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Effects of altitude on the chemical composition of grapes and wine: a review

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ABSTRACT

Of the geographical parameters in a winegrowing site, altitude is an important determinant of wine composition and quality. Grape polyphenols and volatiles comprise a large and varied group of compounds that contribute considerably to the sensory and health-promoting properties of wine. This review surveys the impacts of altitude and its related climatic characteristics on the phenolic and aroma compounds of grapes and wine through the examination of existing literature. Furthermore, this review highlights the challenge of distinguishing the effects of parameters, such as air temperature, variety, vine water status, soil and UV radiation, from the altitude effect. Overall, high-altitude growing sites can favour an increase - albeit at different intensities - in content of many chemical compounds found in grapes and wine, such as total polyphenols, total monomeric anthocyanins, catechins, quercetin derivatives and cyanidin-derived anthocyanins, trihydroxylated flavonols, carotenoids, isoamyl acetate and ethyl hexanoate. However, the altitude factor seems to be cultivar-dependent; in fact, it can exert a positive effect on the concentrations of acylated anthocyanins and of total aroma compounds in some cultivars (e.g., Ekşikara and Glera) and a negative effect on the same components in other cultivars (e.g., Merlot and Cabernet-Sauvignon). Its influence on the polyphenol content can also differ between different parts of the same cultivar; for instance, an increase in skin tannins and a decrease in seed tannins have been found to be concomitant with an increase in altitude in Syrah grapes. Moreover, at higher altitude, the effect of an increase in UV-B radiation can lead to an enhancement in colour intensity due to an increase in the synthesis of anthocyanins, flavonols and tannins. Due to their cool climate, high-elevated winegrowing regions represent favourite cultivation sites under current and future global warming.

KEYWORDS: altitude, grape, polyphenols, aromas, varieties, weather

INTRODUCTION

The term "terroir", derived from the Latin word "terre" or "territoire", is very popular in wine literature. It is related to the interactions between environmental factors and applied vitivinicultural practices that provide uniqueness to the produced wine (Edo-Roca *et al.*, 2013; Van Leeuwen and Seguin, 2006). OIV, the International Organisation of Vine and Wine, defined the vitivinicultural terroir in the Resolution OIV/VITI 333/2010 (OIV, 2010). One of the factors that contributes to the terroir of a region's wine, influencing physicochemical behaviour, phenolic and volatile compound content of grape berries and consequently the sensory characteristics of the resulting wine, is altitude (Xing *et al.*, 2016). The altitude of a growing site, which affects temperature, humidity, UV-B radiation, sunlight hours, water deficits and other environmental factors, can strongly influence climatic conditions (Gutiérrez-Gamboa *et al.*, 2021). The impacts of geographical parameters, such as altitude, on the main chemical components of grapes is an important research area due to their beneficial impacts on product sensory attributes and human health, such as antioxidant activities (Cory *et al.*, 2018). The influence of altitude on grape berry chemical composition (in terms of, for example, sugars, acids, non-flavonoid compounds including copigments (hydroxycinnamic and hydroxybenzoic acids) and antioxidants (stilbenes), flavonoid compounds including anthocyanins, oligomers and polymers of flavan-3-ols, and flavonols, as well as volatile organic compounds) has been recognised and highlighted in only a few recent papers (Alessandrini *et al.*, 2017; Barreto de Oliveira *et al.*, 2019; Gutiérrez-Gamboa *et al.*, 2021; Rienth *et al.*, 2020); therefore, up to now, impacts of altitude on grape and wine chemical composition has been poorly investigated. It is important to underline here that global warming could lead to changes in wine geography, and an upward shift of the growing regions has been forecast (Pomarici and Seccia, 2016). In fact, growing vines at high altitudes is one of the most effective new viticultural strategies for mitigating the negative impacts of global warming on grape and wine quality, particularly because it delays grape ripening. (Gutiérrez-Gamboa *et al.*, 2020). The possibility of cultivating wine grapes in high-altitude regions characterised by a cooler climate under the future predicted higher temperatures needs to be studied. This review aims to explore recent studies related to the effects of altitude on the chemical components - mostly polyphenols and volatile compounds - of grapes and wine, as well as to gain new insights for future research on the effect of climate change on global viticulture.

1. Phenolic compounds in grapes and wine

Polyphenols are a group of organic molecules that are widespread within the plant kingdom and in our diet. They comprise complex structures of several thousand compounds, ranging from small compounds with only one single aromatic ring attached to one to three hydroxyls to several of such structural units (De Pascual-Teresa and Clifford, 2017). Through secondary metabolism, plants produce phenolics during normal growth and as a defense response to stress conditions like wounding, infection and UV radiation (Naczk and Shahidi, 2006). Either non-flavonoid or flavonoid, there are many classes of phenolic compounds according to their structure, which differs in the number and position of hydroxyl and methoxyl groups on the basic backbone.

Non-flavonoid compounds include phenolic acids, which are classified as benzoic and cinnamic acids, as well as other phenolic derivatives; for example, stilbenes, the most well-known molecule of which is resveratrol. Flavonoid compounds are mainly composed of anthocyanins and flavonols, which predominantly exist in grape skins, and of flavan-3-ols, which are found in grape seeds and skins (Xing *et al.*, 2016).

Anthocyanins are flavonoid pigments that are water soluble, favouring their transfer into the must and wine during vinification (Moreno and Peinado, 2012). They are responsible for the colour of the produced wine, which is an important sensory attribute (Mateus *et al.*, 2002).

Flavan-3-ols exist in grapes as oligomers and polymers, which are the common names given to condensed tannins or proanthocyanidins. Flavonols are pale yellow pigments containing a pyrone heterocycle; out of all grape flavonoids they are found in the lowest concentrations. They can serve as a natural sunscreen for grapes and are found in grape skin in glycosylated forms.

2. Aroma compounds in grapes and wine

Volatile organic compounds are generally classified as: varietal aroma compounds when linked directly to the grapes, prefermentative aroma compounds when formed during grape processing, fermentative aroma compounds when formed by yeast and bacteria and postfermentative aroma compounds when formed during the conservation and ageing of the wine (Zhu e*t al.,* 2016). Aroma-active volatiles can be classified as terpenes, methoxypyrazines, alcohols, aldehydes, esters, fatty acids, ketones and volatile thiols; they impart different aromas to wine when higher than their odour perception threshold. Terpenes occur in grapes as both free and, more frequently, odourless glycosylated precursors linked to sugar moieties; a substantial number is responsible for fruity and floral aromas, while others have resin-like odours, such as alpha-terpinene, p-cymene, myrcene and farnesol (González-Barreiro *et al.*, 2015). Methoxypyrazines are nitrogen heterocyclic compounds found in both grapes and wine and they result from the metabolism of amino acids; 3-isobutyl-2-methoxypyrazine (IBMP) is an important compound which contributes to the characteristic bell pepper odour of Sauvignon blanc cultivar (Styger *et al.*, 2011).

A number of higher alcohols are produced during fermentation either from grape amino acids or directly from sugars, and the increase in fermentation rate due to several factors, such as oxygenation and high temperature, will lead to an increase in their formation (Ribéreau-Gayon *et al.*, 2000). C6 and C9 aldehydes and alcohols are involved in the plant defense response to pests, diseases and wounds (Lin e*t al.,* 2019). During the winemaking and aging processes, aldehydes and alcohols can be converted into the respective acetate esters, which have an impact on the aroma quality of the resulting wine. These molecules are considered the most important of the volatile aroma compounds and their production during fermentation mainly affects the fruity flavours associated with wine. Volatile thiols or mercaptans, produced from yeasts during wine fermentation, contribute to the varietal character of wine (Styger *et al.*, 2011). Although many thiols (mercaptans) generate off-putting odours, not all sulfur-containing compounds, or even all thiols, are detrimental to wine quality (González-Barreiro *et al.*, 2015).

3. Effect of altitude on grapes and wine

Along with its associated environmental conditions, altitude has an important influence on vine physiology and fruit chemistry in winegrowing sites. The key findings from studies on the impact of altitude on grapes and wine are listed in Table 1.

Most of the literature reported above shows the effects of lower air temperatures and increased UV radiation on the chemical composition of grapes and wine from high-altitude grapevines.

The production of high-quality grapes depends on the daily thermal amplitude resulting from the lower night-time temperatures usually associated with high elevation plots (Gutiérrez-Gamboa *et al.*, 2020). Grapevines that are cultivated in vineyards with low night temperatures have a higher potential for containing colour and volatile compounds (Gutiérrez-Gamboa *et al.*, 2018). In cool-climate viticulture, the best expression of terroir is achieved when the precociousness of the grapevine variety allows it to ripen its fruit at the end of the growing season (Van Leeuwen and Seguin, 2006), when the grapes contain balanced levels of soluble solid, acidity, phenolic, nitrogenous and aroma compounds. The wines produced from high-altitude sites are generally fresh, with high acidity, high aromatic quality and a lower alcohol degree (Gutiérrez-Gamboa *et al.*, 2020).

The altitude effect is linked to the mass of the atmospheric column through which sun rays reaching the earth's surface must pass; at high altitudes, there are fewer air masses and consequently solar UV-B levels are higher (Gutiérrez-Gamboa *et al.*, 2021). UV levels increase by around 10 % for every 1000 m gain in altitude (WHO, 2016). Vineyards cultivated in the Andes of Argentina, where the effect of low cloud cover is paired with the effect of high altitude, receive high levels of radiation (van Leeuwen *et al.*, 2020).

3.1. Effect altitude on physicochemical behaviour of grapes and wine

3.1.1. Effect of air temperature

Temperature decreases with altitude creating a more temperate climate due to adiabatic cooling of the air (Gutiérrez-Gamboa *et al.*, 2021). 'Chasselas' grapes cultivated on steep terraced slopes at altitudes of between 375 and 575 m were monitored by Rienth *et al.* (2020) in the AOC-Lavaux region in Switzerland. For all three of the consecutive study years, altitude was the main driver of precocity and was consistently associated with the date of budburst and flowering. The temperature decreases with altitude, usually in the range of 0.65 to 1.0 °C for 100 m gain in elevation, were associated with plots at higher elevations showing a delay in budburst and flowering. Because the vineyards at higher altitude ripen later during the cooler periods of the year, they have the highest potential for producing high-quality grapes (with higher acidity and lower alcohol levels) under future warmer temperatures, leading to maximum terroir expression.

Cabré and Nuñez (2020) used indices related to air temperature to evaluate the impacts of future climate on Argentinean winegrowing regions, including the Cool Night Index (CNI) and the average growing season temperature (GST) index. CNI is considered as the mean minimum night temperature in the later maturity stages of the ripening period; it gives a measure of ripening potential, indicating the suitability of a winegrowing region notably in relation to the secondary metabolites (polyphenols, aromas) in grapes and wines. GST is used to determine a cultivar's suitability in a given site and its projected changes could be useful for identifying the best appropriate grapevine varieties for current and future locations. These authors showed that CNI and GST are projected to increase (more than 6 °C for CNI and between 4 and 7 °C for GST) mainly in a distant future in the most pessimistic emission scenario for greenhouse gases (RCP8.5). They also reported that more and new suitable areas may be available for cultivating cool climate varieties, while less suitable areas may be available for warm and hot climate varieties to maintain their current quality.

Major biochemical changes occur during grape ripening, in particular the accumulation of total soluble solids (TSS), increased pH and decreased acidity (Almanza-Merchán *et al.*, 2012). Total titratable acidity (TTA) decreases in grapes with increasing temperatures. Meneghelli *et al.* (2018) showed that a vineyard at 500 m a.s.l. and with higher mean air temperature exhibited lower TTA and higher pH and TSS/TTA ratios in 'Niágara Rosada' and 'Isabel' cultivars when compared to the same values obtained for a vineyard at 650 m altitude. However, in the same study, relatively high values of TTA were obtained at 250 m altitude and this was attributed to the excess of leaf nitrogen that increases vine vigour. Vigorous vines increase shading in the bunch area, which decreases the temperature of the grapes, extends the vegetative growth period and delays fruit maturity.

In a study conducted on 'Syrah' grapes, higher temperatures at the lower altitude regions (350 m a.s.l.) led to a degradation in malic acid and an increase in the concentrations of glucose and fructose compared to the vineyards at higher altitude (1100 m a.s.l.) (Barreto de Oliveira *et al.,* 2019). Regina *et al.* (2010) reported that 'Pinot Noir' grapes from a high-site vineyard (1150 m a.s.l.) characterised by lower temperatures showed higher concentrations of malic acid compared to the same variety cultivated at 873 m a.s.l. (8.04 g/L vs 4.45 g/L in 2008). This suggested that low temperatures are more favorable for producing sparkling wines of high organoleptic quality.

Table 1. Effect of increasing altitude on physicochemical behaviour and on phenolics and aromas of grapes and wine. Table 1/3

Cultivar	Affecting features	Effect on Grapes	References
Chasselas	Weather: lower temperature	Acidity ↑ and alcohol levels↓	Rienth *et al.* (2020)
Ni‡gara Rosada and Isabel	Weather: lower temperature	No effect on TSS. TTA ↑, pH and TSS/TTA ↓	Meneghelli *et al.* (2018)
Syrah	Weather: lower temperature	Malic and succinic acid ↑ Citric acid, glucose and fructose ↓	Barreto de Oliveira *et al.* (2019)
Ancellotta, Garganega and Fiano	Weather: lower temperature	At harvest, TSS reached satisfactory values for producing quality wines	Malinovski *et al.* (2016)
Lambrusco, Negroamaro and Nero d'Avola		At harvest, TSS did not reach satisfactory values for producing quality wines	
Chardonnay	Weather: lower temperature. Higher precipitations	Acidity ↑ TSS ↓ in the first year of the study No effect on TSS in the second year of the study At harvest, TSS reached satisfactory values for balancing acidity values	Regina *et al.* (2010)
Pinot Noir		Acidity ↑, TSS ↓ At harvest, TSS did not reach satisfactory values for balancing acidity values	
Not reported	Weather: lower temperature	In the Argentinian region, where the highest grapevine production is concentrated, the annual mean temperature is expected to increase from 4 to 7 ¡C by 2099 under RCP8.5 emission of greenhouse gases scenario. High-altitude sites and cool climate varieties will likely benefit	Cabré & Nuñez (2020)
Muscat of Bornova	Higher percentage of lime in the soil	Trans-caftaric and trans-coutaric acids ↓	Karaoğlan *et al.* (2015)
	Higher solar radiation	Quercetin-3-O-glycoside ↑	
Carignan	Weather: higher evapotranspiration, higher annual accumulated growing degree days and higher average temperature. Limited water access Higher solar radiation	Anthocyanins and TPI ↑ SM ↓	Edo-Roca *et al.* (2013)
Grenache	Weather: lower temperature	No significant effect on anthocyanins and SM TPI ↓	Edo-Roca *et al.* (2013)

↑ = increased; ↓ = decreased; TSS = total soluble solids; TTA = total titratable acidity; TPI = total polyphenol index; SM = seed maturity index; TP = total polyphenols; Cat = catechin monomers; PC = procyanidin oligomers; TPA = total proanthocyanidins; MIBP = 2-methoxy-3-isobutylpyrazine.

Table 2/3

Ekşikara	Weather: lower temperature Higher solar radiation	<u>The following parameters ↑:</u> anthocyanins in skins and whole berries; tannins and trans-resveratrol in skins and seeds; TP and antioxidant activity in skins, seeds and whole berries; petunidin-3-O-glucoside, cyanidin-3-O-glucoside, peonidin-3-O-glucoside, acylated anthocyanins, gentisic acid, catechin, rutin and isorhamnetin-3-glucoside in whole berries; caffeic acid in seeds; chlorogenic acid in seeds and whole berries; epicatechin in skins. <u>No effect on the following parameters:</u> gallic acid in seeds and whole berries; rutin and isorhamhetin-3- glucoside in skins and seeds; procyanidin B1 and procyanidin B2 in seeds and whole berries. Malvidin-3-O-glucoside in skins and whole berries ↓	Coklar (2017)
Cabernet-Sauvignon	Weather: lower temperature and large diurnal temperature range. Brown sandstone soil	Quercetin derivatives and cyanidin-derived anthocyanins ↑ Myricetin derivatives and delphinidin-derived anthocyanins ↓	Li *et al.* (2011)
Cabernet-Sauvignon, Carmenere, Syrah and Merlot	Weather: lower temperature, humidity and rainfall. Higher diurnal temperatures	Anthocyanins and trihydroxylated flavonols ↑ Dihydroxylated flavonols and acylated anthocyanins ↓	Liang *et al.* (2014)
Cabernet-Sauvignon	Weather: lower temperature and humidity, and higher diurnal temperatures. Stronger sunlight and abundant UV-B radiation	Cyanidin-type anthocyanins and quercetin-type flavonols ↑. No effect on flavan-3-ols	Xing *et al.* (2016)
Syrah	Weather: lower temperature and bigger temperature difference between daytime and night-time	Total phenols, non-flavonoids, flavonoids, total anthocyanins and skin tannins ↑ Trans-resveratrol and seed tannins ↓	Barreto de Oliveira *et al.* (2019)
Touriga Nacional and Touriga Francesa	Weather: lower temperature, higher humidity	Carotenoids ↑	Oliveira *et al.* (2004)
Merlot	Weather: lower temperature and bigger temperature difference between daytime and night-time	Isoamyl acetate and ethyl hexanoate ↑. Total aroma compounds ↑ from 214 m to 450–600 m then ↓ up to 1100 m	Jiang *et al.* (2013)
Cabernet-Sauvignon		Isoamyl acetate, ethyl hexanoate and ethyl octanoate ↑ Total aroma compounds ↓	

↑ = increased; ↓ = decreased; TSS = total soluble solids; TTA = total titratable acidity; TPI = total polyphenol index; SM = seed maturity index; TP = total polyphenols; Cat = catechin monomers; PC = procyanidin oligomers; TPA = total proanthocyanidins; MIBP = 2-methoxy-3-isobutylpyrazine.

Table 3/3

Cultivar	Affecting features	Grape stems	References
Moscatel	Weather: lower temperature and absence of significant thermal stress. Absence of water stress	Total phenols, ortho-diphenols, flavonoids, most of individual phenolics, and antioxidant activity ↓	Gouvinhas *et al.* (2020)
Cultivar	**Affecting features**	**Grapes and wine**	**References**
Touriga Nacional	Weather: lower temperature	Anthocyanins in skins and in wine ↑ Cat and PC in skins ↓ TPA in skins and seeds ↓ PC, color and astringency of wine ↓	Mateus *et al.* (2001)
Touriga Francesa	Weather: lower temperature	Anthocyanins in skins and in wine ↑ Cat PC and TPA in skins ↓ Cat and TPA in seeds ↑ Color and astringency of wine ↓	Mateus *et al.* (2001)
Cabernet-Sauvignon	Weather: lower night-time temperature. Stronger sunshine	No significant effect on aromatic profile. Isoamyl acetate, ethyl octanoate and fruity aromas ↓	Jiang *et al.* (2012)
Merlot	Weather: lower temperature. Higher rainfall and diurnal temperatures	Total phenolics, total flavonoids, total anthocyanins, sum of individual phenolics, salicylic acid and antioxidant capacity ↑ No effect on quercetin, trans-resveratrol and tannins	Jin *et al.* (2017)
Cabernet-Sauvignon	Higher sunshine hours and increased UV radiation	Total phenolics, total flavonoids, total anthocyanins, sum of individual phenolics, salicylic acid, antioxidant capacity, quercetin, trans-resveratrol and tannins ↑	Jin *et al.* (2017)
Glera	Weather: higher heat accumulation degrees	Total aroma compounds, elegance and floral aroma ↑	Alessandrini *et al.* (2017)
Cabernet-Sauvignon	Weather: lower temperature	MIBP ↑ No effect on α- and β-ionone and β -damascenone	Falcão *et al.* (2007)

↑ = increased; ↓ = decreased; TSS = total soluble solids; TTA = total titratable acidity; TPI = total polyphenol index; SM = seed maturity index; TP = total polyphenols; Cat = catechin monomers; PC = procyanidin oligomers; TPA = total proanthocyanidins; MIBP = 2-methoxy-3-isobutylpyrazine.

3.1.2. Choice of grape variety

The altitude effect should be evaluated separately for each grape variety. Malinovski *et al.* (2016) showed that the effects of high-altitude regions in Água Doce in Brazil on the viticultural performance of six Italian native grapevines differ from one cultivar to another. 'Ancellotta', 'Garganega' and 'Fiano' varieties showed satisfactory levels of TSS (i.e., above 18 °Brix), for the production of quality wines. In contrast, the TSS values of 'Lambrusco', 'Nero d'Avola' and 'Negroamaro' at harvest were below 18 °Brix, thus likely compromising the quality of the wines to be produced from these three cultivars.

In the same study, 'Nero d'Avola' and 'Negroamaro' cultivars originating from Sicily and Apulia respectively in Southern Italy, had difficulties in developing their berry components, like sugars and acidity, during ripening; this may be due to the annual air temperature being lower than in their region of origin. Meanwhile, the 'Ancellotta' cultivar, originating from Central Italy with similar thermal conditions to Água Doce, stood out for its good qualitative indices and high adaptability to the local area.

Bolivian viticulture is mostly carried out at altitudes of between 1660 and 2360 m a.s.l, and 'Tannat' grapes as well as Mediterranean cultivars (e.g., 'Grenache', 'Carignan', 'Tempranillo' and 'Sangiovese') have been shown to adapt well to the subtropical conditions of the Central Valley of Tarija, Bolivia. However, other cultivars (e.g., 'Cabernet-Sauvignon', 'Merlot', 'Pinot Noir', 'Chardonnay', 'Syrah' and 'Malbec') are not well-adapted due to their need for very cold winter conditions. Therefore, understanding the differences in chilling needs could help grapevine breeders and growers adapt to the expected climate change (Gutiérrez-Gamboa *et al.*, 2021).

3.2 Altitude effect on phenolic and aroma compounds in grapes and wine

3.2.1. Effect of air temperature

High altitude and the related lower air temperature have an influence on the ripening and polyphenolic composition of grapes (Xing *et al.*, 2016). Coklar (2017) found that under the effect of low temperatures in high elevation vineyards, the total monomeric anthocyanin content in 'Ekşikara' whole berries and skins was significantly higher than that at lower altitude. The author also found that tannin levels in grape seed and skin for the high site were significantly higher than those at the low site. Moreover, higher total phenolic content in whole berries, skins and seeds were obtained for the high site.

The high-altitude regions and their associated climatic conditions seem to be favourable for the production of certain types of phenolic compounds, whereas the climatic conditions in low-altitude regions appear to be favourable for the production of other types. Higher levels of anthocyanins monoglucosides and trihydroxylated flavonols in skins of 'Cabernet-Sauvignon', 'Carmenere', 'Syrah' and 'Merlot' were generated in the western regions in China (up to 1214 m a.s.l.) characterised by large day- and night-time temperature differences. However, the grapes from the lower altitude eastern regions near the sea characterised by higher daily minimum temperatures and small day- and night-time temperature differences, had a higher proportion of acylated anthocyanins and dihydroxylated flavonols (Liang *et al.*, 2014). Furthermore, Coklar (2017) reported that with decreasing altitude, the relative amount of malvidin-3-O-glucoside in both skin and whole berry of 'Ekşikara' grapes increased, whereas that of petunidin-3-O-glucoside, cyanidin-3-O-glucoside, peonidin-3-O-glucoside and acylated anthocyanins in whole berry decreased. This study, however, did not decouple the effect of temperature from UV radiation.

In another study performed by Barreto de Oliveira *et al.* (2019), the difference in altitude had a significant impact on 'Syrah' grapes. The concentrations of total phenols (1,440 mg/ kg fresh fruit), non-flavonoids (200 mg/kg), flavonoids (1,240 mg/kg) and total anthocyanins (890 mg/ kg) at the site at 1100 m a.s.l. were significantly greater than those at the site at 350 m altitude (450, 130, 320 and 350 mg/ kg fresh fruit respectively). This result could be explained by the fact that the high-altitude region is characterised by large day- and night-time differences in temperature and by the fact that the maximum temperatures during the productive cycle stayed below 30 °C, thus favouring the accumulation and preservation of phenolic compounds during the grape ripening period. The grape skins at the high site contained higher levels of total condensed tannins, including monomeric, oligomeric, and polymeric 3-flavanol, whereas the grape seeds contained higher levels of the same compounds at the low site. On the other hand, the concentrations of trans-resveratrol in the first and the second year of the study were 5.71 and 8.17 mg/Kg fresh fruit respectively at the low site and 4.11 and 4.72 mg/Kg fresh fruit respectively at the high site. The synthesis of stilbenes is induced by environmental stresses; therefore, the maximum daily temperatures that exceeded 30 °C during berry growth and ripening in the low-altitude area may have stressed the vines, resulting in higher resveratrol levels.

'Cabernet-Sauvignon' wines made from grapes grown at different altitudes (774, 960, 1350 and 1160-1415 m a.s.l.) were studied by Falcão *et al.* (2007) in Santa Catarina State, Brazil. Altitude did not affect the concentrations of α- and β-ionone and β –damascenone in the produced wines. However, in both winter and summer, the highest levels of 2-methoxy-3-isobutylpyrazine (MIBP) were found in wines of the highest site (1415 m a.s.l.), where the temperature was lower in comparison to the other studied sites. Consequently, these wines were correlated with a "bell pepper" aroma, whereas wines from the lowest altitude (774 m a.s.l.) were correlated with a "red fruits" aroma. Grape MIBP content is closely linked to viticulture parameters, like the growing temperature (Allen *et al.*, 1994); in a previous study, lower temperatures during the period preceding véraison had a greater impact on the MIBP content than after the grapes had matured (Lacey *et al.*, 1991).

However, in some winegrowing regions and depending on the geographic location of the vineyards, it is possible for a higher altitude cultivation site to have warmer conditions that affect the sensory attributes of the produced wines; for instance, in a study performed by Alessandrini *et al.* (2017), the high site (380 m a.s.l.) was warmer than the low one (200 m.a.s.l.) due to its higher heat accumulation degrees favouring the accumulation and preservation of the aroma compounds and enhanced the elegance and the floral aroma of the produced wine. The levels of volatiles were most likely temperature-dependent rather than altitude-dependent. The minimum air temperatures at the low site were approximately 2 ˚C lower than those at the high site and were thus considered to be the main limiting factor for the biosynthesis of the aroma compounds at the lower altitude.

Rotundone is described by Ferreira (2012) as being an important wine aroma-impacting compound, and the anecdotal evidence that rotundone was more common in 'Shiraz' wines from cool climate locations was corroborated in an Australian red wine survey (Black *et al.*, 2015). Geffroy *et al.* (2016) evaluated the variability of its concentrations in 'Gamay N' wines in four French wine-growing areas. The results showed that Auvergne - the coolest vineyard over the whole wine-growing season and ripening period - had the highest rotundone concentrations and the most intense peppery notes. Peppery aroma scores and the concentration of rotundone in wine were shown to be significantly correlated. However, the effects of temperature and vine water status were not totally differentiated in this study: the vineyard with the highest rotundone content was also the wettest during the véraison-harvest period.

In cooler vintages and vineyards, higher levels of rotundone are expected to accumulate in 'Vespolina' grapes (Caputi *et al.*, 2011). The highest levels of rotundone were obtained in 'Shiraz' berries from vines exposed to cooler temperatures, showing a within-vineyard variation and that the topography of the vineyard, particularly the aspect, was the most important factor in the formation of rotundone (Scarlett *et al.*, 2014). In another study, rotundone was typically present at the top and in shaded areas of bunches of 'Shiraz' grapes, which correlates with lower grape surface temperatures, and its concentration was negatively affected by fruit temperatures above 25 °C (Zhang *et al.*, 2015a). Furthermore, a study on fifteen vintages of 'Shiraz' wine produced from the same vineyard block at the same winery showed that wines from cooler seasons tend to contain higher levels of rotundone (Zhang *et al.*, 2015b). Water abundance was another influential factor in this study, since a higher amount of rotundone was detected in wetter vintages.

3.2.2. Effect of UV radiation

The increase in UV radiation noted at higher altitudes promotes the synthesis of skin anthocyanins; this can explain why wines produced from high-altitude regions have a higher colour intensity (Jin e*t al.,* 2017). At higher altitudes, the increase in UV-B radiation can reach 8 % per decade leading to the enhancement of colour, flavonol and tannin synthesis in red grapes on the one hand (van Leeuwen and Darriet, 2016), and to higher concentrations of 1,1,6-trimethyl-1,2-dihydronaphthalene (TDN) - which can give the wine an intense and sometimes unpleasant smell of hydrocarbons - on the other.

UV-B up-regulates the biosynthesis of anthocyanin in grapevines, counteracting the negative effects of increasing atmospheric carbon dioxide and increased temperature on anthocyanin content in berries (Gutiérrez-Gamboa *et al.*, 2021). Exposure to UV-B has been found to slow down berry growth and increase the biosynthesis of anthocyanins and flavonols (Martínez-Lüscher *et al.*, 2016). It also leads to an increase in levels of both total bound glycosidic secondary metabolites and phenolics (Keller and Torres-Martinez, 2004; Lafontaine *et al.*, 2005), and in the synthesis of anthocyanins in grape skins (Berli *et al.*, 2008; Carbonell-Bejerano *et al.*, 2014).

In Bolivia and Argentina, some wines produced from vineyards located higher than 1500 m a.s.l. were found to have higher total antioxidant capacity and phenolic content (including resveratrol) than wines produced from vineyards located at a lower altitude (Osorio-Macías *et al.*, 2018). UV-B radiation activates the phenylpropanoid biosynthesis pathway, resulting in phenolic-based resistance against *Botrytis cinerea* that causes grey mould or botrytis bunch rot in grapes (Elmer and Reglinski, 2006; Gutiérrez-Gamboa *et al.*, 2021). Plant responses to heat stress at high altitudes may be regulated by abscisic acid and salicylic acid (Larkindale and Huang, 2005). Abscisic acid plays a role in the response of grape leaf tissues to UV-B radiation by augmenting the synthesis of UV-absorbing compounds, antioxidant enzymes and membrane sterols (Gutiérrez-Gamboa *et al.*, 2021). Salicylic acid might be synthesised by the grapes as a defense response to stress conditions, such as UV radiation that increases with increasing altitude; Jin e*t al.* (2017) found that its amount increased dramatically with altitude in the wines produced from 'Merlot' and 'Cabernet-Sauvignon'.

The phenolic content of 'Carignan' grapes grown in two different locations, referred to as early and late ripeness parcels corresponding to a higher (370 m a.s.l.) and lower (305 m a.s.l.) altitude respectively, was studied by Edo-Roca *et al.* (2013). The total leaf area (TLA) in the early (warm) parcel (3.4 m^2/vine) was smaller than the TLA in the late (moderate) parcel (4.8 m^2/vine). As a result, the grapes in the warm parcel were more exposed to solar radiation and synthesised larger amounts of anthocyanins. Furthermore, flavonol compounds can serve as natural sunscreen for grapes; their synthesis is induced by light and their levels are positively related to radiation. Karaoğlan *et al.* (2015) showed that the highest amount of quercetin-3-O-glycoside (5.16 mg/L) was obtained for the 'Muscat of Bornova' wine from the site at the highest altitude and with the highest solar radiation (587,465 W/m^2). Furthermore, the amounts of quercetin-3-O-glycoside found in 2.22 and 3.88 mg/L of lower altitude wines correlated with solar radiation values of 542,875 and 553,782 W/m^2 respectively).

Plants accumulate large quantities of various types of compatible solutes and important osmoprotectants (e.g., proteins, proline and carbohydrates) in response to diverse stresses, caused by, for instance, low temperature and UV radiation. These osmoprotectants protect plants from stressing conditions by adjusting cellular osmosis, protecting membrane integrity and contributing to the detoxification of reactive oxygen species and the stabilisation of proteins/enzymes activities (Hayat *et al.*, 2012). Indeed, Berli *et al.* (2013) showed that the application of a high solar UV-B treatment under field conditions to 'Malbec' grapevine leaves in a high-altitude vineyard (1450 m a.s.l.) in Argentina augmented the levels of photoprotective pigments and proline, thereby increasing the antioxidant capacity of leaves.

3.2.3. The combined effect of soil and vine water status

In many studies, the effect of soil and vine water status cannot be clearly distinguished from the altitude factor. Vines with limited access to water in a vineyard cultivated with 'Carignan' grapes at a higher altitude and characterised by a shallow stony soil produced smaller berries with higher anthocyanin content compared to another vineyard at a lower altitude with a deeper soil (Edo-Roca *et al.*, 2013).

Soil and water availability affect the branch points of the biosynthetic pathway of flavonoids in grape berries, which are regulated by a number of enzymes (Li e*t al.,* 2011): Flavonoid 3'-hydroxylase (F3'H) and flavonoid 3', 5'-hydroxylase (F3'5'H) convert dihydrokamepferol into dihydroquercetin and dihydromyricetin, in addition to their derivatives, respectively. Cyanidin-derived anthocyanins and delphinidin-derived anthocyanins are synthesised from dihydroquercetin in the F3'H branch pathway and dihydromyricetin in the F3'5'H branch pathway respectively in the downstream pathways of both branches. Li e*tal.* (2011) found that the regional 'Cabernet-Sauvignon' wines from vines at an altitude of 1900-3500 m a.s.l. in China contained the greatest levels of both quercetin derivatives and cyanidin-derived anthocyanins, while the regional wines from vines at an altitude of 214 m a.s.l. contained the second highest level of myricetin derivatives and the highest levels of delphinidin-derived anthocyanins. The authors related this result to different factors, such as soil and water availability, which might have promoted the directional flow of carbon into the myricetin synthetic branch or to the quercetin synthetic branch. The region at the highest altitude is characterised by a brown sandstone soil and a specific water retention curve (the relationship between soil water content and soil water pressure head). This could incite the flow of more carbon to the F3'H branch pathway, leading to higher concentrations of quercetin derivatives and cyanidin-derived anthocyanins in the grapes and in the resulting wines. The authors did not exclude possible interference of other factors, like the cool-warm climate existing in the higher altitudes and the warm climate existing in the lower altitudes.

A study performed on wines from 'Muscat of Bornova' grapes grown in Turkey found that phenolic levels were the highest in wines of the Halilbeyli sub-region (115 m a.s.l.), followed by wines of the Menderes (90 m a.s.l.) and Kemaliye (245 m a.s.l.) sub-regions (Karaoğlan *et al.*, 2015). In particular, the concentrations of trans-caftaric and trans-coutaric acids in the produced wines from the Kemaliye sub-region (39 and 5.8 mg/L respectively) were lower than those of the Menderes sub-region (55 and 23.6 mg/L respectively) and the Halilbeyli sub-region (80 and 25.3 mg/L respectively). The lowest values obtained at Kemaliye may be related to the soil composition of this sub-region, which is characterised by having the highest percentage of lime, which affects water retention and drainage.

3.2.4. The effect of other parameters

Many studies have shown that other factors, such as humidity, vintage and grapevine variety, are closely associated with temperature, UV radiation and vine water status. The lower humidity of the high cultivation sites (at approximately 2900 m a.s.l.) in southwest China induced an increase in the production of cyaniding-type anthocyanins and quercetin-type flavonols from the F3'H branch of the flavonoid biosynthetic pathway in 'Cabernet-Sauvignon', when compared with sites at lower altitudes (2300 and 2150 m a.s.l.) (Xing *et al.*, 2016). Another study on the effect of altitude on carotenoids of 'Touriga Franca' and 'Touriga Nacional' grape varieties was conducted by Oliveira *et al.* (2004) in the Douro Valley. The altitudes ranged from 85 and 145 to 180 m a.s.l. for 'Touriga Franca' and from 90 and 155 to 210 m a.s.l. for 'Touriga Nacional'. High-elevation terraces with higher humidity levels promoted the accumulation of carotenoids, which degrade during the grape ripening period to form odour-active C13-norisoprenoids.

Mateus *et al.* (2001) showed that at the lower cultivation locations (100-150 m a.s.l.), humidity levels of 95-100 % during the night were not favourable for the biosynthesis of total anthocyanidin monoglucosides in the grape skins of 'Touriga Nacional' and 'Touriga Francesa' compared to the higher sites (250-350 m a.s.l.). Nevertheless, higher concentrations of catechin monomers and low-molecular procyanidin oligomers in the grape skins of both varieties, as well as of total extractable proanthocyanidins in the skins of both cultivars and the seeds of 'Touriga Nacional', and of low-molecular procyanidin oligomers in the 'Touriga Nacional' wine, were obtained at the lower altitudes. None of these studies, however, separated the effect of humidity from temperature.

The latitude effect was more pronounced than the altitude effect for 'Malbec' wines produced by different regions in Argentina. The vineyards at latitudes of 31-33° produced the most desired sensory attributes in wine (e.g., floral, sweetness, cooked fruit and raisin) in contrast to regions outside these latitudes which exhibited sourness, bitterness and a strong herbal aroma (Goldner and Zamora, 2007). The levels and the composition of phenolics in grapes vary as a result of vine vigour and water inputs. The variability in microclimatic conditions of the grapevines may be caused by vine vigour heterogeneity (Asproudi *et al.*, 2016). When compared to less vigorous vines, high vigour vines usually have lower fruit exposure and a greater fruit MIBP content (Mendez-Costabel *et al.*, 2014); as a result of increasing water input from rainfall and irrigation, MIBP synthesis can increase (Mendez-Costabel *et al.*, 2014).

Vintage is one of the main factors to influence the concentrations of proanthocyanidins in grapes, in addition to the effect of air temperature, which varies between altitudes. Of the monomeric and the small oligomeric compounds in 'Syrah' seeds, Barreto de Oliveira *et al.* (2019) found higher levels of gallocatechin, epigallocatechin and B1, B2, B3 and B4 dimers at a higher altitude (1100 m a.s.l.) in the first year of their study, and high concentrations of catechin and B2 dimers esterified with gallic acid at a lower altitude (350 m a.s.l.) in the second year. Vintage was observed to have a higher effect than altitude for 'Chardonnay' and 'Pinot Noir' cultivated in Minas Gerais, Brazil (Regina *et al.*, 2010); a greater number of sunny days in the growing season contributed to a greater accumulation of anthocyanins and phenolic compounds in the grapes.

The highest content of total phenols and flavonoids in 'Moscatel' grape stems sampled form three different regions in northern Portugal at 120, 670 and 730 m a.s.l. were found in the lowest altitude region over two consecutive vintages (Gouvinhas *et al.*, 2020) ; nevertheless, they increased significantly in the second year of the study, which was characterised by an atypical summer with a 3-day heat wave (temperatures above 40°C) near the beginning of the harvest. Under these stressful conditions, which scalded the grapes, the plants produced secondary metabolites as a defense mechanism. The obtained lower levels of total phenols and flavonoids in the high-altitude regions may be attributed to the absence of significant water or thermal stresses in these regions. However, higher biological capacities were induced by high precipitations and the climate, which has an Atlantic influence in the low-altitude regions.

The amount of polyphenols in 'Ancellotta', 'Lambrusco', 'Negroamaro', 'Nero d'Avola', 'Fiano' and 'Garganega' cultivated at 1300 m a.s.l. was greater in the year which had a higher number of rainy days (Malinovski *et al.*, 2016). This result was correlated with the fact that fungal diseases are common in areas with high rainfall, inducing plants to produce phenolic compounds as a stress response. The intensity of this response was found to vary depending on the grape varieties, showing that different cultivars respond differently even when subject to the same stressful climatic conditions.

The antimicrobial activity in 'Moscatel' grape stems was shown by the multivariate analysis to be lower in the high-altitude regions (730 m a.s.l.) than in the lower altitude regions (120 m a.s.l.) (Gouvinhas *et al.*, 2020). This antimicrobial activity seemed to be more affected by the genetic characteristics of the grape stem varieties than by the climate conditions and altitude of the growing sites. Jiang *et al.* (2013) concluded that the magnitude of the effect of environmental factors on the volatile compounds in Cabernet-Sauvignon and Merlot wines produced from four wine-growing regions in China (at 214, 450–600, 1036 and 1100 m a.s.l.) may be related to the cultivar.

Different studies have shown that the effects of temperature and sunlight cannot be isolated from the effect of vine water status. In high-altitude areas in China (2282, 2435 and 2608m a.s.l.), due a decrease in temperature and an increase in rainfall and sunlight hours, the quercetin, trans-resveratrol and tannin content in 'Cabernet-Sauvignon' wines increased with increasing altitude (Jin e*t al.,* 2017); however, no significant effect of altitude on the same parameters was found in 'Merlot' wines. Overall, altitude followed by sunlight hours mostly affected the phenolic characteristics and antioxidant activity of tested red wines. Vine water status is a key determinant of terroir expression, which depends on climatic conditions, such as rainfall and evapotranspiration (van Leeuwen *et al.*, 2020). In a study conducted on 'Grenache' berries (Edo-Roca *et al.*, 2013), the effects of vine water status and temperature were not completely differentiated: levels of anthocyanins in grapes declined in the last ripening control in the warmest year of the study, in which dryness and high temperatures occurred during a 3-day heat wave (temperatures reaching an unusual 40 °C) in the period before harvest.

CONCLUSION AND FUTURE PERSPECTIVE

Altitude affects the chemical composition of grapes and wine to a large extent. Some studies have shown that an increase in altitude results in a delay in budburst, flowering and grape ripening, with elevated winegrowing regions being more adapted to climate change. Studies have shown that high-altitude cultivation favours higher acidity and aroma compound content in grapes, and higher anthocyanin, flavonol, total anthocyanidin monoglucoside and condensed tannin content in grape skins. Altitude has also been found to induce the accumulation of total phenolics, flavonoids and anthocyanins, as well as optimal wine sensory characteristics, such as elegance, bell pepper and floral aromas. However, other studies have found the highest phenolic content in grapes, the highest concentration of total aroma compounds and the highest bitterness and astringency in wine in a region between the highest and the lowest regions in altitude. Meanwhile, in other studies, higher condensed tannin and procyanidin compound contents in grape seeds, of flavonols, trans-resveratrol and 3-O-acetylglucoside anthocyanin contents in grape skins, and red fruits aroma and higher colour intensity of the produced wine were obtained at lower altitudes. Other factors that influence berry and wine composition, such as cultivar, vintage and the presence or absence of significant water or thermal stresses, emerged from these studies. As explored in this review, vineyard location (i.e., altitude, latitude, slope and orientation), plant material (i.e., variety, clones and rootstock), training system, soil type and solar radiation are all factors that influence grape and wine quality; it is very difficult to determine how each individual variable affects it, which is why some articles contain contradictory findings in the literature.

More studies on different cultivars in different terroirs are needed in order to increase our knowledge regarding the impacts of altitude on grape and wine quality in relation to climate and the development of phenolic and aromatic compounds during berry ripeness. Moreover, the recent interest in taking altitude into account in strategies for delaying grape ripening and ensuring that ripening occurs at lower temperatures is due to the role of this important viticultural parameter in reducing the negative effects of global warming.

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