

# The Influence of Environmental Conditions and Vineyard Management Practices on the Composition and Content of Carotenoids in Grapevines (*Vitis vinifera* L.). A Review

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**Carotenoids are plant pigments that are important for photosynthesis and photo-protection. In recent years there has been great interest in the role of carotenoids in grapevines. The reason for this interest is that carotenoids are substrates for the synthesis of C13-norisoprenoids, which have a major influence on wine aroma. To optimise the concentration of C13-norisoprenoids in grapes and wine, the environmental conditions and vineyard management practices that may affect carotenoid metabolism in grapes need to be better understood. This paper reviews recent studies on vineyard management practices in terms of carotenoid accumulation, discusses grapevine plasticity, and provides new perspectives for understanding grapevine physiology in response to environmental conditions that affect carotenoid synthesis.**

## INTRODUCTION

Plant pigments are compounds perceptible to humans that can detect reflected or transmitted light with wavelengths between 380 and 730 nm. The most important classes of plant pigments are chlorophylls, anthocyanins and carotenoids. They impart orange/red, purple/blue, yellow and green colour to plants by acting as a visible signal to attract insects, birds and other animals for pollination and seed dispersal (Nzekoue *et al.*, 2022; Sun *et al.*, 2022). They also protect plants against UV and light damage (Matus *et al.*, 2016).

Today, the grape and wine industry is facing new challenges related to climate change. Air temperature, solar radiation, water availability in the soil and CO<sub>2</sub> concentration in the atmosphere are among the most important abiotic factors influenced by global warming, affecting vine development and grape ripening (Rienth *et al.*, 2021). The continuous depletion of the ozone layer over the last 50 years has led to an increase in UV radiation (Mackerness, 2000), forcing changes in plant physiology and development. Climate changes affect the vegetative growth and reproductive development of grapevines and affect the yield and quality of grapes (Van Leeuwen & Darriet, 2016). High and sudden exposure of bunches to sunlight can lead to photo-oxidative damage and sunburn, especially if the ambient temperature is too high (Torres *et al.*, 2021). Sunburn can affect the composition of the grapes, which can lead to significant economic losses due to a reduced yield and quality of the grapes (Yan *et al.*, 2020).

The grape berry has developed adaptations to mitigate the effects of excessive solar radiation, including

the accumulation of secondary metabolites (Gambetta *et al.*, 2022). Carotenoids are lipid-soluble plant pigments synthesised in the chloroplasts and chromoplasts of fruits and vegetables, where they play an active role in protecting plants from increased light intensity (Sun *et al.*, 2022). The composition and content of carotenoids in grapes are regulated by environmental conditions, phenological stage and variety characteristics (Oliveira *et al.*, 2004; Joubert *et al.*, 2016; Young *et al.*, 2016). Lower concentrations of carotenoids may be associated with shaded fruit, either through direct actions such as canopy management or indirectly through increased fertilisation or irrigation, resulting in a more vigorous canopy (Oliveira *et al.*, 2003; Bindon *et al.*, 2007; Gutiérrez-Gamboa *et al.*, 2018). The vine can react to increased solar radiation by changing the composition of the berries (Asproudi *et al.*, 2020) and increasing the concentration of carotenoids (Bureau *et al.*, 1998; Razungles *et al.*, 1996). Stress caused by water scarcity can also lead to an increase in carotenoids, as plants release excess energy from photosynthesis via the xanthophyll cycle in the form of heat (Hirschberg, 2001).

Since carotenoids are substrates for C13-norisoprenoid synthesis (Young *et al.*, 2012), higher carotenoid concentrations, and thus higher substrate availability, can lead to higher concentrations of C13-norisoprenoids in sun-exposed grapes (Mendes-Pinto, 2009). C13-norisoprenoids are secondary metabolites in grapes that have a positive influence on the complexity and quality of wine aroma. Many different C13-norisoprenoids have been identified in grapes and wine, but only a few of them affect aroma.

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These include  $\beta$ -damascenone,  $\beta$ -ionone, TDN, TPB and vitispirane (Yuan & Qian, 2016), which impart fruity and floral notes to wines. Sun exposure, higher temperatures and mild water stress are associated with an improvement in grape quality, and result in grapes with higher levels of sugars, polyphenolic and volatile compounds, and lower total acidity (Diago *et al.*, 2012). This has a positive effect on the sensory characteristics of the wine, as fruit and floral aromas are emphasised while vegetal and green aromas are reduced (Mendes-Pinto, 2009; Young *et al.*, 2016).

The altered microclimate due to climate change leads to stress responses, acclimatisation and altered quality-related metabolites in grape berries (Rienth *et al.*, 2021). High air temperatures can lead to changes in aroma compounds, leading to the conclusion that, with a further increase in air temperature due to climate change, the perception of overripe fruit notes will increase, as is now the case in hot years (Pons *et al.*, 2017). This may affect the organoleptic properties of wine (Van Leeuwen & Darriet *et al.*, 2016). Therefore, the traditional practices of viticulture and winemaking, as well as the typicality of the assortment, sensory characteristics and style of wines from certain wine-growing regions, are increasingly being questioned. For this reason, viticulture must adapt to the new climatic conditions by adopting new cultivation techniques, resistant varieties and ampelotechnical practices, but also finding new regions for the production of certain styles of wine (Fraga *et al.*, 2012).

Understanding vine physiology in response to environmental conditions may allow the exploration of berry metabolic plasticity in relation to desired wine styles

and could help grape growers make appropriate vine-manipulation decisions to produce the desired aromatic wine profile. The present review aims to demonstrate the influence of environmental conditions and vineyard management practices on the composition and content of carotenoids in grapevines, which can serve as a basis for grape growers and oenologists to synthesise aroma compounds in wine (C13-norisoprenoids).

## STRUCTURE AND SYNTHESIS OF CAROTENOIDS

### The structure of carotenoids

Carotenoids are isoprenoid compounds that belong to the family of terpenes with 40 carbon atoms (tetraterpenes). More than 700 carotenoids have been identified in plant tissues. Most carotenoids consist of eight isoprene units with a 40-carbon skeleton. Their general structure usually consists of a polyene chain with nine conjugated double bonds and an end group at both ends of the polyene chain. The carbon-carbon double bonds can be in the *cis* or *trans* isomer configuration, depending on the arrangement of the substituents. Based on their structure there are two classes of carotenoids, namely carotenes and xanthophylls (oxygenated carotenes). The structure and synthesis of carotenoids has been studied in detail by Tanaka *et al.* (2008) (see Fig. 1).

### The synthesis of carotenoids

Carotenoids are synthesised from isopentenyl pyrophosphate (IPP), which is derived from glyceraldehyde-3-phosphate and pyruvate via the methyl erythritol-4-phosphate (MEP) pathway in the plastids (Tanaka *et al.*, 2008). The condensation of four IPPs produces geranylgeranyl

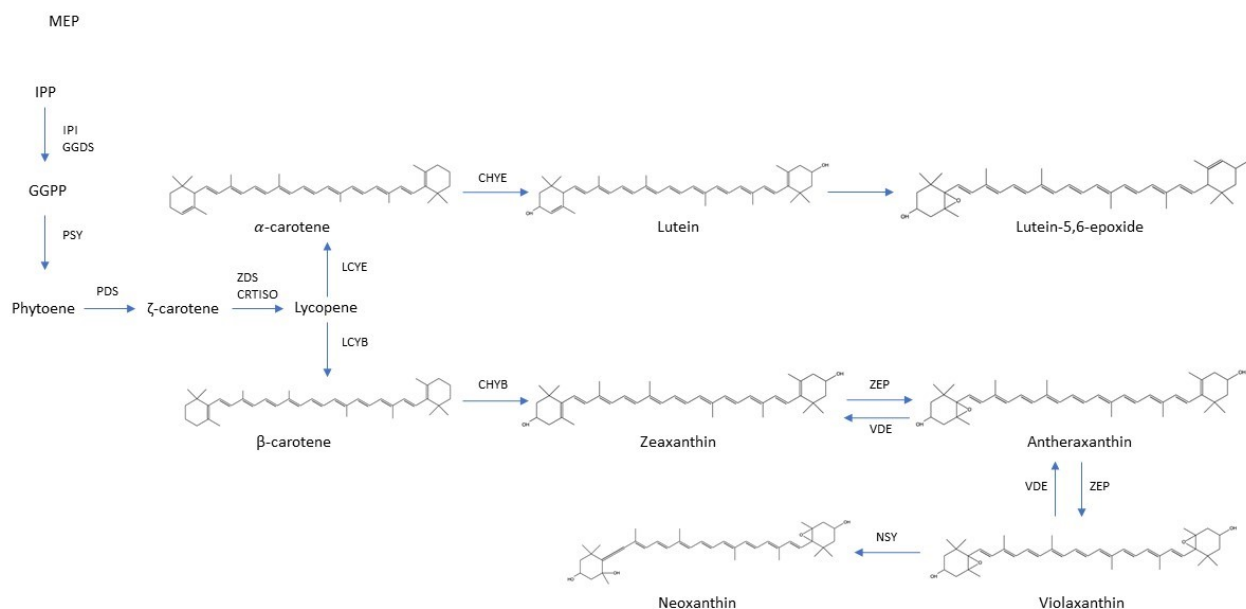


FIGURE 1

Synthesis and structure of different grape carotenoids: MEP – methyl erythritol-4-phosphate pathway; IPP – isopentenyl pyrophosphate; IPI – isopentenyl pyrophosphate isomerase; GGDS – geranylgeranyl diphosphate synthase; GGPP – geranylgeranylpyrophosphate; PSY – phytoene synthase; PDS – phytoene desaturase; ZDS –  $\zeta$ -carotene desaturase; CRTISO – carotenoid isomerase; LCYE – lycopene  $\epsilon$ -cyclase; LCYB – lycopene  $\beta$ -cyclase; ZEP – zeaxanthin epoxidase; VDE – violaxanthin de-epoxidase; NSY – neoxanthin synthase.

pyrophosphate (GGPP), and two GGPPs form phytoene, the first C40 carotenoid. Two enzymes, phytoene desaturase (PDS) and  $\zeta$ -carotene desaturase (ZDS), are responsible for the formation of phytofluene,  $\zeta$ -carotene, neurosporene and lycopene by adding conjugated double bonds. An increase in the number of conjugated double bonds leads to the formation of red lycopene, resulting in the formation of carotenoids with one  $\beta$ - and one  $\epsilon$ -ring ( $\alpha$ -carotene and its derivatives) or two  $\beta$ -rings ( $\beta$ -carotene and its derivatives).  $\alpha$ - and  $\beta$ -carotenes are further modified by hydroxylation or epoxidation, resulting in a variety of compounds (Tanaka *et al.*, 2008). The most important xanthophylls include neoxanthin, lutein, and flavoxanthin. The epoxidation of zeaxanthin catalysed by zeaxanthin epoxidase (ZEP) produces violaxanthin, which can be converted to neoxanthin by neoxanthin synthase (NSY) (Keller, 2010). The formation of violaxanthin from the conversion of  $\beta$ -carotene by activation of the xanthophyll cycle is described in Baumes *et al.* (2002).

The most abundant carotenoids in grapes are  $\beta$ -carotene and lutein (in the order of mg/kg), which account for 60% to 85% of the total carotenoid concentration in grape berries, while neochrome, neoxanthin, violaxanthin, luteoxanthin, flavoxanthin, lutein-5,6-epoxide, zeaxanthin and *cis*-isomers of lutein and  $\beta$ -carotene are present in smaller amounts (in the order of  $\mu$ g/kg) (Guedes de Pinho *et al.*, 2001; Mendes-Pinto, 2009; Fariña *et al.*, 2010; Kwasiewski *et al.*, 2010). Carotenoids are generally concentrated in the skin of the grapes (65%), while the rest is concentrated in the pulp (Guedes de Pinho *et al.*, 2001). The abundance of  $\beta$ -carotene and the xanthophylls neoxanthin, neochrome a, flavoxanthin and lutein is well documented in grape berries before véraison, while their concentrations decrease before or at véraison (Razungles *et al.*, 1996, 1998; Oliveira *et al.*, 2003, 2004; Bindon *et al.*, 2007; Yuan & Qian, 2016), which is due to the increased activity of carotenoid cleavage dioxygenase (CCD). The gene responsible for this, VvCCD1, was identified in research by Mathieu *et al.* (2005) and is induced in the early stages of grape berry development. Three other xanthophylls, namely violaxanthin, luteoxanthin and lutein-5,6-epoxide, appear in grapes after véraison, when the sugar concentration reaches about 160 g/L (Razungles *et al.*, 1996), although Yuan and Qian (2016) showed that neochrome b and violaxanthin may be synthesised from the pea-size stage until véraison, and then degraded after véraison. Carotenoids lutein,  $\beta$ -carotene and xanthophylls were also identified in grapevine leaves (in order of mg/kg). They are also synthesised during the first stage of berry growth and slowly decrease during ripening (Filimon *et al.*, 2016; Nzekoue *et al.*, 2022).

#### THE ROLE OF CAROTENOIDS IN PLANTS AND IN HUMAN HEALTH

Carotenoids are secondary metabolites that are responsible for various biological functions. They play an important role as plant pigments, giving flowers and fruits a yellow to red colour (Osorio, 2019). Carotenoids are essential for the production of the plant phytohormones abscisic acid (ABA) and strigolactone (Cazzonelli, 2011).

Carotenoids are natural plant pigments that play an important role in photosynthesis and photoprotection. They

accumulate in photosynthetic tissue as part of the photosystem II to protect tissues from light damage (Sun *et al.*, 2022). When too much oxygen is produced during photosynthesis in response to increased light intensity, it becomes toxic due to the formation of free radicals, so carotenoids, especially lutein and  $\beta$ -carotene, act as singlet oxygen scavengers (Hirschberg, 2001). They are also involved in dissipating excess light energy and converting it into heat by converting violaxanthin to zeaxanthin via antheraxanthin in the so-called xanthophyll cycle, a process that is controlled by increased light intensity. When the light intensity decreases, zeaxanthin is converted back into violaxanthin (Hirschberg, 2001). For this reason, the concentration of zeaxanthin and antheraxanthin in grapevine leaves increases in the morning and decreases in the evening (Keller, 2010).

Carotenoids have a positive effect on human health as they have antioxidant and anti-cancer properties (Pezzuto, 2008).  $\alpha$ - and  $\beta$ -carotene are important sources of vitamin A in the human diet, which is important for the eyes and the immune system. Carotenoids are widely used as food colorants and in the pharmaceutical industry (Tanaka *et al.*, 2008).

#### DEVELOPMENT OF C13-NORISOPRENOIDS FROM CAROTENOIDS

Carotenoids are unstable compounds due to their double-bonded conjugated structures. Therefore, their degradation in the berries during grape ripening seems to be due to a process of bioconversion of these compounds. This process produces different compounds, such as C13-norisoprenoids, which are responsible for the typical aromas of some grape varieties. These mechanisms are enzymatic or non-enzymatic reactions (Baumes *et al.*, 2002; Winterhalter *et al.*, 2002). The non-enzymatic reactions are stimulated by environmental conditions: light, temperature and oxygen. The enzymatic reaction is catalysed by carotenoid cleavage dioxygenase (CCD) (Mathieu *et al.*, 2005), followed by its degradation, either directly or via glycosylated intermediates (aroma precursors) (Baumes *et al.*, 2002). The aroma compounds are then released during fermentation and wine ageing by enzymatic and acid hydrolysis (Skouroumounis & Sefton, 2000).

Many different C13-norisoprenoids have been identified in grapes and wine, but only some of them affect aroma. These include  $\beta$ -damascenone,  $\beta$ -ionone, TDN, TPB and vitispirane.  $\beta$ -damascenone is responsible for fruity and floral notes in wine, while  $\beta$ -ionone gives a violet aroma to red wine (Darriet *et al.*, 2012). TDN has a detrimental effect on aroma due to its kerosene-like odour, while vitispirane imparts camphor/eucalyptus aromas to wine (Eggers *et al.*, 2006).

The correlation between carotenoids and C13-norisoprenoids in grape berries is compound-dependent, suggesting a dependence on enzyme activity and specificity (Yuan & Qian, 2016). The formation of TDN from lutein under acidic conditions has been illustrated in research by Marais (1992), while neoxanthin may be an important precursor for the formation of  $\beta$ -damascenone (Mendes-Pinto, 2009). In a study by Mathieu *et al.* (2005), the possible formation of  $\beta$ -ionone from zeaxanthin was investigated.

The researchers Guedes de Pinho *et al.* (2001) and Mendes-Pinto *et al.* (2005) even found carotenoids in Port wines from the Douro Valley. These possibly were extracted from the berry skin by ethanol added during alcoholic fermentation, but their concentration was lower than in the grapes. While the wines had lower levels of lutein and  $\beta$ -carotene, they were richer in oxygenated xanthophylls such as neoxanthin, violaxanthin and luteoxanthin.

#### DIFFERENCES BETWEEN GRAPEVINE VARIETIES IN CAROTENOID COMPOSITION AND CONTENT

The concentration of carotenoids in grapes and leaves can vary depending on environmental conditions, phenological stage and variety (Oliveira *et al.*, 2004; Filimon *et al.*, 2016; Joubert *et al.*, 2016; Young *et al.*, 2016). Although research shows that lutein and  $\beta$ -carotene are the most abundant carotenoids in grapes, their ratio depends on the grape variety and wine region. Higher levels of  $\beta$ -carotene compared to lutein were found in Tempranillo and Garnacha, with  $\beta$ -carotene ranging from 77% in Tempranillo to 81% in Garnacha, and lutein ranging from 17% in Garnacha to 21% in Tempranillo. Zeaxanthin was the least abundant carotenoid, varying between 1.3% (in Tempranillo) and 2.5% (in Garnacha), in the Rioja wine region in northern Spain (Gutiérrez-Gamboa *et al.*, 2018). Similar results were obtained by Crupi *et al.* (2010), who found that the concentrations of  $\beta$ -carotene in Chardonnay, Merlot, Primitivo and Negroamaro grown in the Italian region of Apulia were two to four times higher than those of lutein. Yuan and Qian (2016) discovered that the major carotenoids in Pinot noir grapes were lutein and  $\beta$ -carotene, with the lutein content almost twice that of  $\beta$ -carotene, while neochrome a, neochrome b, neoxanthin, violaxanthin and flavoxanthin were found in smaller amounts. In Nebbiolo (Asproudi *et al.*, 2020) and in Petit Verdot and Cabernet franc (Hickey *et al.*, 2018), the concentration of the two carotenoids was very similar. The concentration in the leaves was similar to that in the grapes. The levels of lutein ranged from 32 mg/g to 66 mg/g and those of  $\beta$ -carotene from 19 mg/g to 49 mg/g of dry weight (Castagna *et al.*, 2017).

In the study by Asproudi *et al.* (2020), the concentration of lutein and  $\beta$ -carotene varied between 3.5 and 9.7 mg/kg in the berries of Nebbiolo grapes. Oliveira *et al.* (2004) studied the concentrations in eight varieties from the Douro Valley, with concentrations of lutein and  $\beta$ -carotene ranging between 300  $\mu$ g/kg and 800  $\mu$ g/kg in the berries and of neoxanthin, violaxanthin and luteoxanthin ranging between 10  $\mu$ g/kg and 60  $\mu$ g/kg in the berries. Similarly, Yuan and Qian (2016) showed concentrations of lutein and  $\beta$ -carotene from 100  $\mu$ g/kg to 600  $\mu$ g/kg in the berries and of neoxanthin, violaxanthin and flavoxanthin from 10 to 60  $\mu$ g/kg in the berries of Pinot noir grapes.

#### THE INFLUENCE OF ENVIRONMENTAL CONDITIONS ON THE COMPOSITION AND CONTENT OF CAROTENOID IN GRAPEVINES

Grape varieties respond to changes in the environment and viticultural practices by altering the composition of the berries, which means they can produce different types and styles of wine (Young *et al.*, 2016). This ability of a single

genotype to produce alternative phenotypes as a result of environmental changes is referred to as phenotypic plasticity (Bradshaw, 1965; Arnold *et al.*, 2019). The concentration of carotenoids in grapes and leaves is related to the physiological processes of the vine, which depend on environmental conditions such as temperature, solar and UV radiation, soil properties, vineyard management, phenological stage and variety (Razungles *et al.*, 1996; Oliveira *et al.*, 2004; Kwasniewski *et al.*, 2010; Berli *et al.*, 2013; Castagna *et al.*, 2017; Gutiérrez-Gamboa *et al.*, 2018; Hickey *et al.*, 2018; Asproudi *et al.*, 2020; Doupis *et al.*, 2020; Rienth *et al.*, 2021). To better understand plasticity in relation to carotenoid synthesis, it is important to study grape varieties under different environmental conditions and at different stages of berry development.

#### Sunlight and temperature

The influence of sunlight on grape berry metabolism is complex. Solar radiation can modulate the development of the vine and influence metabolic processes in the berries. Direct sunlight can cause stress due to dehydration and increased temperature (González-Barreiro *et al.*, 2015), but it can also have a positive effect by causing a greater accumulation of sugars, anthocyanins and other polyphenolic compounds, as well as photosynthetic pigments (Fariña *et al.*, 2010; Song *et al.*, 2015).

Carotenoids are photosynthetic pigments whose synthesis in grapes continues from the early stages of berry development until véraison (Oliveira *et al.*, 2003). Sunlight exposure increases the concentration of carotenoids until véraison, and then affects their degradation (Razungles *et al.*, 1996; Bureau *et al.*, 1998). Solar radiation stimulates the photosynthetic activity of plants and consequently affects the biosynthesis of carotenoids, especially the activity of phytoene synthase, an enzyme responsible for the first step of the carotenoid biosynthetic pathway (Hirschberg, 2001), while the degradation of carotenoids in the final stage of berry development may be due to the VvCCD1 gene, which encodes the activity of the enzyme carotenoid cleavage dioxygenase (CCD) (Mathieu *et al.*, 2005).

Since carotenoids are substrates for C13-norisoprenoid synthesis (Young *et al.*, 2012), higher carotenoid concentrations, and thus higher substrate availability, may result in higher concentrations of C13-norisoprenoids in sun-exposed grapes (Mendes-Pinto, 2009). Some studies have shown that grapes exposed to sunlight may have a higher concentration of C13-norisoprenoids (Razungles *et al.*, 1998), while others showed no effect of sun exposure on C13-norisoprenoid concentration (Kwasniewski *et al.*, 2010; Song *et al.*, 2015). This difference can be explained by the effect of sunlight on the synthesis of the individual compounds in grapes, as different reactions can take place in each specific period during ripening, depending on the variety and microclimatic conditions (Asproudi *et al.*, 2020). In warm climates, grapes may have higher carotenoid concentrations due to higher solar radiation (Fariña *et al.*, 2010). However, the effects of temperature and light intensity on grape composition are complex, and the effects can vary. Other researchers have shown that higher temperatures (> 30°C) and higher solar radiation can promote the degradation



of berry carotenoids post-véraison (Oliveira *et al.*, 2004; Hickey *et al.*, 2018; Asproudi *et al.*, 2020). In the research by Gashu *et al.* (2022), the degradation of carotenoids was associated with increased temperature and solar radiation, and the relationship was dependent on the variety.

Under conditions of increased solar radiation, berries respond by adapting their metabolism to the specific stage of berry development, ensuring normal berry growth and development (Young *et al.*, 2016). In other words, the adaptation is reflected in the fact that the typical ripening process of the grapes is not affected, such as the physical parameters (berry weight and diameter) and the concentrations of primary metabolites (sugars and organic acids), but the perceived stress is managed by the synthesis of secondary metabolites predominant in the specific stage of development (Joubert *et al.*, 2016). In the pre-véraison stage of berry development, the secondary metabolites carotenoids are upregulated in response to increased light exposure, protecting photosynthetic membranes and ensuring the maintenance of photosynthesis, even under conditions of severe stress (De Oliveira *et al.*, 2019). After véraison, the increased light exposure leads to the synthesis of monoterpenes and phenols (Song *et al.*, 2015; Young *et al.*, 2016; Wang *et al.*, 2020). Plants use solar radiation for photosynthesis and energy production, but also as a source of information about the environment (Joubert *et al.*, 2016).

Increased sunlight intensity appears to affect the ratio of epoxyxanthophylls to non-epoxyxanthophylls by influencing the conversion of the epoxyxanthophyll violaxanthin to the de-epoxidised xanthophyll zeaxanthin as part of the xanthophyll cycle when excess light energy is dissipated (Hirschberg, 2001; Düring & Davtyan, 2002). In the study by Young *et al.* (2016), the content of zeaxanthin and antheraxanthin increased when grapes were exposed to sunlight by leaf removal, resulting in a larger xanthophyll pool (zeaxanthin, antheraxanthin and violaxanthin), and consequently in an increase in the de-epoxidation state of the xanthophylls (see Fig. 2). On the other hand, lutein epoxide concentrations were significantly lower in the exposed berries, with de-epoxidation of lutein epoxide to lutein

occurring after light exposure (Young *et al.*, 2012). Lutein had a higher degradation rate during grape ripening and a lower concentration of  $\beta$ -carotene at harvest under higher solar radiation and temperature conditions (Asproudi *et al.*, 2020).

### UV radiation

Ultraviolet (UV) radiation, including UV-A (315 nm to 400 nm) and UV-B (280 nm to 315 nm), represents a very small part of the solar spectrum, but has a very large biological effect. The amount of UV radiation changes depending on altitude, latitude, season, time of day and cloud cover (Matus, 2016). However, due to the damage to and thinning of the ozone layer, UV radiation increases and becomes more harmful, leading to forced changes in the life cycle of plants (Mackerness, 2000).

UV-B radiation is generally considered harmful to plants because it affects DNA and chlorophyll degradation, reduces photosynthesis and growth, and causes oxidative stress (Mackerness, 2000). However, most of the studies on it were conducted under unrealistic conditions, with excessively high doses of UV-B radiation (Del Castillo *et al.*, 2020). Instead, grapevine varieties are relatively well adapted to UV exposure under field conditions and generally show acclimatisation, as ecologically relevant doses of UV-B radiation act as environmental modulators and regulate gene expression, metabolism and growth (Downey *et al.*, 2003; Berli *et al.*, 2010; Hideg *et al.*, 2013; Joubert *et al.*, 2016). This new concept opens the possibility to explore different canopy management practices through UV manipulation. One of the most important measures to influence the UV exposure of grapes is leaf removal (Anić *et al.*, 2021). By improving microclimatic conditions through increasing light transmission and temperature in the fruit zone (Feng *et al.*, 2015; Young *et al.*, 2016), basal leaf removal can activate defence responses by increasing the concentration of stress-related defence molecules – polyphenols, monoterpenes and carotenoids (Joubert *et al.*, 2016; Hickey *et al.*, 2018) – which are associated with wine quality traits such as aroma, astringency, colour and stability (Downey *et al.*, 2003;

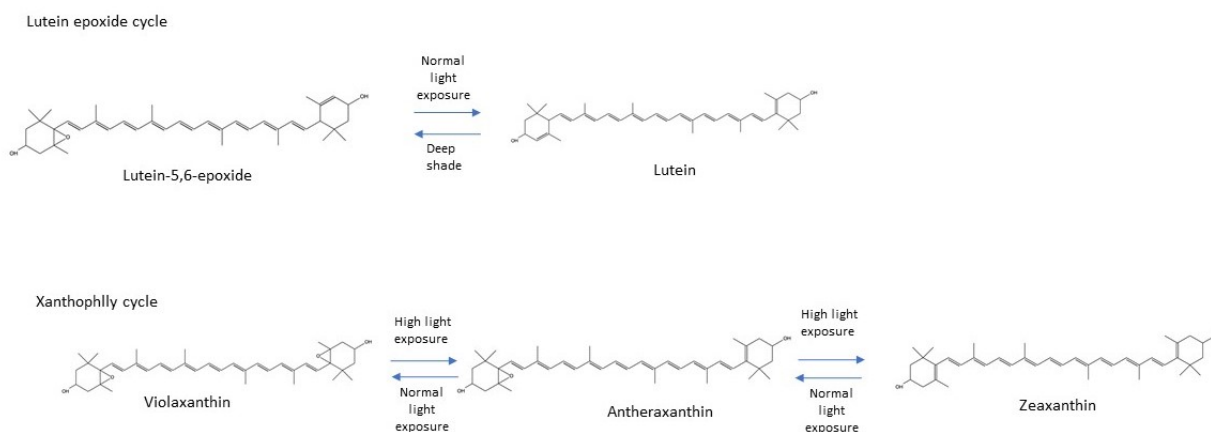


FIGURE 2  
Xanthophyll and lutein epoxide cycles.

González-Barreiro *et al.*, 2015; Wimalasari *et al.*, 2024).

The biosynthesis of secondary metabolites, especially polyphenols such as flavonols, is stimulated by UV radiation (Gregan *et al.*, 2012). Polyphenols have the function of absorbing and shielding UV-B radiation (Berli *et al.*, 2010), as it has been reported that grape exposure to UV radiation can increase the expression of genes involved in the regulation of flavonol accumulation via the phenylpropanoid metabolic pathway (Carbonell-Bejerano *et al.*, 2014; Martínez-Lüscher *et al.*, 2014). Monoterpenes are involved in the protection of berry tissues against UV-B radiation and other biotic and abiotic stresses (Joubert *et al.* 2016), and the exposure of grapes to sunlight promotes the expression of monoterpene metabolic genes in the berries (Friedel *et al.*, 2016).

Carotenoids are an important part of the grape UV-response machinery as they act as pigments for light harvesting (Matus *et al.*, 2016). Joubert *et al.* (2016) showed that UV-B can increase the accumulation of carotenoids and xanthophylls in Sauvignon blanc berries. The xanthophylls zeaxanthin and lutein responded most strongly to UV-B radiation in the early stages of berry development. In the absence of UV-B, berries require less zeaxanthin in the exposed environment (leaf removal treatment), and less lutein epoxide in shaded environments (Joubert *et al.*, 2016). Thus, the absence of UV-B could make grapes more susceptible to damage, as they are less acclimatised than grapes exposed to UV-B radiation. The latter grapes normally release higher concentrations of photoprotective xanthophylls and flavonols. Similar results were obtained in grapevine leaves, where the pigments of the xanthophyll cycle (violaxanthin, antheraxanthin and zeaxanthin) increased with an increased sum of UV radiation (Castagna *et al.*, 2016) (see Fig. 3).

### Topography

Topographic characteristics of the vineyard, such as elevation, slope and exposure of the terrain, as well as the orientation of the rows in the vineyard, the vigour of the

vineyard and different viticultural practices, can lead to great variability in microclimatic conditions, especially the quality and intensity of sunlight (Alem *et al.*, 2019). This can have an effect on carotenoid concentrations due to the direct effects on temperature, humidity, and other environmental factors that affect grape ripening (Castagna *et al.*, 2017). It is known that, in the northern hemisphere, slopes with south and southwest exposure of vineyards receive more sunlight. Higher temperatures in the less-vigorous and south-facing vineyards resulted in lower levels of carotenoids, especially lutein and  $\beta$ -carotene, both during ripening and at harvest (Asproudi *et al.*, 2020), while grapes grown on vines with higher vegetative height appear to have higher carotenoid content (Oliveira *et al.*, 2004) because the grapes are better protected from sunlight. In the Douro region of northern Portugal, high-altitude terraces with lower temperatures and higher humidity during the ripening period appear to produce grapes with higher carotenoid concentrations (Oliveira *et al.*, 2004).

### THE INFLUENCE OF VINEYARD MANAGEMENT PRACTICES ON THE COMPOSITION AND CONTENT OF CAROTENOIDS IN GRAPEVINES

#### Canopy management

Apart from environmental conditions, canopy management practices can also influence grape and wine quality by altering the vine microclimate (Hernandez-Orte *et al.*, 2015). Viticultural practices are known to affect grape berry secondary metabolites and regulate vine vigour, water and nutrient supply, and to increase the sunlight exposure of the grapes (Keller, 2010). Defoliation involves the removal of leaves around the cluster to improve air circulation and increase solar radiation and temperature inside the cluster (Alatzas *et al.*, 2023). In the study by Kwasniewski *et al.* (2010), leaf removal in the fruit zone 33 days after berry set was found to increase zeaxanthin concentrations in Riesling berries by 52 days after berry set, but not at harvest. On the

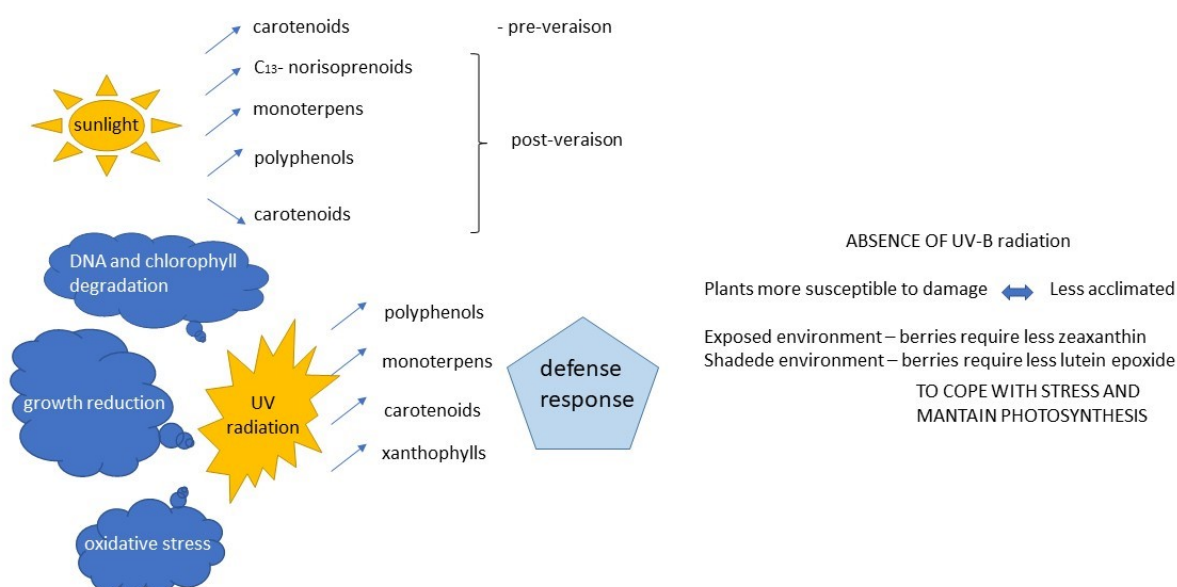


FIGURE 3

Synthesis of secondary metabolites in grapevines effected by sunlight and UV radiation.

other hand, Hickey *et al.* (2018) showed that leaf removal increased zeaxanthin concentration the most compared to all analysed carotenoids. Changes in microclimatic conditions as a result of leaf removal affect berry secondary metabolites (specific xanthophylls, monoterpenes and norisoprenoids) through transcriptional changes that influence enzyme activity and biochemical reactions during berry development and grape ripening, showing metabolic plasticity at different stages of development (Joubert *et al.*, 2016).

#### Irrigation management and tillage treatments

While direct practices such as leaf removal and shoot thinning alter the vine microclimate by modifying the crop level, canopy exposure and canopy density, indirect viticultural practices such as irrigation (Oliveira *et al.*, 2003; Bindon *et al.*, 2007; Jiao *et al.*, 2023) and fertilisation (Gutiérrez-Gamboa *et al.*, 2018) alter vine growth and canopy density by regulating the availability of nutrients and water, thereby influencing carotenoid synthesis in the grapes. The water balance of grapevines depends on soil texture, rainfall, root depth and evapotranspiration (Bois *et al.*, 2020). Depending on the phenological stage, a change in the water balance of the vine can affect vegetative growth, yield, canopy microclimate and the physiology of the berries (Baeza *et al.*, 2019; Chacón-Vozmediano *et al.*, 2020). Excessive water promotes more vegetative growth and reduces yield quality, while water deficit reduces photosynthesis, shoot growth, leaf area and berry size, and long-term water stress negatively affects vine metabolism and impedes ripening (Van Leeuwen & Darriet, 2016). However, moderate water stress can improve grape and wine quality by positively affecting the accumulation of polyphenolic compounds such as tannins and anthocyanins, as well as volatile compounds (González-Barreiro *et al.*, 2015; Van Leeuwen & Darriet, 2016). The water deficit reduces vegetative growth, which alters the vine microclimate and increases the amount of sunlight reaching the grapes, which is associated with higher grape quality (Baeza *et al.*, 2019). The study by Oliveira *et al.* (2003) showed that the irrigation treatment (30% of evapotranspiration (ET(0))) seems to contribute to lower carotenoid content in grapes, but only when the vines are planted in a soil with lower water-retention capacity compared to the non-irrigated treatment. Some studies have shown that partial root drying (PRD) could increase sunlight penetration in the fruit zone, possibly affecting the composition of carotenoids and C13-norisoprenoids (Bindon *et al.*, 2007). Under water stress, plants release excess energy from photosynthesis via the xanthophyll cycle in the form of heat (Hirschberg, 2001). This could lead to an increase in carotenoids, and consequently C13-norisoprenoids (Bindon *et al.*, 2007). A water deficit could also increase carotenoid cleavage dioxygenase (CCD) (Deluc *et al.*, 2009). Soil properties can also influence the rate of carotenoid degradation during grape ripening, with greater carotenoid degradation observed in vines in mulched soils than in conventional vineyards (Fariña *et al.*, 2010).

#### CONCLUSION

The grape-growing industry is highly dependent on the ability of grapevines to tolerate and adapt to the consequences of climate change. Among the most important consequences of climate change are high temperatures during grape ripening, a shift in phenological phases, changes in sugar and organic acid concentrations in grapes, and a change in the aroma profile of grapes, which affect grape and wine quality (De Orduña, 2010). Climate change could help lead to the development of appropriate adaptation strategies, which should be planned by the grape growers according to local environmental conditions. A major challenge for winegrowers and winemakers is therefore how to adapt to climatic changes while preserving the specificity and typicality of the sensory characteristics of a given region (Rienth *et al.*, 2021). This review contributes to knowledge of the influence of environmental conditions and vineyard management practices on the composition and content of carotenoids in grapevines in order to adapt canopy management strategies to maintain grape quality in warmer climates and produce the desired aromatic wine profile.

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