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Review

An overview about the impacts of agricultural practices on grape nitrogen composition: Current research approaches

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An overview about the impacts of agricultural practices on grape nitrogen composition: Current research approaches

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Abstract

Nitrogen is a structural component of proteins, nucleic acids, chlorophyll, hormones and amino acids. The last one and ammonium are important primary metabolites in grapes and are key compounds in winemaking since they are primary sources for yeast fermentation. Currently, grape quality has been affected due to the negative impacts of global warming and anthropogenic activity. Certain studies have reported a significant decrease in the free amino acids content and an increase in berry soluble solids and in proline biosynthesis in grapes in some grapevine varieties cultivated under warm climate conditions and water restriction. Proline is not metabolized by yeasts and stuck and sluggish fermentations can occur when the content of yeast assimilable nitrogen is low. Nitrogen composition of grape is mainly affected by variety, edaphoclimatic conditions of the vineyard and agricultural practices performed to the grapevines. This review summarized the most current research carried out

to modify the nitrogen composition of the grape and give an overview of the technical and scientific aspects that should be considered for future research in this field.

Keywords: amino acids; arginine; climate change; nitrogen uptake; proline; viticulture

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Abbreviations

Ala: alanine

Arg: arginine

Asn: asparagine

Asp: aspartic acid

Cys: cysteine

DAP: diammonium phosphate

Gaba: γ -aminobutyric acid

Gln: glutamine

Glu: glutamic acid

Gly: glycine

His: histidine

HoPro: hydroxyproline

Ile: isoleucine

Leu: leucine

Lys: lysine

Met: methionine

N: nitrogen

NO_3^- : nitrate

NO_2^- : nitrite

NH_4^+ : ammonium

Orn: ornithine

Phe: phenylalanine

Pro: proline

Ser: serine

Thr: threonine

Trp: tryptophan

Tyr: tyrosine

Val: valine

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1. Introduction

The use of nitrogen fertilizers has increased global food production and nitrogen losses, resulting in degradation of water quality and climate pollution (Grizzetti, Pretato, Lassaletta, Billen, & Garnier, 2013; Khalsa et al., 2020). Agriculture is responsible for a large share of surface-water pollution and is responsible almost exclusively for groundwater pollution by nitrogen (FAO, 2013). Nitrogen excess in soils can leach into groundwater or move via surface runoff into waterways (FAO, 2017; Wang et al., 2019). A better understanding of nitrogen application rates and crop and environmental response is needed to optimize management of agroecosystems (Salazar et al., 2019; Khalsa et al., 2020).

Nitrogen assimilation is the process in which inorganic nitrogen acquired by the grapevine is incorporated into the organic carbon compounds necessary for growth and development (Keller, 2020). Nitrogen is an essential macronutrient for plant growth since this element has the highest demand, which often limits plant growth. However, its metabolism is complex and varies according to the species (Kliewer, 1967; Mansour, 2000; Rentsch, Schmidt, & Tegeder, 2007). Plants depend almost entirely on the dissolved forms of organic nitrogen in their soil environment for supplying the needs of this element (Pate, 1973). Organic nitrogen is originated from microbial decomposition and it is present as amino acids in soils, while inorganic nitrogen is present in different available forms such as nitrate (NO_3^-) and ammonium (NH_4^+) (Mansour, 2000). The first step of NO_3^- assimilation is its reduction by the nitrate reductase enzyme to nitrite and subsequently by nitrite reductase to NH_4^+ (Mansour, 2000; Keller, 2020). However, these compounds are toxic, but NH_4^+ is converted into glutamine and glutamate, and subsequently, in others amino acids (Bell & Henschke, 2005; Keller, 2020).

Pro and Arg, are usually the most abundant amino acids synthesized by *Vitis vinifera* grapevines varieties (Bell & Henschke, 2005). Arg is one of the most important nitrogen sources by yeast due to its easy assimilation, while Pro is the least preferred amino acid for *Saccharomyces* yeast (Mauricio & Ortega, 1997; Butzke, 1998; Cramer, Vlassides, & Block, 2002; Gobert et al., 2017). At low nitrogen content in musts, stuck and sluggish fermentations may occur at the wine cellar, leading to wine spoilage (Bisson & Butzke, 2000; Childs, Bohlscheid, & Edwards, 2015; Gutiérrez-Gamboa, Liu, & Pszczółkowski, 2020a). Diammonium phosphate (DAP) addition to the fermented musts is a widespread practice performed into the wine cellar that allow to improve fermentation rate and decrease fermentation duration (Sablayrolles, 2009; Butzke & Park, 2011). However, a production of considerable amounts of hydrogen sulfide (H_2S) in wines is provoked by the addition of high levels of DAP into the musts, giving sometimes to the wine undesirable rotten egg and sewage aromas (Ugliano, Kolouchova, & Henschke, 2010; Gutiérrez-Gamboa et al., 2020a). Typical recommendations for yeast assimilable nitrogen (YAN) content in musts are in order to 150-200 mg N/L since concentrations as low as 70 – 140 mg N/L are necessary to avoid any detectable residual nitrogen, whereas concentrations close to 267 mg N/L are recommended to avoid residual sugar at the end of fermentation (Bell & Henschke, 2005; Waterhouse, Sacks, Jeffery, 2016).

Throughout alcoholic fermentation, volatile fermentative compounds including higher alcohols, medium and long chain volatile acids, acetate and ethyl esters, aldehydes, among other families of chemical volatile compounds containing in wines are synthesized by yeast (Gutiérrez-Gamboa, Garde-Cerdán, Rubio-Bretón, & Pérez-Álvarez, 2020b; Seguinot et al., 2020). Higher alcohols can be synthesized either from intermediates of sugar metabolism, through anabolic reactions, or from branched-chain amino acids, through a multi-step catabolic reaction, the Ehrlich

pathway (Bell & Henschke, 2005; Molina, Swiegers, Varela, Pretorius, & Agosin, 2007; Swiegers & Pretorius, 2007). Some amino acids are precursor of some higher alcohols and esters, which may be responsible for the fruity character of the wines or contribute to diminish the fruit and oak aroma in wines (Cameleyre, Lytra, Tempere, & Barbe, 2015; de la Fuente-Blanco, Sáenz-Navajas, & Ferreira, 2016; de la Fuente-Blanco, Sáenz-Navajas, & Ferreira, 2017).

Ethyl carbamate is a genotoxic and carcinogenic compound that originates from alcoholic beverages, including wines, that is synthesized from urea and ethanol (Weber & Sharypov, 2009; Jiao, Dong & Chen, 2014). Ethyl carbamate has been classified as a group 2A carcinogen, “probably carcinogenic to humans”, by the World Health Organization’s International Agency for Research on Cancer (IARC) in 2007 (Weber & Sharypov, 2009). Biogenic amines are formed by lactic acid bacteria from precursor amino acids, mainly by the microbial decarboxylation (Costantini, Vaudaco, Pulcini, Carafa & García-Moruno, 2019). The presence of these compounds plays a key role in oenology since excessive amounts of them in wines may lead to health problems (Cilliers & van Wyk, 1985; Guo, Yang, Peng, & Han, 2015). The synthesis of these undesirable compounds in wines is associated with a high nitrogen concentration from the grapevines and the high nitrogen rates added in the winemaking procedures at wine cellar (Bell & Heschke, 2005).

Nitrogen composition of the musts and by consequence of wines depends fundamentally of the grapevine variety, edaphoclimatic conditions of the vineyard, viticultural practices, berry ripening and nitrogen additions along winemaking procedures (Gutiérrez-Gamboa et al., 2020a). Therefore, this overview mainly concentrates on the effects of edaphoclimatic conditions and agronomic practices on the synthesis of grape amino acids and illustrates the caused current problems due to the negative effects of climate change in scientific knowledge so that future

investigations can focus on them. Nitrogen compounds, which are produced during winemaking are not considered in this review although some researches were reported to be, otherwise, relevant.

2. Nitrogen absorption by grapevines

2.1. Nitrate absorption

Nitrate (NO_3^-) transport begins with its absorption from the soil solution by epidermal, cortical and endodermal root cells (Barberon & Geldner, 2014), although it can also occur in the leaves (Wermelinger, Baumgärtner, & Gutierrez, 1991), which is an important aspect for foliar nitrogen fertilization. NO_3^- absorption has two transport systems: i) the high affinity nitrate transport system (HATS), which allows ion absorption when the external concentration is low (less than 1 mM), and ii) the low affinity nitrate transport system (LATS) that is activated when the external concentration of NO_3^- is greater than 1 mM (Crawford & Glass, 1998). In grapevines, the genes that code for HATS-type transporters correspond to the NRT2 family, while the genes that code for LATS-type transporters belong to the NRT1 family (Tomasi, Monte, Varanini, Cesco, & Pinton, 2015). Grapevine genome contains 44 NRT1 members (Wittgenstein et al., 2014) and 4 NRT2 members (Pii, Alessandrini, Guardini, Zamboni, & Varanini, 2013; Cochetel et al., 2017). HATS in grapevines respond more slowly than herbaceous species such as corn (*Zea mays* L.) or arabidopsis (*Arabidopsis thaliana*), but faster than other woody species such as cherry (*Prunus avium* L.) (Pii et al., 2013). VvNRT2.4A gene shows greater fluctuation in the level of transcripts, suggesting that this could be the main gene responsible for the HATS response to NO_3^- in grapevines (Pii et al., 2013). Genotype is usually an important factor in the absorption of NO_3^- , since some grapevine varieties present a higher absorption rate in the high affinity transport system (Tomasi et al., 2015). Rootstock selection favored the response of low- and high-affinity transport

systems to external nitrate in grapevines and was also dependent on the characteristics of the scion (Tomasi et al., 2015).

After absorption, NO_3^- is reduced to nitrite (NO_2^-) in the cytoplasm by the nitrate reductase (NR) enzyme. NO_2^- is reduced to ammonia (NH_4^+) in the plastid by the nitrite reductase enzyme (ammonium manages to enter directly in this step) for its subsequent assimilation, which is carried out by the enzyme glutamine synthetase (GS) (Coleman, Cánovas, Man, Kirby, & Mansfield, 2012; Castro-Rodríguez et al., 2015). In addition, nitrogen assimilation processes can also be transcriptionally regulated under nitrogen starvation (Ruffel et al., 2008; Krapp et al., 2011).

2.2. Ammonium absorption

Ammonium (NH_4^+) is an important source of soil nitrogen (N) for plants and it is transported radially through the root tissue (Keller, 2020). Nitrogen assimilation requires the reduction of nitrate (NO_3^-) to NH_4^+ , followed by NH_4^+ assimilation into amino acids (Masclaux-Daubresse et al., 2010). NH_4^+ is generated by reduction of NO_3^- , deamination of organic compounds during protein turnover, lignin biosynthesis, photorespiration or amino acid recycling (Masclaux-Daubresse et al., 2010). NH_4^+ is also absorbed by the roots from the soil, and since it requires less energy than NO_3^- for its assimilation, it is the preferential form of absorption when plants are subject to nitrogen deficiency (Bloom, Sukrapanna, & Warner, 1992). However, high concentrations of NH_4^+ can be toxic causing a reduction in growth and competition for other cations, which is reason why the absorption of NH_4^+ is strictly regulated (Marschner, 1995; Britto & Kronzucker, 2001; Kronzucker, Britto, Davenport, & Tester, 2001). In this way, NH_4^+ can be toxic to plants even at 1 mg/kg on a dry weight basis in plant tissues (Britto & Kronzucker, 2001).

However, plant species have different tolerance to ammonium accumulation (Britto & Kronzucker, 2001). The exposition to 30 mM $\text{NH}_4^+ \text{NO}_3^-$, lead to a severe senescence of the grapevine cuttings, or more specifically symptoms resembling ammonium toxicity (Parish, 1996).

As well as NO_3^- , NH_4^+ also presents a high and low affinity transport system given by proteins of the AMT/Rh/Mep family that intercede the transport of NH_4^+ through membranes (Ludewig, Neuhäuser, & Dynowski, 2007). The high affinity transport system is mediated by the AMT1 family transporters (von Wirén, Gazzarrini, Gojon, & Frommer, 2000; Yuan, Loqué, Ye, Frommer, & von Wirén, 2007), while the low affinity transport system is mediated by the AMT2 family (Guether et al., 2009). Although there is little information about AMT transporters in grapevines, AMT3.1 and AMT3.3 members have been found to be down-regulated in grapevine roots when plants are subjected to high dosages of nitrate (Cochetel et al., 2017). Despite the expression these genes mainly occurs in roots, the expression of AMT in leaves can be essential since photorespiration generates a large amount of NH_4^+ , which suggests that the expression of AMT genes may be important to guarantee the recycling of NH_4^+ during photorespiration (Li, Cong, Lin, & Chang, 2015). Upon absorption in the root cells, NH_4^+ is assimilated into amino acids or amides to make it available to the plant through the concerted action of the enzymes glutamine synthetase (GS) and glutamine oxoglutarate aminotransferase (GOGAT) to supply the specific nitrogen needs of different plant organs (Cánovas, Avila, Canton, Canas, & de la Torre, 2007; Masclaux-Daubresse et al., 2010).

3. Biosynthesis of nitrogen compounds

Nitrogen compounds in grapes include ammonium and nitrogen organic compounds, such as amino acids, biogenic amines, peptides, nucleic acids and proteins (Cosme, Gonçalves, Ines,

Jordão, & Vilela, 2016). As the grapes ripen, organic nitrogen accumulates progressively (Figure 1), while the ammonia content slightly decreases (Cosme et al., 2016). The synthesis of amino acids, peptides and proteins occurs during the last six or eight weeks of grape ripening (Cosme et al., 2016). Glutamine is the main nitrogen compound transport in grapevines (Keller, 2020). Thus, aminotransferase enzymes convert grape glutamine into the other amino acids (Figure 2), of which, arginine and proline together represent between 60 and 80% of the free amino acids present in ripe grapes (Keller, 2020; Gutiérrez-Gamboa, Garde-Cerdán, Gonzalo-Diago, Moreno-Simunovic, & Martínez-Gil, 2017a). However, there may be marked differences in the composition of amino acids between grape varieties (Bouzas-Cid, Trigo-Córdoba, Orriols, Falqué, & Mirás-Avalos, 2018a, Bouzas-Cid, Falqué, Orriols, & Mirás-Avalos, 2018b; Gutiérrez-Gamboa, Garde-Cerdán, Rubio-Bretón, & Pérez-Álvarez, 2020c). In this sense, most of the accumulation of proline in grapes arises at the end of ripening, about four weeks after the veraison (Stines et al., 2000). On the contrary, the accumulation of arginine begins before the veraison and continues until maturity, excluding the proline accumulator grapevine varieties (Stines et al., 2000; Bell & Henschke, 2005). Proline is synthesized in plant tissues in order to protect cells from excessive osmotic stress (Haider et al., 2017; Canoura, Kelly, & Ojeda, 2018). Thus, the accumulation of proline during ripening could be related to the osmotic pressure caused by the accumulation of hexose sugars (Gomes, Oliva, Mielke, Almeida, & Aquino, 2010; Chun, Paramasivan, & Chandrasekaran, 2018). The accumulation of proline could also contribute to the increase in the pH of the must because its production from glutamate may involve the release of hydroxide (Smith & Raven, 1979). In addition to proline, certain proteins such as chitinases and taumatins also accumulate after the veraison and continue to grow during grape ripening. This accumulation probably occurs in response to osmotic stress derived from the increase in sugar concentration, occupying an enlarging

fraction of the total berries' proteins (Murfhey, Spayd, & Powers, 1989; Salzman, Tikhonova, Bordelon, Hasegawa, & Bressan, 1998; Giribaldi, Perugini, Sauvage, & Schubert, 2007; Monteiro, Piçarra-Pereira, Loureiro, Teixeira, & Ferreira, 2007; Negri et al., 2008; Keller, 2020).

4. Edaphoclimatic conditions

4.1. Climate conditions

Climatic conditions of the vineyard can affect both (i) the process of nitrogen mineralization in the soil and (ii) the synthesis of amino acids in grapes (Huang & Ough, 1989; Gutiérrez-Gamboa et al., 2018a). In this sense, the grapevines that grow in cool sites based on different bioclimatic indices such as average mean temperature of the warmest month ($< 20.7^{\circ}\text{C}$) and cold night index ($< 12^{\circ}\text{C}$), can prolong their maturation time by promoting the synthesis of amino acids in grapes (Gutiérrez-Gamboa et al., 2018a). It has been shown that the synthesis of several amino acids in grapes such as Asp, Arg, Gaba, Glu, Ile, Leu, Met, Le, Phe, Trp, Tyr and Val are favored by the decrease of the minimum temperatures during the month prior to harvest (Gutiérrez-Gamboa et al., 2018a). Additionally, according to different bioclimatic indices, the Carignan vineyards located in warm climates produced grapes with higher content of Pro than Arg compared to the vineyard placed in cool sites (Gutiérrez-Gamboa et al., 2018a).

4.2. Soil properties

Soil physical, chemical and biological properties affect the content of N in it (Udom & Omovbude, 2019). Soils have different retention properties depending on their texture and organic matter, in this way, sandy soils have less retention than clay soils since they have less silt and clay, resulting in a lower cation exchange capacity (Witheetrirong, Tripathi, Tipdecho, & Parkpian,

2011). Soils with important amounts of silt, clay, and organic matter can retain more NO_3^- than the soils without much levels of silt and clay (Witheetrirong et al., 2011). Soil texture also affects water permeability or percolation rate of a soil and in sandy soils, nitrate (NO_3^-) leaches into groundwater faster (Wang et al., 2019). Organic matter content is the most determining factor in the total N content available in the soil (Wang, Wang, Cao, Bai, & Qin, 2016). Microbes use organic matter containing in soils as substrate in the process of N mineralization, which is a fundamental soil process that plays a major role in determining the supply of soil inorganic N for plants (Osterholz et al., 2017).

Generally, most of the vineyards that produce high quality wines receive little or no nitrogen fertilization (van Leeuwen, 2010; Gutiérrez-Gamboa et al., 2018a). The absorption of nitrogen by the grapevine depends largely on the amount of nitrogen that the soil supplies to them, through the mineralization of organic matter (Keller, 2020). In this sense, the accessibility of nitrogen for rainfed grapevines is determined, among other factors, by the presence of sufficient water in the soil, which accumulates mainly during winter rains and/or early spring (Gutiérrez-Gamboa et al., 2018a). Nitrate moves with other salts in the soil solution, so its concentration may vary dramatically depending on the distance and depth of the emitter from the nearest dropper (Gutiérrez-Gamboa et al., 2018a). In this way, irrigation viticulture has an advantage over rainfed viticulture because nitrogen can be available for the grapevines when necessary, without being conditioned by rainfall (Gutiérrez-Gamboa et al., 2018a). Thus, a limitation in the absorption of nitrogen reduces the vigor of the grapevine, the weight and yield of the berries and increases the concentration of sugar, anthocyanins and tannins in the berries (Choné, van Leeuwen, Chéry, & Ribéreau-Gayon, 2001; Hilbert et al., 2003; Gutiérrez-Gamboa et al., 2018b). These effects are beneficial for the quality potential of the grape for the production of wines.

5. Agricultural practices

5.1. Grapevine variety

Arginine and proline generally constitute the highest proportion of the total concentration of amino acids present in grapes (Table 1) and, their concentration, depends primarily on the variety (Stines et al., 2000; Lasa et al., 2012; Garde-Cerdán et al., 2014; Hannam et al., 2016; Pérez-Álvarez, Garde-Cerdán, García-Escudero, & Martínez-Vidaurre, 2017; Garde-Cerdán, Gutiérrez-Gamboa, Fernández-Novales, Pérez-Álvarez, & Diago, 2018a; Gutiérrez-Gamboa et al., 2018b; Gutiérrez-Gamboa & Moreno-Simunovic, 2019; Gutiérrez-Gamboa, Pérez-Álvarez, Rubio-Bretón, & Garde-Cerdán, 2019a; Palčić et al., 2020). In this sense, the proline to arginine ratio reflects the proportion of non-assimilable nitrogen (proline) to assimilable (arginine) by yeasts, providing an index of the nutritional value of the must of each particular variety (Bell & Henschke, 2005). Thus, grapevine varieties can be classified into categories according to their ability to accumulate arginine or proline. In this respect, two varieties may have the same total concentration of amino acids, but the one that accumulates a greater proportion of proline in relation to arginine will have lower easily assimilable nitrogen (Bell & Henschke, 2005). Among the grapevine varieties, Chardonnay, Cabernet Franc, Cabernet Sauvignon, Carignan, Merlot, Riesling, Semillon, Syrah, Tempranillo and Zinfandel have a high proline to arginine ratio, while others, such as Airén, Chenin Blanc, Grenache, Gewürztraminer, Mencía, Montepulciano, Muscat Gordo, Pinot Noir and Sauvignon Blanc have a low proline to arginine ratio (Huang & Ough, 1989, 1991; Stines et al., 2000; Bell & Henschke, 2005; Garde-Cerdán et al., 2014, 2017a, 2018a; Bouzas-Cid et al., 2015, 2018a; Sánchez-Gómez et al., 2016; Gutiérrez-Gamboa et al., 2017a, 2018; Gutiérrez-Gamboa, Portu, Santamaría, López, & Garde-Cerdán 2017b). However, this

relationship is influenced by the level of maturity of the grape, the viticultural practices carried out in the vineyard and the edaphoclimatic conditions of each site (Huang & Ough, 1989, 1991; Bell & Henschke, 2005; Garde-Cerdán et al., 2014; 2018a) (Figure 3). In the early stages of ripening of the grape, the Garnacha variety can be classified as an accumulative variety of arginine, however, towards later stages of maturity, this variety tends to store a greater amount of proline than arginine (Kliewer, 1970; Bell & Henschke, 2005). In addition, it has been documented that certain varieties such as Sauvignon Blanc and Tempranillo can behave as arginine or proline accumulators depending on the edaphoclimatic conditions of each site or vintage (Huang & Ough, 1989, 1991; Garde-Cerdán et al., 2014; Garde-Cerdán, Gutiérrez-Gamboa, López, Rubio-Bretón, & Pérez-Álvarez, 2018b).

5.2. Rootstock influence

The adoption of rootstocks in viticulture can also affect the content of nitrogen compounds in grapes (Huang & Ough, 1989; Bell & Henschke, 2005; Gutiérrez-Gamboa et al., 2018a). Rootstocks differ in the capacity to capture water and nutrients, and therefore can modify some variables in the grapevines such as vigor, productivity and chemical composition of the berries (Serra, Strever, Myburgh, & Deloire 2014; Ibacache, Verdugo-Vásquez, & Zurita-Silva, 2020). Frequently, more vigorous rootstocks result in higher N levels on the grafted cultivar in different species (Albornoz et al., 2020; Ibacache et al., 2020). In this sense, it has been shown that the musts of Chardonnay grapevines grafted on vigorous rootstocks such as St. George, Harmony, SO4 and 5A had higher total amino acid contents, while the musts of the grapevines of this variety grafted on less vigorous rootstocks such as 110 R showed a lower total amino acid content (Huang & Ough, 1989). In another report, it has been shown that the rootstock did not affect the amino acid

content of the musts of the Cabernet Sauvignon grapevines, probably because the soil already contained high levels of nitrogen, so this element was readily available to be absorbed by the radical system (Huang & Ough, 1989). On the other hand, grapes harvested from Carignan grapevines grafted on roots of the Listán Prieto grapevine variety tended to have a lower concentration of amino acids than grapes harvested from ungrafted Carignan grapevines (Gutiérrez-Gamboa et al., 2018a). The vegetative groundcover and rootstock selection are important practices for grapevine production in humid climate vineyards. Noiret (interspecific *Vitis* sp., hybrid) grapevines grafted onto medium vigor rootstocks showed higher reductions in vegetative (40 % v/s 19 %) and reproductive (22 % v/s 0 %) behavior compared to grapevines grafted onto low vigor rootstocks under the presence of groundcover (Fleishman, Eissenstat, & Centinari, 2019). These authors suggested that in a wet vintage, young grapevines grafted onto low vigor rootstocks may be more tolerant of groundcover competition than those grafted onto medium vigor rootstocks.

5.3. Foliar fertilization

Foliar nitrogen applications to the grapevines have become an important strategy to improve the content of amino acids and ammonium in musts compared to the fertilization of nitrogen applied to the soil due to its rapid and efficient assimilation by the leaves (Lacroux et al., 2008; Lasa et al., 2012; Garde-Cerdán et al., 2014; Hannam et al., 2016; Gutiérrez-Gamboa et al., 2017a). In this sense, urea has been one of the most used nitrogen sources that have been commercially applied in viticulture due to its easy solubility and low cost (Lasa et al., 2012). It has also been shown that the application of urea supplemented with sulfur and certain commercial products to Sauvignon Blanc, Cabernet Sauvignon and Petit Manseng grapevines has allowed the improvement of the synthesis of amino acids in grapes, increasing its content in the producing

wines (Lacroux et al., 2008; Gutiérrez-Gamboa et al., 2017a; Kelly et al., 2017). Foliar nitrogen applications can improve grapevine nitrogen status and enhance aroma expression in Sauvignon blanc wines without the negative impact on vigour and Botrytis susceptibility (Lacroux et al., 2008). Urea applied foliarly to grapevines increased the concentration of amino acids in musts of different grapevine varieties, such as Merlot, Sauvignon Blanc, Pinot Gris and Tempranillo (Lasa et al., 2012; Garde-Cerdán et al., 2014; Hannam et al., 2016). However, the foliar application of urea to Cabernet Sauvignon grapevines barely affected the amino acid content of the grape (Gutiérrez-Gamboa et al., 2017a). The differences in the effectiveness of the application of urea to the grapevines in the amino acid content of the grape depend on the needs of nitrogen by the grapevines at the time of the foliar nitrogen application (Gutiérrez-Gamboa, Romanazzi, Garde-Cerdán, & Pérez-Álvarez, 2019b). Therefore, the foliar application of urea to the grapevines makes it possible to increase the amino acid content in grapes of grapevines with high nitrogen requirements, and not in grapevines with low nitrogen requirements.

5.4. Cover crops

Cover crops use in viticulture can have different objectives (from a nutritional point of view) depending on the time of establishment, species and management (García et al. 2018). In vineyards with low vigor, the use of cover crops during the post-harvest with their incorporation (mowing, decomposition and mineralization) in winter can increase the availability of nitrogen for the grapevine, by increasing the content of organic matter in the soil. On the other hand, cover crops utilization in vigorous vineyards can reduce the excessive vegetative growth of the grapevines, improving the quality of the grapes (Pérez-Álvarez, Pérez-Sotés, García-Escudero, & Peregrina, 2013). The study of cover crops in viticulture is booming due to its positive effects on

the physical, chemical and biological characteristics of the soils compared to conventional tillage (Ghimire, Norton, Stahl, & Norton, 2014). The use of barley as a cover crop can lead to a decrease in the availability of nitrate for grapevines throughout the vegetative season compared to conventional tillage (Pérez-Álvarez et al., 2013). The grapevines managed under conventional tillage system produced grapes with a higher concentration of several amino acids, such as Asp, Glu, Gly, Lys, Met, Pro, Ser, Thr, Trp and Tyr than the grapevines cultivated with cover crops (Pérez- Álvarez, Garde-Cerdán, Santamaría, García-Escudero, & Peregrina, 2015).

Cover cropping with nitrogen (N) fixing forage legumes is increasingly being used in vineyard production systems in different wine growing regions (Ovalle, del Pozo, Peoples & Lavín, 2010). Cover crops are often cultivated in between vineyard rows to reduce soil erosion, increase soil fertility, and improve soil structure (Cheng & Baumgartner, 2004). The forage legumes species differ in their capacity to symbiotically fix atmospheric N₂ (Ovalle et al., 2007). Roots of both grapevines and cover crops form mutualistic symbioses with arbuscular mycorrhizal (AM) fungi, which are interconnected by AM hyphae leading to direct transfer of N via mycorrhizal hyphae connections between the roots of legumes and their neighboring grapevines (Cheng & Baumgartner, 2004; Ovalle et al., 2007). In this way, grape dry matter production was increased significantly by 48–61 % and the amount of N accumulated in grape bunches was enhanced by 74–105 % after 2 years of legume cover crop (Ovalle et al., 2010). In addition, it was reported that leguminous cover crops have the potential to supply nitrogen to grapevines during the times of peak nitrogen demand (Figure 4) in early spring and fruit set (Patrick, Smith, Keck & Berry, 2004). However, different authors suggested the overall contribution of cover crop nitrogen to total grape-leaf nitrogen content was small compared to cover crop nitrogen uptake by younger grapevines or annual crops (Patrick et al., 2004; Ovalle et al., 2010).

5.5. Diseases management

Currently, the management of diseases in viticulture is mostly carried out through the use of synthetic pesticides (Pertot et al., 2017). It has been demonstrated that foliar application of fungicides to Monastrell grapevines decreases the concentration of ammonium and several amino acids in grapes (Oliva, Garde-Cerdán, Martínez-Gil, Salinas, & Barba, 2011). Thus, the application of synthetic fungicides such as famoxadone, fenhexamide and quinoxifen decreased the concentration in grapes of various amino acids, such as Ala, Arg, Asp, Glu, His, Ile, Lys, Phe, Pro, Ser y Thr (Oliva et al., 2011).

Elicitation in viticulture is a novel strategy that allows to improve grapevine defense responses against vineyard diseases (Delaunois et al., 2014). Methyl jasmonate (MeJ) is one of the most researched elicitors in viticulture (Vezzulli, Civardi, Ferrari, & Bavaresco, 2007; D'Onofrio, Matarese, & Cuzzola, 2018). However, the majority of the researches carried out has focused on its effect on the phenolic compounds in grapes (Gutiérrez-Gamboa et al., 2019b). This is probably due to the exogenous application of elicitors, mainly jasmonates, inducing the activation of enzymes involved in the synthesis of phenolic compounds (Delaunois et al., 2013; Gutiérrez-Gamboa et al., 2019b). Paladines-Quezada, Moreno-Olivares, Fernández-Fernández, Bautista-Ortín and Gil-Muñoz (2019) showed that the application of MeJ and benzothiadiazole (BTH) to Monastrell, Merlot and Cabernet Sauvignon caused significant changes in various components of the grape skin cell walls, such as phenolic compounds, proteins and structural sugars. These authors reported that these elicitor treatments increased the proteins and phenols in the cell wall of the skins of the Monastrell and Cabernet Sauvignon berries, while the structural integrity of the Merlot variety berry skin tended to decrease.

The researches that have been carried out studying the effect of MeJ on the amino acid content of grapes do not show conclusive results (Gutiérrez-Gamboa et al., 2019b). Garde-Cerdán, Portu, López and Santamaría (2016) showed that the total amino acid content was not affected by the application of MeJ, however, the concentration of certain amino acids such as His, Ser, Trp, Phe, Tyr, Asn, Met and Lys increased as a result of the application of MeJ on grapevines of the Tempranillo variety. Gutiérrez-Gamboa et al. (2017b) observed that the application of MeJ on Tempranillo grapevines barely affected the concentration of amino acids in grapes.

Biotic elicitors such as chitosan and yeast extract applied to Tempranillo grapevines decreased the concentration of several amino acids in the musts, negatively affecting its total amino acid content (Gutiérrez-Gamboa et al., 2017b). In addition, Garde-Cerdán et al. (2017a) reported that biotic elicitors applied to Montepulciano grapevines decreased the content of several of the amino acids studied in grapes. These results suggest that induction of resistance through the foliar application of biotic elicitors may result in physiological costs for the grapevines associated with a degradation or compartmentalization of the amino acids synthesized in grapes in other reserve organs through the grapevine.

5.6. Irrigation

Continuous changes of N occur in soils through mineralization and immobilization processes, which usually results in a net release of mineral N available to plants (Raath, & Saayman, 2017; Cheng et al., 2019). N mineralization is a microbiological process in which NH_4^{+} -N is converted into NO_3^{-} -N by two groups of gram-negative chemoautotrophic bacteria (Ghosh & Kashyap, 2003). This process is affected by soil properties, and environmental factors and human factors (Raiesi, 2006). Fertilization and irrigation are the dominant human activities that can

change the mineralization process (Shang, Ren, Yang, Li, & Ma, 2015). The available N pools ($\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$) are produced through N-mineralization, which thus governs the supply rate of N to plants (Ghosh & Kashyap, 2003). In this way, irrigation may increase ammonia N pools, nitrification potential and N mineralization (White, Balachandra, Edis, & Chen, 2007; Brackin, Buckley, Pirie, & Visser, 2019).

Regarding the effects of the grapevine water deficit irrigation in the amino acid content in the grapes, it has been shown that the grapevines accumulate a high amount of Pro in the grapes in response to water stress (Canoura et al., 2018). In this sense, it has been shown that water stress causes the expression of genes that regulate the biosynthesis of Pro in grapevines (Haider et al., 2017). On the other hand, Bouzas-Cid et al. (2018b) observed that irrigation did not affect the total concentration of amino acids in Treixadura musts, but it affected the content of certain amino acids such as Asn, Met, Pro, Ser, Trp and Tyr. However, these authors suggested that the differences obtained in the content of amino acids were more influenced by the climatic conditions of the vintage than by the irrigation applied to the grapevines.

The application of fertilizers through irrigation water is a common strategy in the horticultural management to supply the water and nutrient requirements by plants (Conradie & Myburgh, 2000; Vilanova, Fandiño, Frutos-Puerto, & Cancela, 2018). Since the correct amount of fertilizer can be applied at the right time and rapidly in the grapevine root zone, nutritional efficiency may be improved compared to conventional broadcasting (Conradie & Myburgh, 2000). The fertigation applied in a Niagara vineyard using 46:0:0 (NPK) from bud break to flowering, followed by 20:20:20 (NPK) from fruit set to veraison improved N and P levels in the leave petioles compared to grapevines fertigated with only 46:0:0 (NPK) either from bud break (Reynolds et al., 2005). These results suggest that the formulation of the nutrient can be of a wide importance since

both treatments received 80 kg N/ha (Howell & Conradie, 2013). Fertigation applied to Syrah grapevines using elicitors enriched with amino acids improved gas exchange balance and N assimilation, while increased yeast assimilable nitrogen and also enhanced the aromatic profile of the grapes (Roda et al., 2019). Thus, a soil-plant-atmosphere assessment throughout the whole season allows accurate irrigation/fertigation practices minimizing fertilizer leaching losses, therefore reducing the negative environmental impacts of irrigation (Fuentes et al., 2008).

5.7. Leaf removal

Severity and timing of leaf removal directly affect light exposure and berry temperature, impacting sink to source relationships (Song, Wang, Xie, & Zhang, 2018). Leaf removal improve light penetration and air circulation around the clusters, which could improve temperature conditions of berries and effectiveness of biostimulants and fungicides formulations, decreasing grapevine diseases incidence (Ivanišević, Kalajdžić, Drenjančević, Puškaš, & Korać, 2020). Basal leaf removal applied 72 days after flowering of Sauvignon Blanc grapevines at 50 % of severity level promoted the synthesis of Ala, Arg, Asp, Gaba, Pro and Ser in grapes, and showed the highest content of total amino acids, whereas the leaf removal applied 72 days after flowering at 100% of severity level showed the lowest content of amino acids in grapes (Yue et al., 2019). Additionally, these authors reported that the content of Cys, Gly, Lys, Met and Tyr in grapes were not affected by the timing or severity of basal defoliation in grapevines (Yue et al., 2019). Among these amino acids, the content of Lys and Cys is similar along the berry ripening, whereas the content of Gly decreases as berry maturation increases (Garde-Cerdán et al., 2018a). Therefore, these amino acids could be involved in the synthesis of other secondary metabolic in grapes. Despite the important

differences shown by the authors, these results consider the data obtained in only one vintage, so they could change by the climatic conditions of the season.

Rossouw et al. (2017) evaluated the response of root and leaf primary metabolism after defoliation treatments applied to potted Syrah grapevines during ripening. These authors showed that partial and full defoliation increased the contribution by root carbohydrate sources to berry sugar accumulation through the starch remobilization. Rossouw et al. (2017) also reported that full defoliation induced the activation of the shikimate pathway, allowing the accumulation of aromatic amino acid in roots. Phenylalanine ammonia-lyase is an important enzyme in plant tissues that eliminates ammonia from phenylalanine to form *trans*-cinnamic acid, a precursor of phenylpropanoid secondary products, such as lignins, flavanoids, and coumarins (Hyun, Yun, Kim & Kim, 2011). Berry content of aromatic amino acids increase along the ripening with a minimum concentration around 10-15 °Brix, and a maximum content close to 20-25 °Brix (Garde-Cerdán et al., 2018a). Genes related to the synthesis of aromatic amino acids are expressed at post-veraison stages in grapevine berries (Berdeja et al., 2015; Rossouw et al., 2017). Therefore, roots may contribute as an aromatic amino acid source to berries after the exclusion of the leaf source (Rossouw et al., 2017).

6. Agronomic considerations

Nitrogen fertilization program must consider the growth cycle of the grapevine, the nutritional contributions of the system (soil, irrigation water) and the needs of the grapevine, based on the expected yield and nutritional status (reserves) (Figure 4). Regarding the growth cycle, nitrogen fertilizers must be applied to soil when the roots are in active growth, which occurs after flowering and in post-harvest (Figure 4). Soil nitrogen applications in winter are not recommended

since the roots are not fully functioning, and soil temperatures are still low, which reduces the rate of solubilization and absorption by grapevines. Nitrate uptake and respiration declined considerably quickly as increasing root age, which corresponded with a strong decline in root nitrogen concentration, suggesting the translocation of nitrogen out of the roots (Volder, Smart, Bloom, & Eissenstat, 2005).

During the post-harvest period, nitrogen is remobilized from the senescing leaves to be stored in perennial organs such as trunks, cordons or canes (Ferrara, Malerba, Matarrese, Mondelli, & Mazzeo, 2018). As is shown in Figure 4, nitrogen is remobilized from these perennial structures to developing organs in spring before root nitrogen uptake becomes the main process to sustain tree nitrogen needs (Masclaux-Daubresse et al., 2010; Ferrara et al., 2018). Nitrogen absorption is significant in warm climates (relative to Huglin's Heliothermal index), where there is a long post-harvest season, so it is important to assure an important quantity of nitrogen to the grapevine for its translocation to perennial organs (Figure 4). However, this recommendation is not valid for very long cycle grapevine varieties or in vineyards cultivated in cold climates (relative to Huglin's Heliothermal index). Nitrogen coming either from senescing leaves or roots contribute to nitrogen storage pools and to efficient nitrogen management and the movement of nitrogen into grape berries and shoots during the season (Masclaux-Daubresse et al., 2010).

Root nitrogen uptake and internal nitrogen cycling are the two major sources of nitrogen that contribute to vegetative and reproductive development (Carranca, Brunetto, & Tagliavini, 2018). The optimization of external and internal nitrogen sources is a key factor for a sustainable fruit production, since nitrogen use efficiency by trees is generally low and losses of nitrogen by fertilizers may occur with negative economic and environmental consequences (Carranca et al., 2018). Therefore, different potential strategies, considering plant genotype, soil management and

nitrogen fertilization practices may be carried out to enhance the nitrogen use efficiency of fertilizers by grapevines.

Although soil is usually the main source of nutrients for grapevines, foliar fertilization may rapidly and efficiently satisfy the nutritional needs during the critical growth stages of development (Lasa et al., 2012; Hannam et al., 2016). Plants can absorb nitrogen as urea, when it is applied to foliage and even by roots (Gooding & Davies, 1992). However, in soils, urea gets hydrolyzed quickly and is not available for absorption (Prasad & Shivay, 2016). It has been reported that it is more effective to correct nitrogen deficiencies in the vineyard with foliar urea applications during veraison than during flowering (Verdenal et al., 2015). Additionally, the effectiveness of foliar nitrogen applications to grapevines depends mainly of the nitrogen needs of the grapevines (Gutiérrez-Gamboa et al., 2019b). As is shown in Figure 4, around veraison a large part of the nitrogen uptake by the grapevines is translocated to grapes (Conradie, 1986). Due to these reasons, foliar nitrogen applications to grapevines at veraison stage could be an important alternative to correct nitrogen deficiencies in the vineyard (Figure 4).

For a correct program, analyzes must be carried out throughout the season (Figure 4) that allow quantifying and diagnosing the nutritional status of the grapevine with respect to nitrogen. It is recommended to carry out soil analysis every 3-4 years, at the end of the season (post-harvest) or before the start of the new season (winter), quantifying the total nitrogen in the soil (organic and inorganic). Additionally, the amount of nitrogen provided by the irrigation water must be determined, for which a water analysis must be made during the season (Figure 4). A high level of nitrate (NO_3^-) in water reduces further usage of water for irrigation and drinking since levels of NO_3^- close to 10 mg/l in water causes serious health threat to infants and adults (Alslaibi, Abunada, Abu Amr, & Abustan, 2018). The two previous analyzes will reveal the nitrogen supply by the

soil-water system. Regarding the nutritional status of the grapevine, it is important to quantify during the winter the amount of arginine in the roots (reserve analysis, Figure 4), and during the season to carry out foliar analyzes (petiole at flowering and blade at veraison) that allow adjustments to be made to the nitrogen fertilization program.

7. Current approach

Negative effects of climate change and the indiscriminate use of water in very demanding crops and in other industrial sectors such as mining have resulted in a considerable decrease in water for agriculture, as well as in its quality, giving place to drought events, largely in the Mediterranean agroclimatic zones (Oertel, Meza, & Gironás, 2020; Peña-Guerrero, Nauditt, Muñoz-Robles, Ribbe, & Meza, 2020). From a winemaking approach, a classical postulate in viticulture declares that small grapes will produce high quality wines. However, it has been reported that wines made from grapes with a greater proportion of skins contain higher amounts of phenolic compounds, terpenes, volatile acids, acetate esters and polysaccharides (Gil Cortiella, Úbeda, Del Barrio-Galán, & Peña-Neira, 2020). Although the drought and the decrease in irrigation water in viticulture could lead to smaller berries, its effect on the quality of the grapes and wine is debatable. Gutiérrez-Gamboa et al. (2020c) showed that grapevines growing with irrigation water limitations produced musts with low content of ammonium and amino acids and with high concentration of proline compared to the grapevines growing without water constraints. As was previously stated, proline is not metabolized by yeasts during alcoholic fermentation and stuck and sluggish fermentations can occur when the content of yeast assimilable nitrogen is less than 140 mg N/L (Bell & Henschke, 2005). This problem can occur more often due to the current climatic conditions and water availability, which would lead to significant economic losses in the winery,

especially if proline accumulator grapevine varieties are used for winemaking, such as Cabernet Sauvignon, which is the most-planted grapevine variety (*Vitis vinifera*), covering close to 341,000 ha, and distributed mainly in China, France, Chile, the United States, Australia, Spain, Argentina, Italy and South Africa (OIV, 2017). Therefore, an accurately prevention and diagnostic of stuck and sluggish fermentations must be carried out at the wine cellar since the resumption of fermentations is a long and expensive process.

Certain interesting researches have been carried out with the goal to avoid the negative effects of the current global warming in viticulture, exposing the necessity to grapevine adaption to climate change (Webb et al., 2010; Gu, Jacobs, McCarthy, & Gohil, 2012; Duchêne, 2016; Martínez de Toda, García, & Balda, 2019; Ollat et al., 2019; Pou, Balda, Albacete, & Martínez de Toda, 2019; van Leeuwen, Pieri, Gowdy, Ollat, & Roby, 2019; Delrot et al., 2020). These consider viticultural practices performed in established vineyards such as the reduction of vineyard density in dry lands and the forcing grapevine regrowth with the aim to reduce irrigation water and to delay ripening, respectively (Martínez de Toda et al., 2019; van Leeuwen et al., 2019). Additionally to these viticultural techniques, other solutions may be carried out in this field, depending on an economic-technical feasibility by the viticulturists with the aim to avoid the negative effects of warm temperatures in the vineyard and thus, the degradation of amino acids in grapes, such as i) applying irrigation if water is available, ii) planting late ripening varieties into warm climate zones, iii) using late ripening clones and more vigorous rootstocks, according to their local vegetative and productive behavior, iv) diversifying the production of autochthonous varieties, v) adaptation of training systems and vi) late pruning if it is possible. However, these viticultural practices may not be enough to avoid the negative effects of the current warm climate and other considerations in

relation to vineyards not established should be taking into account such as moving vineyards to colder climatic and soil depth/fertility conditions.

8. Conclusions

The addition of nitrogen compounds is a frequent practice in wineries that allows to improve the fermentation rate as well as to reduce its duration. However, its incorporation may lead to the synthesis of sulfur compounds that could affect the organoleptic qualities of the wine by generating undesired aromas. Furthermore, compounds derived from amino acid decarboxylation may appear, such as biogenic amines, whose concentration must be kept low due to their influence on human health. Nonetheless, as winemakers knows well, other factors such as the strain of lactic acid bacteria added and especially the wine pH play also a very important role on the production of these undesirable compounds in wines.

The different distribution of the amino acid fraction is a particular feature of each variety. Moreover, said amino acid concentration is conditioned by antecedents such as climatic conditions of the vineyard and by consequence, the phenological state of the grapes. The grapevines can absorb nitrate throughout both the root and leaf tissues, thus facilitating their fertilization. The high and low affinity transporters allow the entry of nitrogenous compounds in grapevine tissues, in the form of NO_3^- and/or NH_4^+ . The transporters responsible for carrying out this distribution are the HATS and LATS proteins for nitrate and AMT1 and AMT2 in the case of ammonium. Reasonably, the expression of these proteins is not only reduced to the root tissues but also appears in the leaves where they have a key role in photorespiration.

A further point to bear in mind in the assimilation of nitrogen is the influence of the physical, chemical and biological properties of the soil. Thus, the availability of nitrogen may be

affected by the composition of the soil or the availability of irrigation. By manipulating these variables, the quality of the wine grape could be increased. These parameters may also vary along diverse grape varieties. Therefore, vine varieties could be classified into two separate categories based on their ability to assimilate higher levels of arginine (Airen, Chenin Blanc, Grenache, Gewürztraminer) or proline (Chardonnay, Cabernet Franc, Cabernet Sauvignon, Carignan), hence obtaining a correlation between the ratio of assimilable and non-assimilable nitrogen, respectively. This classification would be a bare approximation since, as said before, there are several conditioning variables in the accumulation of these compounds in plants (maturity of the grape, viticultural practices carried out in the vineyard and the edaphoclimatic situation of the field). Within agricultural practices, the effect of the rootstock on the absorption of nutrients through the roots should also be assessed. Foliar application of fertilizers has been one of the most common practices in increasing the amino acid content in crops with high nitrogen requirements. This technique has proven to be an effective solution to nitrogen deficiencies when carried out during veraison. Another possible approach would be the use of vegetal covers that control the availability of this element in the soil depending on the objective pursued, being able to prioritize increasing the vigor of the vineyard or reducing it in exchange for obtaining higher quality grapes. The possible side effect of the application of pesticides in the vineyard must also be considered, since the concentration of available ammonia and amino acids may vary, as well as the synthesis of compounds with phenological interest in the berries. The concentration of certain amino acids could also be altered by subjecting plants to water stress, which would result in an increase in proline levels, or by removing leaves after flowering, thus allowing enrichment of aromatic amino acids in berries.

Future research should therefore focus on mitigating the effects of climate change and carrying out responsible water use since drought will be one of the main determining factors of the quality of the wine grape and, therefore, that of the musts. Consequently, modifying current winemaking techniques will be a priority in pursuance of adapting crops to future climatic conditions, as well as introducing grape varieties that are better adapted to warm temperatures and water scarcity.

Conflicts of interest

The authors declare that they have no conflicts of interest when publishing this review.

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The authors declare that they have no conflicts of interest.

Journal Pre-proofs

Figure captions

Figure 1. Amino acid content (mg N/L) throughout the accumulation of soluble solids in grapes (°Brix) in an arginine accumulator grapevine variety. **Footnote:** Data obtained from those published by Garde-Cerdán et al. (2018a).

Figure 2. Overview of the biosynthesis of amino acids in plants. Alanine is derived from the glycolysis intermediate pyruvate in a single transamination step. Ribose-5-phosphate is produced in the cycle of the oxidative pentose phosphate. **Footnote:** Figure obtained from those published by Buchanan, Gruissem and Jones (2015).

Figure 3. Model of the relationship among the genetic makeup, environmental conditions and agronomical practices on grape composition at harvest. **Footnote:** The model indicates directions of direct and indirect effects.

Figure 4. Requirements and nitrogen dependence of the grapevines throughout its physiological maturation. **Footnote:** the black squares correspond to the physiological stages throughout grapevine ripening, the blue squares indicate technical considerations for the nitrogen application to the vineyard, the red squares correspond to the needs and consumption of N by grapevines throughout ripening, the orange squares indicate the different types of analysis that should be carried out during the growing season for a correct program of nitrogen fertilization.

Table 1. Range of concentration of amino acids in grape juices and wines.

Amino acid	Range of concentration in grape juice (mg/L)	Range of concentration in white wine (mg/L)	Range of concentration in red wine (mg/L)
Alanine	8.9 – 227	2.1 – 238	0.10 – 90.2
Arginine	3.6 – 2,322	3.55 – 1,075	0 – 153
Asparagine	1 – 171	0.66 – 86.7	1.86 – 75.8
Aspartic acid	0.8 – 138	3.9 – 74.8	0.28 – 80.9
Citrulline	0.1 – 83	0 – 32.6	2.23 – 26.5
Cysteine	0.2 – 18.5	0.13 – 6.73	0.94 – 8.39
γ -aminobutyric acid	20.8 – 189.9	1.46 – 444	1.33 – 61.44
Glutamine	9 – 4,499	0 – 16.6	0.58 – 19.9
Glutamic acid	1.3 – 454	4.9 – 140.2	5.69 – 112
Glycine	1 – 20	2.1 – 42	1.3 – 45.3
Histidine	1.6 – 197	1.02 – 79.4	0.06 – 75.2
Isoleucine	1 – 117	0 – 18	0.14 – 10.89
Leucine	1.1 – 160	1.4 – 44.5	0.2 – 16.22
Lysine	0.1 – 45	1.91 – 78.8	1.15 – 46.9
Methionine	0.04 – 33	0.22 – 37.3	0 – 33.2
Ornithine	0.1 – 27.2	0 – 55	0.43 – 67.2
Phenylalanine	1.9 – 138	0.92 – 52.5	0.4 – 29.71
Proline	2.0 – 2,912.7	24.9 – 1,391	17.86 – 4,415
Serine	10.0 – 330	1.14 – 48	0.18 – 31.9
Threonine	5.7 – 284	1.16 – 62.6	0.75 – 19.3
Tryptophan	0.2 – 57.9	0 – 9.84	0.54 – 12.29
Tyrosine	0.4 – 33	0.68 – 45.9	0.26 – 9.18
Valine	2.5 – 116	0 – 37.5	0.11 – 18.2

Data obtained from to the results published by Gutiérrez-Gamboa, Garde-Cerdán, Moreno-Simunovic and Pérez-Álvarez (2019c).

Table 2. Range of concentration of amino acids in grape juices by variety.

Amino acid (mg/L)	Cabernet Sauvignon	Merlot	Carignan	Grenache	Tempranillo	Monastrell	Graciano	Pinot Noir	Chardonnay	Sauvignon Blanc	Riesling
Ala	27.0-74.7	10.0-68.8	9.8-53.0	9.6-65.0	68.4-93.6	81.4-109.9	170.6-206.4	46.0	83.0-262.0	90.0	5.2-67.3
Arg	36.0-354.5	28.5-400.0	20.3-219.3	78.4-1063.6	318.1-705.2	350.1-472.8	587.0-665.3	93.0-332.7	53.0-603.0	147.0-447.2	18.5-164.1
Asp	18.3-155.7	11.0-22.0	2.1-33.0	6.0-29.2	19.5-86.5	6.6-8.8	10.7-11.9	16.0-52.3	25.4-40.1	29.0-49.5	7.1-52.7
Cys	5.8-10.8	NF	2.5-6.1	0.7-28.9	7.1-9.1	7.4-10.9	17.4-19.3	NF	NF	NF	NF
GABA	161.0-273.7	190	59.4-109.8	10.6-134.3	64.4-161.8	125.2-273.5	225.0-235.7	NF	44.9-68.1	NF	6.9-139.6
Gln	27.0-71.5	4.5-131.0	13.0-68.4	27.1-185.2	155.6-262.6	86.8-94.0	270.0-326.6	16.0-71.3	57.0-385.0	59.0-145.7	30.7-132.3
Glu	40.5-230.0	52.0-85.1	7.0-96.2	6.2-55.3	85.2-158.5	16.8-24.1	81.3-92.9	139.3	114.0-171.0	167.7	18.9-51.0
Gly	2.1-19.8	5.0-5.2	0.0-6.4	1.9-12.5	5.5-7.3	6.9-9.0	17.6-21.7	5.67	3.0-20.0	2.5	1.1-2.1
His	8.7-314.2	11.2-29.4	4.4-68.0	7.4-74.1	22.2-137.4	37.3-42.6	85.1-96.9	5.0-38.7	12.7-104.0	13.5	5.8-17.4
Ile	7.6-45.1	10.5-12.2	3.6-14.3	2.0-14.2	3.1-4.6	8.0-8.9	8.0-8.2	3.5	5.3-25.6	9.0- 40.6	1.0-39.3
Leu	9.8-102.3	15.0-18.9	3.9-16.6	0.1-28.1	8.0-12.0	20.1-21.4	18.5-19.2	4.2	5.0-16.7	10.5	1.7-52.3
Lys	2.0-4.3	0.9-14.95	0.9-2.3	1.1-14.9	2.2-13.7	4.1-5.1	5.1-5.9	1.2-15.4	1.9-9.7	3.2- 11.9	1.0-1.5
Met	1.0-75.5	1.2-10.6	0.1-14.3	0.3-13.5	6.0-25.2	2.2-2.5	9.0-10.3	1.4-12.8	2.8-14.8	2.9-9.3	2.1-9.3
Phe	5.61-60.6	6.5-19.3	1.0-7.0	1.5-33.1	7.5-23.4	8.4-17.6	9.3-9.6	4.3-24.4	9.3-28.3	19.0- 36.0	2.3-51.2
Pro	105.1-2178	738.0-1840.0	212.0-484.8	90.8-709.9	302.3-699.7	829.5-972.7	505.2-678.2	80.0-118.7	305.0-1096.0	308.0-351.7	2.5-260.4
Ser	17.0-42.8	15.6-46.5	10.0-35.0	9.8-33.1	45.0-60.1	39.2-52.9	97.2-108.6	17.0-60.0	53.0-233.0*	41.0-71.5	7.8-39.8
Thr	20.0-57.3	12.0-54.0	5.7-27.6	3.9-28.5	22.2-72.3	38.6-44.1	74.0-79.1	32.0-96.3	38.0-117.0	48.0- 69.0	7.4-53.6
Trp	6.2-15.5	NF	6.2-21.4	5.1-49.1	20.9-31.1	27.1-32.4	12.5-14.4	NF	NF	NF	4.5-19.3
Val	13.0-39.0	21.0-24.8	4.9-22.7	1.7-24.7	12.2-14.8	20.5-21.9	20.9-22.3	7.0	10.0-38.8	19.0	10.2-37.2

Data obtained from to the results published by Ough and Tabacman (1979). Huang and Ough (1989), Treeby, Holzapfel, Walker and Nicholas (1998), Hernández-Orte, Cacho and Ferreira (2002), Hernández-Orte, Ibarz, Cacho and Ferreira (2006), Friedel, Stoll, Patz, Will and Dietrich (2015), Garde-Cerdán, Gutiérrez-Gamboa, Portu, Fernández-Fernández and Gil-Muñoz (2017b), Gutiérrez-Gamboa, Portu, López, Santamaría, and Garde-Cerdán, (2018c) and Ju et al. (2018).

Figure 1.

Figure 2.

Figure 3.

Figure 4.

Highlights

- Current reports show a decrease in the amino acid content of grapes.
- Proline biosynthesis in grapes has been related to warm climate and water restriction
- Stuck and sluggish fermentations can occur when the YAN content is low
- We summarized the current research carried out to modify the N content of grapes
- Technical and scientific aspects are discussed for future research in this field