stresses. They can be found in the peels, stems and seeds of grapes, and red varieties seem to present higher stilbene contents than white varieties. The structure of stilbenes is composed of two aromatic rings connected by an ethylene bridge forming a C6-C2-C6 chain (Teixeira *et al.* 2014). The two aromatic rings could be substituted by functional groups such as methoxyl, hydroxyl, geranyl or prenyl groups. Moreover, monomeric units can also be coupled, leading to the formation of more complex oligomers, including dimers, trimers and tetramers (Takaya *et al.* 2005). According to record reports, the main stilbenes found in grapes are cis- and trans-resveratrol, piceid, piceatannol, and viniferins (Gutiérrez-Gamboa *et al.* 2021). Among the identified stilbenes, resveratrol is the most popular compound, conferring its anti-inflammatory, anti-oxidative, and anti-aging properties in humans (Corpas *et al.* 2019, Benbouguerra *et al.* 2021). Additionally, the concentration of stilbene in grape berries mainly depends on the ripening stage, generally after véraison and continuing throughout the ripening stage (Adrian *et al.* 2000). Since they are associated with plant resistance, infection with fungal diseases, such as *Botrytis cinerea*, can induce the production of resveratrol, ε-viniferin and piceid (Jeandet *et al.* 1995, Bavaresco *et al.* 1997). Furthermore, infection by *Plasmopara viticola* or other stress factors, such as UV radiation, can induce the synthesis of δ-viniferin and ε-viniferin (Błaszczyk *et al.* 2019).

Aroma compounds: Aroma compounds are secondary metabolites of grape berries that determine the quality of grapes and wines and, hence, for consumer acceptance. More than 1000 volatile aroma compounds with different polarities were detected in grapes and wines, at concentrations ranging from hundreds of milligrams per litre to a few picograms per litre (Ferreira 2010). Part of them are biosynthezised in berries, and the other part results from winemaking and aging (Alem *et al.* 2019). They are classified into three categories according to their source or origin: primary aromas, also known as grape aromas or varietal aromas, are derived from the grapes themselves; secondary (or fermentation) aromas arise from yeast metabolism; and post-fermentative (or aging) aromas arise from chemical reactions that take place during the wine's aging process (Ruiz *et al.* 2019). Aroma compounds are usually located in both the pulp and skin of grapes and are classified into the free aroma and bound (glycosylated) aroma. The free forms are volatile compounds that possess volatile properties, thus contributing to the aroma of berries. On the other hand, the bound glycoside forms comprise non-volatile components that do not directly affect the overall grape or wine aroma; however, they are commonly known as aroma precursors since they undergo hydrolysis to odor-active forms, thereby generating the active odor molecules and enhancing the aromatic characteristics of grapes (Ghaste *et al.* 2015, Yao *et al.* 2021).

Aroma is the result of a complex mixture of multiple compounds (terpenoids, C13-norisoprenoids [Carotenoids], benzenoids, esters, methoxypyrazines, and thiols) (D'Onofrio *et al.* 2018, Garde-Cerdán *et al.* 2018). Among them, terpenoids and C13 norisoprenoid have the lowest perception threshold, thus contributing importantly to the aroma (Román *et al.* 2020). Meanwhile, terpenes, esters and benzenoids are strongly linked to fruity and floral characteristics; C6-aldehydes and alcohols are known to contribute to green leafy aroma characteristics; and meth-

oxypyrazines possess green capsicum characteristics (WU *et al.* 2016). Furthermore, C13-norisoprenoids are generally responsible for different flavors in fruits and wines, such as berry, tobacco, honey, balsamic and violet aromas (PEINADO *et al.* 2004, YUAN and QIAN 2016). Thiols are derived from fatty acid molecules and are usually bound with cysteine or glutathione and are odorless until enzymatic release. At low concentrations, they can provide desirable blackcurrant, citrus and passion fruit aromas to wines (ALEM *et al.* 2019). In recent years, many authors have studied the effects of agronomic practices and environmental factors on aroma compounds, with the aim of being able to modulate and improve the chemical composition of the grape aroma (ALEM *et al.* 2019, PETRETTO *et al.* 2021, VAN LEEUWEN *et al.* 2018).

Stresses positively influence the biochemistry of grape berries

Generally, stresses negatively influence plant growth and development in multiple ways. However, grapevines (*Vitis* spp.) like other plants, have an internal adaptive mechanism to combat abiotic and biotic stress. In viticulture, studies have demonstrated that certain degrees of stress, such as water deficit, low/high temperature, UV radiation, pathogens or other microbe attack, are beneficial for improving grape qualities and characteristics. The biochemical traits impacted by various stresses in grape berries are partially summarized in Tabs 1 and 2.

W a t e r   s t r e s s : Due to global warming, water deficit has become an increasing factor limiting grape production, especially in the dry and warm Mediterranean region of Europe (CHAVES *et al.* 2007). The impacts of water stress on grape quality have been extensively investigated in recent decades. Studies have demonstrated that severe water stress hinders grape development, resulting in physiological disorders and decreasing the grape berry quality. However, large-scale transcriptome and metabolome analyses revealed the metabolic responses to water stress, and many of these modified metabolites positively improved gape quality and characteristics. Certain degrees of water deficit benefit the overall berry quality and have been applied in practices *via* vineyard water management in viticulture (CHAVES *et al.* 2010; CALDERAN *et al.* 2021, CHACÓN-VOZMEDIANO *et al.* 2021). Irrigation of vineyards is strictly controlled or even prohibited under the administration of commercial organizations in high-quality wine producing regions or countries such as Bordeaux, France. In general, mild to moderate water stresses result in smaller berries, and therefore increase the ratio of skin to pulp (ROBY and MATTHEWS 2004, CONDE *et al.* 2007, CALDERAN *et al.* 2021, ZHANG *et al.* 2021). However, total phenol, anthocyanin, proanthocyanidin, aroma compounds and sugar concentrations in berries usually increased compared with well-watered conditions (CHAVES *et al.* 2007, SONG *et al.* 2012, BONADA *et al.* 2015, SAVOI *et al.* 2017, CÁCERES-MELLA *et al.* 2018, ZOMBARDO *et al.* 2020, CALDERAN *et al.* 2021). Flavonol concentration can increase when stress is applied before pre-véraison (CASTELLARIN *et al.* 2007a, DELUC *et al.* 2009 BRILLANTE *et al.* 2017, in 'Chardonnay') or is unaffected (DELUC *et al.* 2009 in 'Caber-

net Sauvignon', SAVOI *et al.* 2017), but may decrease when stress is applied after véraison (CASTELLARIN *et al.* 2007a, ZARROUK *et al.* 2012). With the adoption of large-scale metabolite and transcript analyses, as well as multi-omics and integrated network analyses, studies have indicated that the metabolic response of the grape berries to water stress is related to the complex regulation of several metabolic pathways, possibly determined by common or specific molecular signals (CASTELLARIN *et al.* 2007b, DELUC *et al.* 2009, HOCHBERG *et al.* 2015, ROBY and MATTHEWS 2004, SAVOI *et al.* 2017). SAVOI *et al.* (2017) revealed that the concentrations of phenylpropanoids, carotenoids, zeaxanthin and monoterpenes were upregulated gene expression in response to water stress. Similar results were obtained with the white grape 'Tocai Friulano'. Grapevine berries respond to drought by stimulating the production of phenylpropanoids, monoterpenes, and tocopherols (SAVOI *et al.* 2016). In addition, water-stressed grapevines increased aroma compound concentrations in berries, but decreased undesirable aroma compound concentrations, such as free C6 compounds (hexanal, trans-2-hexenal, and 1-hexanol) (SONG *et al.* 2012).

However, the response of grape to water stress is complex. On the one hand, the effect of secondary metabolites varies with the timing and intensity of stress applied. Pre-véraison water stress treatment performed generally better than post-véraison treatment based on the majority of experiments, resulting in an increase in partial metabolites compared with normal or full water status, although berry size was reduced to some degree (DELUC *et al.* 2009, INTRIGLIOLO *et al.* 2012, ROMERO *et al.* 2013, ZARROUK *et al.* 2016). Post-véraison water stress, in contrast, was less remarkable than pre-véraison treatment on berry secondary metabolites, although it had some positive effects (ROBY and MATTHEWS 2004, INTRIGLIOLO *et al.* 2012, CASASSA *et al.* 2015). Nonetheless, there was still much disagreement among the reported literature, which may be due to differences in the severity and duration of water stress, vine cultivar, climate, soil and altitude.

The grape response to water stresses might be somewhat cultivar-dependent. The effects of water stress on 'Cabernet Sauvignon' seem to differ from those observed in 'Chardonnay' (DELUC *et al.* 2009). Water stress activated the expression of transcripts associated with proline biosynthesis and the phenylpropanoid pathway, with increases in ABA, proline, sugar and anthocyanin concentrations in 'Cabernet Sauvignon', while partially activating the phenylpropanoid, carotenoid and isoprenoid metabolic pathways, promoting the synthesis of flavonols and aromas in 'Chardonnay'. Under similar deficit irrigation, HOCHBERG *et al.* (2015) showed cultivar-specific responses in metabolites between 'Shiraz' and 'Cabernet Sauvignon'. 'Cabernet Sauvignon' (compared with 'Shiraz') exhibited milder metabolic alteration of berry-skin primary metabolites, as well as less variation in °Brix and berry weight, which coincided with the research carried out between 'Tempranillo' and 'Graciano' (NICULCEA *et al.* 2014).

T e m p e r a t u r e : Likewise, heat stress, which is often accompanied by drought, has attracted attention as viticulture is sensitive to climate changes (HANNAH *et al.*

T a b l e 1

Effects of moderate water deficit on the biochemical parameters of grape berries at harvest. Berry weight (BW) or volume (BV), percentage soluble solids (%SS) or °Brix, titrable acidity (TA), total phenols (TP), anthocyanins (As), flavonols (Fs), proanthocyanidins (PAs), abscisic acid (ABA), and aroma. –, not assessed; ↑, increase; ↓, decrease; =, no significant change

Authors	Cultivar(s)	The time applied	Effects on								
			BW/BV	°Brix	TA	TP	As	Fs	PAs	Aroma	ABA
Bonada et al. (2015)	Shiraz	After berry set	↓	↑	↓	↑	↑	-	↑	↑	-
Brillante et al. (2017)	Cabernet Sauvignon	Before véraison	=	↓	↓	-	↑	↑	↑	-	-
Bucchetti et al. (2011)	Merlot	After berry set	↓	=	=	-	↑	-	=	-	-
Cáceres-Mella et al. (2017)	Cabernet Sauvignon	Before véraison	-	=	=	↑	↑	-	↑	-	-
Cáceres-Mella et al. (2018)	Cabernet Sauvignon	Before véraison	-	↑	↑	↑	↑	-	-	↑	-
Casassa et al. (2013)	Cabernet Sauvignon	After berry set	↓	=	↓	-	↑	-	↑	-	-
Casassa et al. (2015)	Cabernet Sauvignon	Before véraison	↓	↓	↓	-	↑	-	↑	-	-
		After véraison	↓	↓	↓	-	=	-	↓	-	-
Castellarin et al. (2007b)	Merlot	Before véraison	↓	=	=	-	↑	-	-	-	-
Castellarin et al. (2007a)	Cabernet Sauvignon	Before véraison	=	↑	-	-	↑	↑	↑	-	-
		After véraison	↓	↑	-	-	↑	↓	↑	-	-
Chaves et al. (2007)	Moscatel	After berry set	↓	=	↓	↑	-	-	-	-	-
	Castelao		↓	↑	↓	↑	-	-	-	-	-
De Royer Dupré et al. (2014)	Grenache Noir	Before véraison	-	-	-	-	-	-	↑	-	-
		After véraison	-	-	-	-	-	-	↑	-	-
Deluc et al. (2009)	Cabernet Sauvignon	Before véraison	↓	↑	=	-	↑	=	-	↑	↑
	Chardonnay		↓	=	↓	-	-	↑	-	↑	↑
Intrigliolo et al. (2012)	Tempranillo	Before véraison	↓	=	↓	↓	↑	-	-	-	-
		After véraison	=	↓	=	↓	↓	-	-	-	-
Koundouras et al. (2009)	Cabernet Sauvignon	After berry set	↓	↑	-	↑	↑	-	=	↑	-
Kyraleou et al. (2016, 2017)	Syrah	After berry set	↓	↓	=	-	↑	-	↑	-	-
Matthews and Anderson (1988)	Cabernet franc	Before véraison	↓	↓	↓	↑	↑	-	-	-	-
		After véraison	↓	↓	↓	↑	↑	-	-	-	-
Olle et al. (2011)	Shiraz	Before véraison	=	-	-	-	↑	-	=	-	-
		After véraison	↓	-	-	-	↑	-	=	-	-
Ou et al. (2010)	Merlot	After berry set	-	↑	↓	-	-	-	-	↑	-
Qian et al. (2009)	Merlot	After berry set	-	-	-	-	-	-	-	↑	-
Santesteban et al. (2011)	Tempranillo	After berry set	↓	=	↓	↑	↑	-	-	-	-
		After véraison	=	=	↓	↑	↑	-	-	-	-
Savoi et al. (2016)	Tocai Friulano	After berry set	↓	↑	=	↑	-	-	↓	↑	-
Savoi et al. (2017)	Merlot	After berry set	↓	↑	=	↑	↑	=	↑	↑	-
Song et al. (2012)	Merlot	After berry set	↓	↑	↓	↑	↑	-	-	↑	-
Talaverano et al. (2018)	Cabernet Sauvignon	Before véraison	-	↑	=	-	-	-	-	↑	-
Vilanova et al. (2019)	Verdejo	Before véraison	↓	=	=	-	-	-	-	↑	-
Zarrouk et al. (2012)	Tempranillo	After berry set	=	=	=	↑	↓	↓	=	-	↑

2013), and the grapevine response to heat stress might also be cultivar dependent (Gashu et al. 2020). Research has helped uncover the effects of temperature on the accumulation of secondary metabolites as well as the biosynthetic pathways involved in their biosynthesis. Grape berry metabolism is sensitive to heat at the flowering and ripening stages. Generally, anthocyanin is suppressed by high temperatures, accompanied by lower acidity and higher sugar concentrations in berries (Mori et al. 2005b and 2007, Yamane et al. 2006, Azuma et al. 2012, Shinomiya et al. 2015, Abeysinghe et al. 2019, Arrizabalaga-Arriazu et al. 2020, Venios et al. 2020). Photosynthesis was also greatly reduced with the consequences of berry size and weight reduction (Hale and Buttrose 1973, Coombe 1987, Camps and Ramos 2012). High temperature affects not only the synthesis but also the stability of existing metabolites. High temperature increased the degradation rate of anthocyanin as well as the inhibition of mRNA transcription of anthocyanin biosynthetic genes (Yamane et al.

2006, Mori et al. 2007). In contrast, optimal conditions such as cool nights and mild temperate days might be favored for berry quality. In some grape varieties, exposing whole vines or clusters to cold temperature enhances accumulation or biosynthesis. Mori et al. (2005a) compared the effects on berries under high night temperature (30 °C) and low night temperatures (15 °C), and found that continuous warm nights generally repressed anthocyanin accumulation in berry skin compared to that of berries grown under cool night conditions, owing to the lower activities of anthocyanin biosynthetic enzymes, particularly UFGT. Similarly, during the 'Kyoho' ripening season under continuous 24 °C, 27 °C and 30 °C temperatures, skin coloration and anthocyanin accumulation were sufficient under 24 °C, while 27 °C or 30 °C showed insufficient coloration and low levels of anthocyanin accumulation, ABA concentration, and anthocyanin biosynthetic gene transcript levels (Shinomiya et al. 2015). Although anthocyanins and proanthocyanidins share several steps in the biosyn-

Table 2

Effects of stress on the biochemical parameters of grape berries at harvest. Berry weight (BW) or volume (BV), percentage soluble solids (%SS) or °Brix, titrable acidity (TA), total phenols (TP), anthocyanins (As), flavonols (Fs), proanthocyanidins (PAs), abscisic acid (ABA), and aroma. −, not assessed; ↑, increase; ↓, decrease; =, no significant change

Factors	Effects on									References
	BW/BV	°Brix	TA	TP	As	Fs	PAs	Aroma	ABA	
Low temperature	↑[1,2]=[3]	↓[1,2,4]	↑[2]↓[4,5]	-	↑[1,4,6,7,8,16]	↑[6]=[4]	↓[1,3]	↑[2,9]	↑[6,7,8]	[1]COHEN et al. (2008); [2]JI and DAMI (2008); [3]COHEN et al. (2012); [4]MORI et al. (2005a); [5]GASHU et al. (2020); [6]AZUMA et al. (2012); [7]SHINOMIYA et al. (2015); [8]YAMANE et al. (2006); [9]CAMPS and RAMOS (2012); [10]PLANK et al. (2019); [11]GOUOTA et al. (2019); [12]ARRIZABALAGA-ARRIAZU et al. (2020); [13]ABEYSINGHE et al. (2019); [14]PASTORE et al. (2017); [15]MORI et al. (2007); [16]SPAYD et al. (2002)
High temperature	↓[2,10,11]=[3]	↓[2,4,5,11]↑[12,13,14]	↓[4]↓[2,11,12,14]	-	↓[4,6,7,8,12,14,15,16]	=[4]↓[6,14]	↑[13,11]=[14]	↑[2,9]	↓[6,7]	[1]CORTELL and KENNEDY (2006); [2]DOWNEY et al. (2004); [3]PEREIRA et al. (2006); [4]SPAYD et al. (2002); [5]DAYER et al. (2020); [6]PRICE et al. (1995); [7]ROUBELAKIS-ANGELAKIS and KLIEWER (1986); [8]AZUMA et al. (2012); [9]ZHOU et al. (2018); [10]GUAN et al. (2016); [11]CZEMMEL et al. (2009); [12]PLANK et al. (2019); [13]JEONG et al. (2004); [14]KOYAMA et al. (2012); [15]SPAYD et al. (2002);
Light exposure	↑[1,2]↓[3,4]	=[2]↑[3,5]	↓[3,4,6]	↑[7]	↑[1,2,4,6,7,8,9,10,15,16,17]↓[3]	↑[1,2,3,4,8,11]	↑[12]↓[9]	↓[12]	=[8]	[16]GERDES et al. (2002); [17]MARAIS et al. (1992); [18]GREGAN et al. (2012)
Shading	↓[1,2,6]↑[3,4]	=[2,6]↓[3,5]	↑[3,4,6]	-	↓[1,2,4,6,8,9,10,13,15]↑[3]	↓[1,2,14]↓[9]	↓[1,2,14]↓[9]	↑[12,18]	=[8]	
UV radiation	=[1]↓[2,3]	=[1]↓[2]↑[4]↓[3]	↑[1]=[4,5]	↑[6]↑[2,3,7,8,11,12,13]	↑[1,9,13]↓[2,7,8]	↑[1,5,9,10,11,12]	-	↑[2]	↑[2]	[1]SPAYD et al. (2002); [2]BERLI et al. (2011); [3]BERLI et al. (2015); [4]GUERRERO et al. (2016); [5]BERLI et al. (2010); [6]AZUMA et al. (2012); [7]ALONSO et al. (2016); [8]BERLI et al. (2008); [9]MARTÍNEZ-LÜSCHER et al. (2014); [10]KOYAMA et al. (2014); [11]GREGAN et al. (2012); [12]LIU et al. (2015); [13]PINTO et al. (2022)
Microbiology										
Botrytis cinerea	-	-	-	-	↑[1]	-	↑[1]	↑[1]	↑[1]	[1]BLANCO-ULATE et al. (2015)
PGPR	-	-	-	-	-	-	-	↑[2,3]	↑[2,3]	[2]SALOMON et al. 2014; [3]SALOMON et al. (2016)
Endophytes	-	↑[4]	-	↑[4,6]	↑[5]	-	-	-	-	[4]YANG et al. (2016); [5]YU et al. (2020); [6]ALEYNOVA et al. (2021)

thetic pathway, there are many differences in their regulation and reactivity. Another experiment on 'Merlot' showed that attenuation of the diurnal temperature fluctuations (cooled in daytime and heated at night) led to higher sugar concentrations, berry weights and anthocyanin concentrations, but lower flavonol and proanthocyanidin concentrations at harvest (COHEN et al. 2008). The same authors on the same variety demonstrated the highest proanthocyanidin concentration in heated berries and the lowest in cooled berries only in the third year, and did not vary during the first two years (COHEN et al. 2012). SPAYD et al. (2002) clarified that moderate temperature increased anthocyanin concentrations, while clusters exposed to higher temperatures led to degradation and decreased grape pigments. In addition, cool regions typically produced grapes with higher malic acid concentrations; conversely, grapes grown in warmer regions tended to have lower acidity (KOUNDOURAS et al. 2006). On the other hand, cool temperatures increased the concentrations of C6 volatile aldehydes in 'Traminette' berries, whereas the monoterpene concentrations were higher in hot conditions than in cool conditions (JI and DAMI 2008).

Light/UV radiation: The responses of plants to light are complex. Biosynthesis of phenolic compounds is sensitive to light environments, which reflects the possible role of UV protectants. Adequate, but not excessive, exposure of grapes to sunlight has long been known to be beneficial for grape and wine quality, especially red wine quality. High light exposure can increase the activity of phenylalanine ammonia lyase (PAL) resulting in higher concentrations of phenolics and anthocyanins (ROUBELAKIS-ANGELAKIS and KLIEWER 1986). The C13-norisoprenoid concentration was increased substantially in sun-exposed bunches of 'Riesling' and 'Chenin blanc' berries (GERDES et al. 2002, MARAIS et al. 1992). However, it is often unclear whether sun exposure effects arise from higher density lights or from UV radiation, which are both consequences. Many studies have demonstrated that the synthesis of flavonols is a light-dependent process. In different varieties, such as 'Pinot noir', 'Shiraz' and 'Merlot', light has been confirmed to promote the accumulation of flavonols,

while anthocyanin was not affected. In 'Shiraz', shading applied to bunches of grapes prior to flowering was found to significantly decrease flavonol synthesis, while in the exposed fruit, the per berry flavonol concentration increased during ripening (Downey *et al.* 2004). In 'Merlot', sun-exposed clusters had almost 10 times greater concentrations of total flavonols than shaded clusters (Spayd *et al.* 2002). Interestingly, the results from the same clusters were consistent with the previous results that berries on the sunny side had higher levels of quercetin glycoside than berries from the shade side (Price *et al.* 1995). Light can not only influence flavonol concentrations but can also modulate the expression of flavonol synthase (*VvFLS*), a key flavonol structural gene, and of *VvMYBF1*, a transcriptional regulator of flavonoid synthesis (Downey *et al.* 2004, Czemmel *et al.* 2009, Koyama *et al.* 2012). In addition to flavonols, Cortell and Kennedy (2006) found that cluster shading also reduced the concentration of anthocyanins and proanthocyanidins in the fruit at harvest in 'Pinot noir' grapes. Similarly, Jeong *et al.* (2004) pointed out that the expression of anthocyanin biosynthesis genes was suppressed in shading treatments. Light and low temperature appear to have a synergistic effect on berry quality. Sufficient anthocyanin accumulation was observed under low temperature (15 °C) plus light treatment in grape skin through the regulation of flavonoid biosynthesis pathway genes, whereas high temperature (35 °C) or dark treatment severely suppressed anthocyanin accumulation (Azuma *et al.* 2012). The experiment of exogenous 24-Epibrassinolide (EBR) and light on the mechanism of anthocyanin and proanthocyanidin accumulation in grape berries, showed that a large quantity of anthocyanins accumulated in the grape skins under light treatments, whereas dark treatments significantly suppressed anthocyanin accumulation (Zhou *et al.* 2018).

Additionally, UV plays a relevant role in grapevines in the production of certain important chemical compounds that directly contribute to grape quality. Smart (1987) pointed out that high levels of radiation before véraison would cause sunburn damage on grapes. However, exposure of grape bunches to radiation has shown positive effects on skin phenolic accumulation, also berry aroma and aroma precursor profiles during ripening (van Leeuwen and Destrac-Irvine 2017). In several studies, high levels of UV-B were reported to enhance the accumulation of UV-absorbing compounds, including flavonoids and related phenolics (Berli *et al.* 2008). UV-B was also known to up-regulate some key biosynthetic genes of flavonols and anthocyanins, resulting in an increased sugar and phenolic concentration and a change in their profile (Martínez-Lüscher *et al.* 2014, Alonso *et al.* 2016). Studies showed that flavonol levels, particularly quercetin and kaempferol glycosides, accumulated to maximum concentrations at véraison by exposure to UV-B, while concentrations of methoxypyrazines and amino acids were promoted through canopy shading by leaf retention in the fruiting zone (Gregan *et al.* 2012, Liu *et al.* 2015). Except for compound enhancement, UV-B significantly triggered grape berry ripening (Berli *et al.* 2011). UV-C was applied daily for three days before the harvesting of the table grape variety 'Crimson Seedless',

and an 86-fold stilbenoid level increase in the grapes was achieved (Guerrero *et al.* 2016). In addition, total phenolic compounds, total anthocyanins, and *cis*-resveratrol tended to increase when UV-C radiation was applied to 'Concord' grapes after harvest (Pinto *et al.* 2022). Notwithstanding the above, UV-B is also known to up-regulate genes encoding PAL and chalcone synthase (CHS), which are regulatory enzymes of the phenylpropanoid and flavonoid biosynthetic pathways (Berli *et al.* 2010) .

M i c r o b i o l o g y : In addition to the abiotic factors as discussed above, the effects of ambient microorganisms on grape quality such as pathogens and rhizosphere microbes were also considered (Reynolds 2001, Hong *et al.* 2012, Salomon *et al.* 2016). Well-known 'noble rot' wines (also known as botrytized wines) are made from plant pathogen *Botrytis cinerea*-infected berries, and special components in *B. cinerea*-infected grape berries have been detected (Blanco-Ulate *et al.* 2015). Botrytized wines have been made since the 16th century, primarily in the Tokaj (Hungary), Rheingau (Germany), and Sauternes (France) regions, and are also are produced in increasing amounts in Australia, New Zealand and South Africa. *B. cinerea* is a fungal plant pathogen that causes necrotic lesions on a wide range of plants and fruit, leading to economic and quality losses in wine production. However, unlike bunch rot, noble rot results from *B. cinerea* infections of ripe or overripe grapes under particular climatic (*i.e.* moist nights, foggy mornings, and dry days) and edaphic (*i.e.* low-nutrient and well-drained soils) conditions (Magyar 2011, Blanco-Ulate *et al.* 2015). During ripening, cell wall and cuticle modifications lead to grape berry softening and microfractures on the surface, resulting in vulnerability to pathogen infection (Cantu *et al.* 2008, 2009). *B. cinerea* multiplies on mature grape skin and penetrates into the grape skin for nutrient consumption through the secretion of extracellular enzymes (Valette-Collet *et al.* 2003, Cilindre *et al.* 2008, Hong *et al.* 2012). Hence, infections induce metabolic alterations favoring the synthesis of a variety of compounds that contribute to wine flavor and aroma as well as the concentration of sugars. In a study of *B. cinerea* infected berries of 'Sémillon', noble rot altered the metabolism as well as ripening processes, by promoting the biosynthesis of terpenes and fatty acid aroma precursors (Blanco-Ulate *et al.* 2015). Interestingly, *B. cinerea* altered grape metabolism and induced the synthesis and accumulation of anthocyanins in berries from the white grape variety 'Sémillon' as a result of *B. cinerea* infection (Blanco-Ulate *et al.* 2015).

Furthermore, some of bacteria, such as epiphytic or endophytic plant growth-promoting rhizobacteria, have been reported to enhance plant growth while improving resistance towards biotic and abiotic stress in grapevines (Ait Barka *et al.* 2006, Trotel-Aziz *et al.* 2008). Inoculation with arbuscular mycorrhizal fungi increased the intensity of CO_2 assimilation and stomatal conductance for water in the grapevines tested (Mikiciuk *et al.* 2019). Salomon *et al.* (2014) reported that five bacteria isolated from the rhizosphere and roots of *Vitis vinifera* L. in vineyards of Argentina, act as stress alleviators by diminishing water losses in correlation with increases in ABA. These bacteria

also elicited the synthesis of terpenes, helping grapevines cope with stresses (Salomon *et al.* 2014, 2016). The other microbes, endophytes, abundantly distributed within grape leaves, have been intensively studied during the past several decades for the possible application of endophytic fungi as metabolic regulators in viticulture. Eight strains of fungal endophytes were re-inoculated to field-grown grapevines, and it was found that the physiochemical status of the grapevines was reshaped to different degrees (Yang *et al.* 2016). Yu *et al.* (2020) showed that exposure to fungal endophytes could quantitatively and compositionally modify anthocyanins in grape cells. In another study, after co-cultivation with different strains of endophytic bacteria for 2 weeks, the total stilbene content of the *V. amurensis* cell was increased 2.2-5.3-fold, while it increased 2.6-16.3-fold when co-cultivated with endophytic fungi (Aleynova *et al.* 2021). Additionally, Dwibedi and Saxena (2018) found that some endophytic fungi isolated from the stem and leaf tissues of *V. vinifera* possessed resveratrol-producing ability. Seven strains of endophytic fungi isolated from 'Cabernet Sauvignon' were deduced to have the capability of producing resveratrol, especially the fungus C2J6 which has stable genetic properties and produces high levels of resveratrol (Liu *et al.* 2016). These results attest to the special ability of endophytes to produce the same or similar bioactive substances as host plants. Thus, the interactions between endophytes and grapevines deserve a thorough investigation.

A B A :   a   t o o l   t o   e n h a n c e   g r a p e   q u a l i t y   a n d   t o   c o n t r o l   a b i o t i c   s t r e s s : In addition to ethylene, ABA, known as a stress-associated plant hormone, can be considered to be another ripening regulation factor, for its concentration increased dramatically at the onset of ripening and exogenous ABA application on pre-véraison berries hastened ripening (Coombe and Hale 1973, Deluc *et al.* 2007, Berli *et al.* 2011, Pilati *et al.* 2017). Moreover, exogenous ABA treatments on the berries were reported to enhance the production of several metabolites involved in fruit ripening, thereby promoting fruit ripening (Jeong *et al.* 2004, Giribaldi *et al.* 2010, Koyama *et al.* 2010, Balint and Reynolds 2013, Berli *et al.* 2015). Similar results were obtained by groups Koyama *et al.* (2018) and Vergara *et al.* (2018); the application of exogenous ABA has been shown to increase the expression of the VvMYBA1 and VvMYAB2 transcription factors (involved in the regulation of the biosynthetic genes chalcone isomerase, flavanone 3-hydroxylase gene, and anthocyanidin 3-*O*-glucosyltransferase of the anthocyanin pathway) and give rise to an increase in berry color and anthocyanin synthesis. In addition, exogenous applications of ABA increased the total phenolic compound concentration of xylem sap extracted from 'Pinot noir' vines (Meyer and Kirkpatrick 2011). The application of ABA increased the concentration of skin anthocyanins and proanthocyanidins, although these positive effects were not reflected in 'Monastrell' (syn. 'Mourvedre') wines (Ruiz-García *et al.* 2013); however, in another report, the concentrations of total phenolics, proanthocyanidins, flavonoids and anthocyanins were higher in the wine produced with ABA-treated 'Yan73' grapes than in the wine from untreated grapes (Xi

et al. 2013). The antioxidant capacity, anthocyanins and phenolic concentration of 'Muscadine' grapes were enhanced by ABA treatment, while the average berry weight, TSS and pH of the juice were not affected (Sandhu *et al.* 2011).

To date, considerable progress has been made on the role of ABA in the regulation of fruit ripening. However, the mechanisms of ABA action remain to be elucidated, and there is still much to explore. ABA is also believed to play a crucial role in plant adaptation to adverse environmental conditions, including drought, temperature, light, and salinity (Leng *et al.* 2014). Water stress can increase ABA concentrations in the leaves of grapevine (Okamoto *et al.* 2004). As a determinant factor of stomatal closure, ABA controls both transpiration and assimilation, promoting expansive cell growth by saving leaf water and reducing xylem tension, likely altering structural growth by limiting CO_2 entry (Ferrandino and Lovisolo 2014, Pantin *et al.* 2012). Aquaporins are another target for ABA regulating water and carbon fluxes. In response to water stress, ABA loading by xylem to perivascular tissues acts as a signal to trigger aquaporin-mediated parenchyma-to-xylem radial water flow during embolism refilling (Kaldenhoff *et al.* 2008). Berli *et al.* (2010) suggested that the grape leaf antioxidant defence system was activated by UV-B radiation with ABA acting downstream in the signaling pathway. While in leaves of maize, Tossi *et al.* (2009) suggested that UV-B perception triggered an increase in ABA concentration, which activated NADPH oxidase and hydrogen peroxide generation, and then, a nitric oxide (NO) synthase-like-dependent mechanism increased NO production to maintain cell homeostasis and attenuate UV-B-derived cell damage. Not only can the ABA-mediated effects of water stress and UV-B radiation influence grape berry secondary metabolites, but in addition, a positive effect of ABA-mediation on anthocyanin accumulation in response to heat and cold was demonstrated. Mori *et al.* (2005b) reported that the total anthocyanin concentration of 'Pinot noir' was greatly reduced under high night temperatures (30 °C); however, the suppressive effect was annulled when clusters were sprayed with ABA, and the total anthocyanin concentration was almost the same as under low night temperatures (15 **°C**).

Conclusion and Perspectives

From the above-mentioned overview of published information, one may summarize that grape berries function as a sophisticated biochemical factory. In this factory, they synthesize phenolic and aroma compounds, import and accumulate water, minerals, sugar, organic acids. Abiotic and biotic stress modifies growth and development of grapevine. The accumulation of secondary metabolites in berry pulps, seeds and skins of secondary metabolites is derived by the response to stress at the berry level. Thus, the development of viticulture practices for optimizing primary and secondary metabolites in challenging environments is an important issue, reflecting on an enhancement of table grape and wine quality. To date, by means of

high-throughput transcriptomic, proteomic, metabolomic and phenomic approaches, many scientific advances have achieved in better understanding of berry metabolism and composition, and of their variations; however, the current knowledge on the particular mechanisms is still far from well understood. In the context of climate change, much effort is underway to reveal how endogenous and external signals are perceived by the grape, thus modulating ripening, metabolic pathways, and hence berry composition. In this regard, future investigations involving genetic diversity and metabolic pathways in response to environmental conditions also deserve more attention.

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