UV-B Radiation as a Factor that Deserves Further Research in Bolivian Viticulture: A Review

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Bolivian viticulture has acquired an incipient notoriety in the international wine market due to the production of high-altitude wines with a high antioxidant potential. Andes agricultural regions present an advantage for wine production since UV-B radiation reaching the earth's surface increases with altitude and varies with latitude, promoting the activation of plant defense mechanisms responsible for the synthesis of secondary metabolites. UV-B radiation upregulates the biosynthesis of nitrogen, phenolic and volatile compounds that contribute to wine flavour. It is thought that the incident UV-B radiation in the Bolivian valleys makes it possible to obtain wines with high phenolic and aromatic potential, but the published results are not entirely conclusive. This manuscript addressed the geological and climatic features that affect Bolivian viticulture, and we reviewed the field studies carried out regarding the effects of altitude and UV-B radiation on flavour components of grapes and wines from Bolivian viticultural valleys. A high antioxidant capacity and *trans*-resveratrol content is found in grapes and wines from high-altitude Bolivian vineyards, including if they are compared to those samples from different wine countries. However, high UV-B radiation can result in bunch sunburn affecting some physico-chemical parameters of the produced wines. Scarce number of studies have been developed in this field despite this region present a valuable potential for research in order to quantify the effects of biologically damaging radiation on the synthesis of flavour components in grapes and some of them were not well scientifically controlled.

INTRODUCTION

Currently, viticulture is an important activity of the agriculture in many regions of Andean America (Preston & Clewer, 1993). In 1960, the introduction of new genetic material and production technologies were prioritized in order to intensify and modernize the viticulture sector (Turner & Davidson-Hunt, 2016). The reconfiguration of the regional economy towards viticulture was consolidated during the 1990s through continued capital investment, the establishment of education, a plant nursery and research facilities (Turner & Davidson-Hunt, 2016). These important efforts have resulted in the establishment of the spirit *Singani* as a typical beverage of this region by origin denomination and the famous of wines produced from grapes from high-altitude vineyards to the international wine market to this day.

The total surface area of the vineyards planted in Bolivia is estimated at 2,500 ha of which 65 % is located in the Central Valley of Tarija (Pszczólkowski *et al*., 2010), whose wine ecosystem has production limitations due to complex pedoclimatic conditions (Aguilar & Pszczólkowski, 2012).

Bolivia's sub-equatorial and inter Andean valleys are located mainly at the end of the Andean mountain range which have elevations of between 2,000–4,000 metres above sea level (m. a. s. l.), and latitudes in the range of 10°–20° South (Taquichiri *et al*., 2014). Bolivian viticulture is mostly located at 1,660 to 2,360 m. a. s. l. (Pszczólkowski *et al*., 2010). Based upon latitude and altitude, Bolivian viticulture could be defined as a subtropical, corresponding to a cool semi-arid zone based on Köppen classification, with a large mesoclimatic variability (Pszczólkowski *et al*., 2010).

The viticultural regions of Tarija and the Loayza Province of La Paz receive more intense solar UV radiation is more intense than other places in Bolivia where grapevines are cultivated (Taquichiri *et al*., 2014). UV-B environmental levels are mainly regulated by cloudiness, season and latitude, but also increase with altitude as UV-B passes through a thinner atmosphere to reach the earth's surface (McKenzie *et al*., 2007). There are many studies demonstrating that UV radiation reaching the earth's surface increases with altitude and varies with latitude (Zaratti *et al*., 2003; Pfeifer *et al*.,

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2006). Concerning latitude, UV levels are higher closer to the equator since the sun's rays have a shorter distance to travel through the atmosphere and therefore less of the harmful UV radiation can be absorbed (WHO, 2016). At increasing altitude, less atmosphere is available to absorb UV radiation and, with every 1,000 m in altitude, UV levels increase by approximately 10 % (WHO 2016). Table grapes are produced at altitudes between 400 to 2,000 m. a. s. l. in the Chaco Tarijeño, while wine grapes are cultivated between 1,600 and 2,800 m. a. s. l. in the Valley of Cotagaita (Department of Potosí, Bolivia). Bolivian viticulture therefore lends itself to unique climatic and favourable conditions for the production of grapes and wine with nutritional value listed in Table 1.

Keller & Torres-Martinez (2004) reported that UV radiation reduced early-season shoot growth but stimulated lateral shoot growth later in the season and enhanced root growth. Concerning plant physiology and grape quality, UV radiation had no obvious effect on leaf chlorophyll and gas exchange, but reduced leaf water content and increased carotenoid and flavonoid concentrations (Keller & Torres-Martinez, 2004). Lafontaine *et al*. (2005) showed that chlorophyll degradation in leaves and berry skins occurred rapidly in Riesling grapes subjected to high UV-radiation. These authors also reported that exposure of grapes to UV-B radiation increased both the concentration of total bound glycosidic secondary metabolites and phenolics. The synthesis of flavonoid and non-flavonoid compounds in grape skins can increased when grapes are exposed to sunlight (Gregan *et al*., 2012; Teixeira *et al*., 2013; Blancquaert *et al*., 2019). Flavonols are a class of flavonoids with photo-protection activities since they effectively absorb both UV-A and UV-B wavelengths (Flamini *et al*., 2013). The synthesis of anthocyanins increase in grape skins as a consequence of UV radiation (Berli *et al*., 2008; Carbonell-Bejerano *et al*., 2014). Stilbenes are phytoalexins present in grapes that are associated with health promoting properties (Flamini *et al*., 2013). Synthesis of some stilbenes can also be induced upon grapevine diseases infection or UV irradiation and accumulation of stilbenes may also be stimulated by the UV received at high altitudes (Pezet *et al*., 2004; Berli *et al*., 2011; Carbonell-Bejerano *et al*., 2014).

Some commercial wine cellars with great purchasing power produce wine from grapes grown at high-altitudes such as Shandong and Yunnan in China, Galilee in Israel and Cafayate and Jujuy in Argentina. Recently, Compés and Sotés (2018) mentioned in their report that in Bolivia, a new viticultural country of surprising interest, and a culture of high-altitude vineyards has developed in the Tarija region. Therefore, Bolivian viticulturists use Criolla and Vinifera cultivars for the production of wine, table grapes and spirits (Gutiérrez-Gamboa *et al*., 2020). Singani is a controlled designation of origin, which defines the spirits obtained from Moscatel de Alejandría and produced in certain Bolivian areas (Buitrago Soliz, 2014). Singani is considered the national schnapps of Bolivia and is mainly produced in Tarija, the traditional wine-growing region of Bolivia (Buitrago Soliz, 2014; Gutiérrez-Gamboa *et al*., 2020). This review aims to summarize the effects of altitude on the chemical composition of grapes, i.e. phenolic, volatile and nitrogenous compounds, and to compare altitude impacts with the results obtained under the edaphoclimatic conditions of Bolivian viticulture . It should be noted that there are not many published studies on this geographical area regarding viticultural research. The discussion would compare results from other high-altitude viticultural zones, and discuss the potential impacts under the reality of Bolivian viticulture.

SOIL AND CLIMATE CONDITIONS OF BOLIVIAN VITICULTURE
Soil conditions
The Central Valley of Tarija belongs to the geological structure of the Bolivian Cordillera Orientale and its topography is that of a mountainous and hilly border surrounding the catchment area of the Guadalquivir, Tolomosa and Camacho rivers (Pszczólkowski *et al*., 2010). Tarija soils are frequently and intensely degraded by water and wind erosion (Pszczólkowski *et al*., 2010). The soil loss values provoked by erosion in Tarija are exorbitantly high, even on nearly level surfaces, amounting to up to 65 metric tons per hectare for a single storm and total losses of approximately of 230 metric tons per ha by year (Bastian & Gräfe, 1989).

Generally, Tarija soils are characterized by low levels of fertility and organic matter (≤ 1 % of OM) (Apaza-Gutiérrez *et al*., 2002). These soils also have high salinity, sodium toxicity and pH above 7.5 (Coppus, 2002; Pszczólkowski *et al*., 2010). Since the presence of sodium carbonate, there are frequent manifestations of black alkalinity symptoms, a situation which makes it difficult for the infiltration of rainwater or irrigation water in soils (Pszczólkowski, 2008). This phenomenon is aggravated by the silty texture and laminar structure of the soils (Pszczólkowski *et al*., 2010). In addition, these soils have a high level of Ca and $MgCO_3$, with high contents of active limestone, which promotes iron deficiency (Reyes *et al*., 2006). The most common rootstocks for grapevines used in Central Valley of Tarija are 99 Richter, 110 Richter and 1003 Paulsen, which tolerate up to 17 % of active limestone, and SO4 rootstock that tolerates close to 20 % of active limestone (Pszczólkowski *et al*., 2010). Therefore, it is important to evaluate the conditions that result in chlorosis, by measuring certain parameters such as total carbonates (%), active lime (%) and CPI (chlorotic power index) (Casanova-Gascón *et al*., 2018). CPI means that the quantity of active lime is related to the quantity of Fe extracted by ammonium oxalate (Pavlousek, 2013). Rootstocks that presents *Vitis berlandieri* genetic background are more adapted to calcareous soils than *Vitis riparia* and *Vitis rupestris* rootstocks (Pavlousek, 2013). Based on empirical knowledge, the utilization of other rootstocks like Fercal in combination with irrigation, should be evaluated to solve the aforementioned problems (Pszczólkowski *et al*., 2010).

In Tarija, there is usually a strong soil compaction as a result of the use of mechanization, leading to a limitation of root development by anoxia (Pszczólkowski *et al*., 2010). Contrary to the vineyards cultivated in Santa Cruz de la Sierra valleys, anoxia problems are present in Tarija vineyards mostly located close to the rivers, due to the presence of a surface water table less than 45 cm (Pszczólkowski *et al*., 2010; Aguilar & Pszczólkowski, 2012).

Seeking new productive solutions, different winemakers

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TABLE 1
Range of values of different variables obtained from grapes and wine produced in Bolivia.

Measurement	Matrix	Cultivar	Altitude (m.a.s.l.)	UV radiation	Range
Total antioxydant capacity[a]	Grape	Cariñena	1738	0 to 60 % UV-B attenuation	10.04 to 11.84 DPPH
		Moscatel de Alejandría	1738	1 to 60 % UV-B attenuation	1.84 to 2.25 DPPH
		Syrah	1733	2 to 60 % UV-B attenuation	8.66 to 11.09 DPPH
		Cabernet-Sauvignon	1870	3 to 60 % UV-B attenuation	9.67 to 14.06 DPPH
Total phenolic content[a]		Cariñena	1738	4 to 60 % UV-B attenuation	1.03 to 1.17*
		Moscatel de Alejandría	1738	5 to 60 % UV-B attenuation	0.29 to 0.30*
		Syrah	1733	6 to 60 % UV-B attenuation	0.81 to 1.07*
		Cabernet-Sauvignon	1870	7 to 60 % UV-B attenuation	1.31 to 1.43*
trans-resveratrol[b]		Negra Oliva	2274 to 2935	0.80 to 1.65 W/m^2	0.003 to 0.060 mg/g
		Negra Bordeaux	2276 to 2935	0.80 to 1.65 W/m^2	0.005 to 0.080 mg/g
		Negra Criolla	2274 to 3088	0.80 to 1.65 W/m^2	0.004 to 0.050 mg/g
		Torontel	2825 to 2987	1.30 to 1.65 W/m^2	0.001 to 0.060 mg/g
		Cabernet-Sauvignon	2550 to 2825	1.30 to 1.65 W/m^2	0.004 to 0.050 mg/g
		Moscatel de Alejandría	2825	1.30 W/m^2	0.003 mg/g
Colour Intensity index[c]	Wine	Syrah	1719 to 1800	Not provided	3.8 to 10.6
		Cabernet-Sauvignon	1720 to 1800	Not provided	9.1 to 12.7
Total phenolic index[c,d]		Syrah	1721 to 1800	Not provided	33 to 57
		Cabernet Sauvignon	1722 to 1800	Not provided	49 to 59
		Non-varietal, Cabernet-Sauvignon, Syrah and Tannat	1750 to 2100	Not provided	9.22 to 20.52 mmol/L
Anthocyanins[c]		Syrah	1723 to 1800	Not provided	298 to 736 mg/L
		Cabernet-Sauvignon	1724 to 1800	Not provided	554 to 749 mg/L
Saccharose[d]					<DL to 6.15 g/L
Glucose[d]					1.76 to 8.06 g/L
Fructose[d]					0.52 to 8.51 g/L
trans-resveratrol[d]		Non-varietal, Cabernet-Sauvignon, Syrah and Tannat	1750 to 2100	Not provided	<DL to 7.9 mg/L
Total flavonoids[d]					1.85 to 5.79 mmol/L
Total antioxidant[d] capacity[d]					4.1 to 24.3 mmol/L

* Folin Ciocalteu protocol. DL: Detection limit. [a]Ayarde Mogro *et al.* (2012), [b]Taquichiri *et al.* (2014), [c]Ceppi de Leco and Castillo (2008), [d]Osorio-Macías *et al.* (2018).

have launched a re-invention of Bolivian viticulture in different ecosystems of the district of Santa Cruz through the planting of small vineyards in mountainous areas, which represents close to 175 ha (Aguilar & Pszczólkowski, 2012). The soils present in the wine-growing areas of Santa Cruz is of loam-clay texture with a depth that varies from 1.0 m to 1.5 m, a moderate water holding capacity, and well aerated, which facilitates the infiltration and drainage of water (Aguilar & Pszczólkowski, 2012). These soils have a low organic matter content reaching less than 1 % (Aguilar & Pszczólkowski, 2012).

Santa Cruz soils have favourable physicochemical conditions for grapevines (Pszczólkowski *et al.*, 2010; Aguilar & Pszczólkowski 2012). The soils present low electrical conductivity, low exchangeable sodium percentage and a pH close to 6.8 (Aguilar & Pszczólkowski, 2012). Regarding soil fertility, Santa Cruz soils exhibit phosphorus deficiency due to the retention of clays and the lack of nitrogen by leaching (Aguilar & Pszczólkowski, 2012). In addition, the levels of calcium and magnesium carbonates in soils are low and present absence of active limestone substrate, conditions that reduce the risk of ferric chlorosis that affect the initial development of grapevines (Aguilar & Pszczólkowski, 2012; Gutiérrez-Gamboa *et al.*, 2020; Pszczólkowski *et al.*, 2010). Consequently, Bolivian viticulture is cultivated on diverse types of soils, in terms of physicochemical parameters, such pH, chemical and mineral composition, organic matter and salinity.

Climate conditions

In the Central Valley of Tarija (Fig. 1), the average maximum temperature ranges from 23.8 (in July) to 27.5 °C (in October or November) and the average minimum temperature ranges from 2.3 (in July) to 14.4 °C (in January)

(Pszczólkowski *et al.*, 2010). Day-night thermal amplitude is highest in July reaching a difference of 21.5 °C, and lowest in January with an amplitude of 12.7 °C (Pszczólkowski *et al.*, 2010). The small annual variation in average maximum temperatures is explained by less summer sunshine due to abundant cloudiness and rainfall (November to March), compared to the winter that holds low cloudiness and dryness (Francou *et al.*, 2003; Pszczólkowski *et al.*, 2010).

As in the Central Andes, in the Tarija altiplano and adjacent valleys, 95 % of the annual rainfall falls in spring and summer, specifically between the months of October to April (Preston *et al.*, 2003). During the wet season, rainfall is not evenly distributed, characteristically falling during short, intensive storm events (Preston *et al.*, 2003). Because of this, the lack of irrigation, especially in winter and early spring, is the limiting factor for grapevine cultivation in this region (Pszczólkowski *et al.*, 2010). The amount of rainfall depends on the summer daytime temperature and, to a lesser degree, by the El Niño Southern Oscillation (ENSO) (Preston, 2000). During strong ENSO events, drought commonly occurs on the Andean Altiplano in the austral summer, whereas during anti-El Niño or La Niña phases, rainfall increases (Thompson *et al.*, 1984). However, because of the high degree of variability of rainfalls, wetter than average months occur during dry ENSO periods (Preston, 2000; Preston *et al.*, 2003). In the case of the Central Valley of Tarija, generally, the La Niña seasons are wetter, while the El Niño seasons are drier, which is the opposite of what occurs in the western coast of South America (Pszczólkowski *et al.,* 2010). The vineyards can be affected by flooding when the summer rains are intense, which can cause soil erosion (Pszczólkowski *et al.*, 2010). In addition, in the Central Valley of Tarija, thunder storms occur which is often accompanied by hail (Zamuriano *et al.*, 2019). The use of anti-hail nets is an

FIGURE 1
Wine Regions of Bolivia (Figure obtained by the report published by Wines of Bolivia, 2020).

important current viticultural strategy to solve this problem (López Ávila, 2008). However, in most of the Bolivian viticultural valleys, endemic trees are planted within the vineyard. The foliage of the trees protect the vineyards from hail (Oliva Oller, 2021).

In Tarija, the frost-free period accounts seven months from October to April, whereas in Santa Cruz de La Sierra, it has a duration of eight months from October until May (Pszczólkowski et al., 2010; Aguilar and Pszczólkowski, 2012). In Tarija, the frosts are convective but in Santa Cruz de La Sierra the frost could be radiative or convective (Pszczólkowski et al., 2010; Aguilar & Pszczólkowski, 2012). Hailstorms are frequent in the Andes and hail is typically formed in convective storms both locally and in the Amazon basin, where there is sufficient water vapour and favourable energy conditions (Andrade, 2017). The complex interaction between lakes, surface heating and orography favours deep convection and hailstorm formation (Zamuriano et al., 2019). In Tarija, frost, hailstorms and floods are responsible for grape production losses of between 25 to 50 % per season, a situation which is less critical in the valleys of the department of Santa Cruz since where there is less risk of hailstorms and floods (Pszczólkowski et al., 2010). To curb hailstorms, farmers install anti-hail nets, preferably cover nets, since it allows the mechanization of certain practices, such as pre-pruning, phytosanitary applications and harvesting (López Ávila, 2008) which allows sufficient irradiation and ventilation of grapevines, and also reducing the incidence of cryptogamic diseases by 65 % per hectare (López Ávila, 2008).

An advantage to mitigate global warming is that altitude causes a decrease in temperature, creating a more temperate climate, due to adiabatic cooling of the air at a rate of 0.6 °C every 100 m (Pszczólkowski et al., 2010; Gutiérrez-Gamboa et al., 2020). This altitude-related cooling is attenuated by the effects of strong solar radiation, low cloudiness and low precipitation that characterize winter in Tarija (Pszczólkowski et al., 2010). But in part, these unfavourable conditions for the accumulation of winter temperatures, are

compensated by the wind coming from the inter-Andean valleys, located at the south-east of the Central Valley of Tarija (Pszczólkowski et al., 2010). In this valley, the average accumulation of chilling hours over a series of 45 years was 337 hours (Pszczólkowski et al., 2010). However, the average accumulated of the last ten years is only 269 hours, showing a clear decreasing trend as is reported by Anzanello et al. (2018), Fraga et al. (2019) and Santos et al. (2019).

Previous studies indicate that the chilling exposure necessary for normal bud growing ranges between 50 and 400 hours at temperatures lower than 7 ºC (Dokoozlian, 1999; Dokoozlian et al., 1995). As is shown in Fig. 2, in warm regions where winter temperatures rarely reach below 7 ºC, insufficient chilling can result in delayed and desynchronized budburst (Londo & Johnson, 2014). By consequence, shoot number, bunch number, and fruit ripening rates are all negatively affected, which result in a decrease in vineyard productivity (Dokoozlian et al., 1995; Dokoozlian, 1999; Londo & Johnson, 2014). In the viticultural regions where achieving chilling is problematic, the use of hydrogen cyanamide has proven to improve budburst (Dokoozlian et al., 1995). However, this chemical regulator also advances budburst, increasing the risk of spring frost damage, and therefore, it is not used in Bolivian vineyard management (Pszczólkowski et al., 2010; Gutiérrez-Gamboa et al., 2020).

Pruning practices such as cane pruning, late winter pruning, double-pruning or pruning the spurs leaving one bud, may partially solve heterogeneous budburst by insufficient chilling, without advancing the date of budburst (Pszcolkowski et al., 1983; Pszczólkowski et al., 2010). Pruning to one bud favours the burst of the base bud providing acrotony control (Pszczólkowski & Villena, 2009). Hence, the use of low chill cultivars would likely reduce the need for budburst induction via physical or chemical intervention techniques (Londo & Johnson, 2014). As stated by Pszczólkowski et al. (2010) interspecific hybrids such as Favorita Diaz and Monte Rico (Concord ´ Vitis labrusca) are the most adapted cultivars under the subtropical conditions. Cultivars such as Cardinal, Italia and Red Globe for table

FIGURE 2

Acrotony and heterogeneous bud burst due to the lack of winter cold in Santa Ana la Nueva vineyard in Central Tarija Valley (left). Homogeneous budburst as consequence of pruning practices on Carmenère in Calamuchita vineyard in Central Tarija Valley (right). (Figure obtained by the manuscript published by Pszczólkowski et al., 2010).

grape production are reasonably adapted. Certain Criolla cultivars used for table grape production, wine and spirit production such as Vicchoqueña, Negra Criolla, Blanca Redonda, Rosada Criolla, Moscatel San Juanina, Mollar, as well as Alphonse Lavallée, Ribier, Cereza, Pedro Giménez and Torontel are also reasonably adapted. Vinifera cultivars, i.e. Chardonnay, Cabernet Franc, Cabernet Sauvignon, Carmenère, Merlot, Petit Verdot, Pinot Blanc, Pinot Gris, Meunier, Pinot Noir, Riesling, Sauvignon blanc, Chenin blanc, Colombard, Malbec, Sauvignon vert and Syrah show a deficient adaptation to subtropical conditions due to their need for high winter cold. However, Tannat grapes appears to be well suited to Bolivian viticulture conditions. Some Mediterranean cultivars such as Bonarda, Carignan, Grenache, Nebbiolo, Sangiovese, Tempranillo and Ugni Blanc, present a better adaptation to the subtropical conditions of Central Valley of Tarija than the above mentioned Vinifera cultivars. Therefore, understanding variation in chilling requirements will prepare grapevine breeders and producers for the projected changes in global climate (Londo & Johnson, 2014).

The spectrum of solar UV radiation reaching the surface of the Earth ranges between 290 nm and 400 nm, which are equivalent to quantum energies between 4.278 eV and 3.102 eV (Piazena & *Häder*, 2009). Sun elevation above the zenith changes during the day and seasons, thereby UV-B levels are higher at midday and summertime in the tropics, than in other zones of the Hemisphere (Piazena, 1996). The impact of altitude is related to the atmospheric column mass that solar rays must traverse, and at high altitudes there is less air masses and hence greater solar UV-B levels (Piazena, 1996). In subtropical Andean regions, during the summer months and especially during the wet season, the cloudiness is enhanced, leading to increased incoming long-wave radiation (Francou *et al*., 2003). In general, UV irradiance increases with altitude because of the decreasing quantity in absorbing and scattering material above the observer (Pfeifer *et al*., 2006). At solar elevations between 20° and 90° the increase of the global irradiance is about 8 to 10 % every 1000 m for UV-B and changed from 15 to 7 % every 1000 m for UV-A (Piazena, 1996). Moreover, albedo effect further enhances UV irradiance with altitude since albedo increases with altitude because of increased probability of snow and the change from vegetation to rocks (Pfeifer *et al*., 2006). The column ozone is thinner over the tropics compared to northern mid-latitude, and UV increases in relation to the elevation (Fig. 3), clear skies, and low aerosols (Blumthaler *et al*., 1994). In the high-elevation zones of Bolivia, extreme UV-B (280-315 nm) irradiance equivalent to a UV index of 43.3 was recorded, which is the highest ground value ever reported (Cabrol *et al*., 2014). By consequence, the tropical Andes zones represent a particularly valuable study area for quantifying the effects of biologically damaging radiation (UV-A, UV-B) on crop productivity and quality (Piazena, 1996). The total UV-B irradiance measured at Central Valley of Tarija, is up to 6.2 W m^2 in summer and 2.1 W m^{-2} in winter, corresponding to a UV-B index of 14 in summer and 6 in winter (Taquichiri *et al*., 2014).

UV RADIATION EFFECTS ON THE SYNTHESIS OF PHENOLIC COMPOUNDS IN GRAPES

The common protective response of grapevines against UV-B radiation is the biosynthesis of UV-absorbing compounds that are accumulated in epidermal vacuoles (Kolb *et al*., 2001; Berli *et al*., 2011). Abscisic acid (ABA) is involved in the response of grape leaf tissues to UV-B radiation by enhancing the synthesis of UV-absorbing compounds, antioxidant enzymes and membrane sterols (Kolb *et al*., 2001; Berli *et al.*, 2009). Indeed, previous incidence of high UV-B in grapevines prevented deleterious effects of water deficit on berry weight reduction and decrease of sugar accumulation (Alonso *et al*., 2016). UV-B modulates the accumulation of sugars and upregulates anthocyanin biosynthesis in grapevines and compensated the deleterious
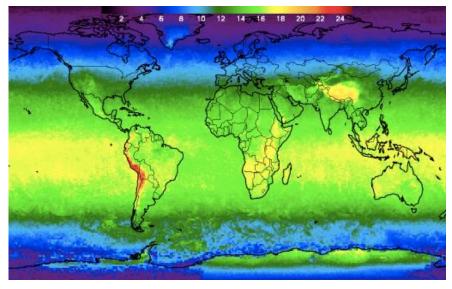

FIGURE 3
Map of peak of UV Index (UVI), using a modified colour scale to highlight the absolute peaks (Figure obtained by the report published by Liley and Mckenzie, 2006).

effect of elevated atmospheric carbon dioxide (CO_2) and increased temperature on berry anthocyanin concentration (Martínez-Lüscher *et al*., 2016). UV-B radiation slowed berry development and upregulated flavonol and anthocyanin biosynthesis (Martínez-Lüscher *et al*., 2016). Moreover, viticultural practices that result in the exposure of grape bunches to UV-B radiation, may alleviate the effect of elevated atmospheric CO_2 and increased temperature on grape anthocyanin concentration, which occur in Bolivia vineyards. Supporting this, a preliminary study showed that photosystem II (PSII) in chloroplasts is protected against UV-B damage by epidermal screening (Kolb *et al*., 2001). These authors suggested that the protection of UV-B inactivation of PSII is because preceding damage is repaired, while those factors determining UV-B inhibition of CO_2 assimilation recover more slowly.

UV-radiation activates specific signalling pathways in grape skins from grapevines established at mid-altitudes and by consequence, the accumulation and synthesis of secondary metabolites that potentially confer cross-tolerance, are specifically triggered (Carbonell-Bejerano *et al*., 2014). Two key biosynthetic genes (*UFGT* and *FLS1*) concomitantly are up-regulated by UV-B radiation, leading to an increase in anthocyanin and flavonol concentration in skins (Gregan *et al*., 2012; Martínez-Lüscher *et al*., 2014). The changes in flavonol and anthocyanin concentration are explained to a large extend by transcript levels of *F3'H, F3'5'H* and *OMT2,* affected by UV-B radiation (Martínez-Lüscher *et al*., 2014). Secondary metabolism related transcripts are induced by UV radiation including *VvFLS1*, *VvGT5* and *VvGT6* flavonol biosynthetic genes, which result in an increase in flavonols accumulation in skin grapes (Carbonell-Bejerano *et al*., 2014). The transcriptional activation of structural (*VvANR*, *VvLAR1* and *VvLAR2*) and regulatory (*VvMYB5a*, *VvMYB5b* and *VvMYBPA1*) genes involved on flavanol biosynthesis in grapes depend on developmental stage in which grapes are affected by UV-radiation, since it enhanced gene expression and flavanol content only in unripen grapes (3 weeks after flowering), compared to the mature grapes (11 weeks after flowering) (Zhang *et al*., 2013). UV-B radiation generates a phenolic-based resistance against *Botrytis cinerea* through the activation of the phenylpropanoid biosynthetic pathway (Demkura & Ballaré 2012; Matus, 2016). Based on literature (Flamini *et al*., 2013; Gindro *et al*., 2017), it is known that grapevine diseases allow the induction of stilbene synthase (STS) in grapevine cells. Therefore, UV-light irradiation can stimulate STS transcript of unripe berries, harvested from Corvina grapevines (Versari *et al*., 2001).

Based on results obtained in vineyards cultivated in Bolivia (Table 1), it was reported that Syrah wines from Pampa Colorada (1.729 m. a. s. l) and Santa Ana (1.800 m. a. s. l) sites had higher alcohol content, colour intensity (CI), total polyphenol index (IPT) and anthocyanins content than the wines from Pampa la Villa (1.719 m. a. s. l) and La Compañía (1.721 m. a .s. l) (Ceppi de Lecco & Castillo, 2008). Cabernet Sauvignon wines obtained from these sites were not significantly different in phenolic composition but wines from Pampa Colorada and Santa Ana showed higher total anthocyanin content than the wines from Pampa la Villa and La Compañía (Ceppi de Lecco & Castillo 2008).

Recently, Arteaga *et al*. (2020) reported that total tannin content in commercial wines from Central Valley of Tarija ranged from 0.21 to 4.97 g/ L. Regarding other compounds, it was reported that some South American wines from grapevines growing at high altitude (higher than 1.500 m. a. s. l as in Tarija and Santa Cruz in Bolivia, and Salta in Argentina) had higher total antioxidant capacity (TAC) and phenolic content, including resveratrol than wines from the low-altitude vineyards (Osorio-Macías *et al*., 2018).

Taquichiri et al. (2014) reported that *trans*-resveratrol content in grapes from Central Valley of Tarija was significantly higher than the grapes collected in the Loayza province and in other viticultural countries (Taquichiri *et al*., 2014). These authors related the differences on solar UV-B radiation levels with the oxidative processes that affect the synthesis of *trans*-resveratrol in grapes. Similar results for *trans*-resveratrol were found in wines from Bolivia (7.7 mg/L), compared to those from other countries (from 1.0 to 3.2 mg/L) by Bustos *et al*. (2012). In addition, Syrah grapes had the highest concentration of *trans*-resveratrol and therefore can be assume that this cultivar is more affected by UV radiation exposure, compared to most of *Vitis vinifera* grapevine cultivars cultivated in Bolivia (Ceppi de Lecco & Castillo 2008; Taquichiri *et al*., 2014). Moreover, it is possible that high UV-B radiation could have a negative effect on the quality of grapes (Fig. 4), causing sunburn damage to grapes, thereby affecting the tonality of the produced wines (Ayarde Mogro *et al*., 2012). Under these conditions, the attenuation of UV-B radiation using anti-hail mesh can be an alternative to reduce sunburn damage (Ayarde Mogro *et al*., 2012).

The high concentration of resveratrol and antioxidants found in Bolivian wines can mainly be attributed to the high altitudes (Andrade *et al*., 1998). However, in some cultivars, delaying ripening can increase the stilbene content of grapes but insufficient extraction of these compounds during winemaking can limit their concentration in wines (Favre *et al*., 2020). In addition, other studies have found direct associations between the UV-B radiation and the increment of the content of flavanols, flavonols and stilbenes and thereby the antioxidant activity in grapes and wines (Taquichiri *et al*., 2014; Alonso *et al*., 2016; Del-Castillo-Alonso *et al*., 2020). Plant defence mechanisms towards UV-B signal, promote the production of antioxidant secondary metabolites, instead of primary metabolites (Takshak & Agrawal, 2019; Liu *et al*., 2020). UV-B radiation decreased net photosynthesis and stomatal conductance, mainly through the limitation in gas exchange, reducing leaf area, net carbon fixation and plant growth (Berli *et al*., 2013). Morphologically, UV-B radiation induces an increase on leaf thickness, including the quantity of photoprotective pigments and proline, thereby increasing the antioxidant capacity of leaves (Berli *et al*., 2013). These authors suggested that UV-B effects on grapevine metabolic responses depend on tissues developmental stage and interplay with total radiation and air temperatures (Berli *et al*., 2013). In this way, high fluence rate UV-B seemed to had regulatory effects on the defence or general multiple-stress responses pathways but low fluence rate UV-B promoted the expression of genes that could be involved in UV-B protection or the amelioration of the UV-B-induced damage. (Pontin *et al*., 2010) These results can be linked to

FIGURE 4
UV-B damage in Muscat of Alexandria bunches. On the left there is a bunch without UV-B attenuation and on the right, the bunch present 60 % UV-B attenuation using anti-hail meshes (Figure obtained by the report published by Ayarde Mogro et al., 2012).

the effect of global warming on viticulture since it has been showed that UV-B alleviated the senescence-related lipid peroxidation induced by elevated CO_2-temperature but not by deficit irrigation (Martínez-Lüscher *et al.*, 2015a,b).

UV RADIATION EFFECTS ON THE SYNTHESIS OF OTHER COMPOUNDS IN GRAPES

Volatile organic compounds (VOCs) are produced by plants as signalling molecules that interact with the physical and biotic environment (Delory *et al.*, 2016, Ninkovic *et al.*, 2020). VOCs protect plant tissues against abiotic stressful factors through the decrease in the oxidative damage by the synthesis of antioxidant compounds and play a key role on grape varietal aroma of wines (González-Barreiro *et al.*, 2015; Faiola & Taipale, 2020). To our knowledge, there is no published reports that studies the effects of UV-B radiation on the synthesis of secondary metabolites other than polyphenols in grapes produced from Bolivian vineyards. However, some national oenologists emphasize the fact that cultivating vines in Bolivia, especially in the Central Valley of Tarija, produce wines with high content of terpenes and intense aromatic wines and distillates due to the exposure of the grapevines to varying UV-B radiation. This opinion contrast to the report by Lafontaine *et al.* (2005) who found that UV-B radiation decreased the content of volatile compounds, i.e. mostly terpenes and norisoprenoids. Radiation intensities depend on the row direction and altitude of the vineyard. For example, N-S orientated rows can receive a maximum photosynthetic active radiation twice a day with approximately 60 µmol m^{-2} s^{-1} inside the canopy and close to 1,000 µmol/m/s radiation outside the canopy during late morning for southern hemisphere. For example, NE-SW orientated rows can receive up to 80 µmol m^{-2} s^{-1} radiation inside the canopy and close to 1300 µmol/m/s radiation outside the canopy during mid-afternoon (Hunter *et al.*, 2016).

Regarding work by other authors, high intensity UV-B irradiation (0.33 W m^2 during the last 4 h of a 16 h day photoperiod) to grapevine leaves grown *in vitro,* allowed the synthesis of α-pinene, 3-carene, terpinolene and nerolidol that are considered a strong antioxidant. (Gil *et al.*, 2013) In addition, UV-B irradiation to Malbec grapes increased the content of terpenes at preharvest stages (90 days after flowering) as well as the content of hexanal and 5-hepten-2-one, whereas terpenes content decreased towards harvest (Gil *et al.*, 2013) Sunlight and UV exposure of grape bunches affected terpene, alcohols, C$_{13}$-norisprenoids and other volatile composition of the wine differently (Song *et al.*, 2015). These parameters enhanced the nerol, geraniol and citronellol content of wine but not linalool. Neither basal leaf removal nor UV transmission treatments, that allowed to increase bunch exposure to radiation, showed any effects on the content of β-damascenone in Pinot Noir wines (Song *et al.*, 2015). Terpene synthase (TPS) genes expression occurs during the later stages of berry development and some researchers suggest that low UV-B irradiance trigger acclimation processes via induction of TPS, resulting in terpene biosynthesis. (Lücker *et al.*, 2004; Gil *et al.*, 2012; Alonso *et al.*, 2016). In contrast, β-D-glucosyltransferases promote the conversion of free terpenes to glycosidic form, allowing the glycosylation of monoterpenes progresses towards harvest (Miao *et al.*, 2020) As a result, the effects of UV on free terpenes in grapes at harvest may be not significant as stated previously (Gil *et al.*, 2012; Liu *et al.*, 2015; Miao *et al.*, 2020). Linalool is one of the most sensitive monoterpene compound to sunlight exposure, whose biosynthesis was inhibited by sunlight exclusion where after it was enhanced by the re-exposure to radiation (Zhang *et al.*, 2017). Glycosylated geraniol and ocimene presented suppressive and stimulative responses to sunlight exclusion, respectively (Zhang *et al.*, 2017). *VvPNLinNer1,*

VvCSbOci, *VvGT7* and *VvGT14* genes are mainly responsible for monoterpene accumulation and sensitivity to sunlight (Zhang *et al*., 2017). *VvDXS2* and *VvDXR* genes are related in certain degree to the differential accumulation of total terpenes under different sunlight treatments performed by sunlight exclusion by bagging clusters in opaque boxes (Zhang *et al*., 2017).

Nitrogen compounds such as amino acids are molecules that play a key position in grapevine metabolism and play a major role in the biological functions of fermentative microbes and as flavour components of wines (Gregan *et al*., 2017). Proteins, proline and carbohydrates are important osmoprotectants that are synthesized in plants in response to adverse environmental conditions (Ashraf, 2010; Dawood *et al*., 2014). These osmoprotectants protect the plants from abiotic stresses adjusting cellular osmosis, scavenging reactive oxygen species, protecting cellular membranes, and stabilizing proteins/enzymes and enzyme activities (Gill & Tuteja, 2010). In this way, Berli *et al*. (2013) showed that proline content increased in grapevine leaves after exposition to specifically UV-B radiation under field conditions. Zhu *et al*. (2017) reported that grapevines exposed to UV-B radiation under glasshouse conditions, decreased the content of total amino acids and some individual amino acids in grapes between 41 to 93 %. Total free amino acid content of Tempranillo grapes harvested from fruit-bearing cuttings, exposed to two UV-B treatments (5.98 and 9.66 kJ m^{-2} d^{-1}) was not affected (Martínez-Lüscher *et al*., 2014). In terms of individual amino acids, UV-B radiation increased the content of gamma-aminobutyric acid (GABA), but decreased threonine, isoleucine, methionine, serine and glycine content, revealing a potential effect of UV-B on the GABA-mediated signalling and amino acid metabolism (Martínez-Lüscher *et al*., 2014).

CONCLUSION

Bolivian vineyards are mostly located at 1,660 to 2,360 metres above sea level which is higher than several of the cultivated vineyards worldwide. Bolivia is characterized by a subtropical altitude viticulture, and according to **Köp**pen classification, the climate corresponds to a cool semi-arid zone, with a large mesoclimatic variability. Under these edaphoclimatic conditions, UV-B radiation increases at 8 to 10 % every 1000 m of altitude. Moreover, the altitude causes a decrease in temperature, creating a more temperate climate, due to adiabatic cooling of the air at a rate of 0.6 °C every 100 m of altitude and could be an effective strategy to face global warming in viticulture. The above-mentioned climatic features open an opportunity to Bolivia to practice viticulture. Grapes and wines obtained from high-altitude Bolivian vineyards have high levels of *trans*-resveratrol and antioxidants, mainly attributed to the effects of UV-B radiation on activation of plant defence mechanisms. The study of secondary metabolites related to wine flavour deserve investigation but is currently limited due to the few public policies developed in relation to wine sciences. Despite the efforts made by the national industry, some trials have not been conducted under controlled conditions and it is possible that research performed under field conditions are not able to generate conclusive information in this regard.

Based on this, Bolivian viticulture represents a valuable study region for quantifying the effects of biologically damaging radiation on grapevine productivity, and grape and wine quality.

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