Chapter 4

Lactic Acid Bacteria Contribution to Wine Quality and Safety

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Abstract

Wine production is a complex biochemical process that brings into play different microorganisms. Among these, lactic acid bacteria (LAB) play a central role in the quality of the final wine. LAB are not only responsible for the malolactic fermentation that usually occurs after the alcoholic fermentation but also contribute for other important biochemical reactions such as esterase and glycosidase activities and citric acid and methionine metabolism. Nonetheless, LAB may also contribute negatively to wine quality by contributing to the production of volatile phenols, biogenic amines, and ethyl carbamate. This chapter aims to integrate the current knowledge about the role of LAB in wine flavor and quality.

Keywords: lactic acid bacteria, winemaking, wine flavor, wine quality, wine safety

1. Introduction

This review focuses on the current knowledge about the impact of lactic acid bacteria (LAB) in wine composition and flavor. In wine, LAB perform a second fermentation consisting of decarboxylating L-malic acid to L-lactic acid, designated by malolactic fermentation (MLF). This fermentation follows the alcoholic fermentation conducted by yeast (*Saccharomyces* spp.). MLF reduces wine acidity and provides microbiological stabilization by lowering nutrient content of wine.

Under favorable conditions, MLF occurs spontaneously after alcoholic fermentation by the growth of indigenous LAB population in wine. However, selected strains of LAB can be inoculated into wine to induce MLF. According to the types of wines produced, this biological deacidification may be considered beneficial or detrimental to wine quality. However, it

should be highlighted that some LAB species in particular homofermentative pediococci and heterofermentative lactobacilli are responsible for wine spoilage [1].

LAB metabolic activity that may have a very significant impact on wine flavor includes the metabolism of citric acid and amino acids, the hydrolysis of grape glycosides, and the synthesis and hydrolysis of esters. Yet, other reactions can lead to the production of biogenic amines and ethyl carbamate by some LAB strains with negative consequences to wine safety.

2. LAB distribution and their succession in musts, in wine, and during vinification

Although it is not possible to have a clear definition of lactic acid bacteria (LAB), this group of bacteria is mainly characterized by the production of lactic acid as a major catabolic end product from glucose [2]. The other main characteristics of LAB are gram-positive cocci or bacilli, non-sporing, generally nonmotile, catalase negative, aerotolerant, acid tolerant, chemoorganotrophic, and strictly fermentative organisms. In some conditions, such as media

Morphology	Fermentation type	Species
Bacilli	Facultative heterofermentative	*Lactobacillus casei*
		L. coryniformis
		L. curvatus
		L. homohoichii
		L. paracasei
		L. pentosus
		L. plantarum
		L. sakei
		L. zeae
		L. nagelli
		L. diolivorans
	Heterofermentative	*Lactobacillus brevis*
		L. buchneri
		L. collinoides
		L. fermentum
		L. fructivorans
		L. hilgardii
		L. kunkeei
		L. sanfrancisensis
		Lactobacillus spp.
		L. vacinostercus
	Homofermentative	*Lactobacillus delbrueckii*
		L. jensenii
		L. mali
		L. vini

Morphology	Fermentation type	Species
Cocci	Homofermentative	*Pediococcus acidilactici*
		P. damnosus
		P. dextrinicus
		P. inopinatus
		P. parvulus
		P. pentosaceus
		Pediococcus spp.
		Lactococcus lactis
		Lactococcus spp.
		Enterococcus spp.
	Heterofermentative	*Leuconostoc citrovorum*
		L. mesenteroides subsp. *dextranicum*
		L. mesenteroides subsp. *mesenteroides*
		Leuconostoc spp.
		Weissella confusa
		W. paramesenteroides
		Weissella spp.
		W. uvarum
		Oenococcus oeni

Table 1. Lactic acid bacteria (LAB) species grouped according to their morphology and fermentative pathway, isolated worldwide from grapes, musts, and wines (adapted from [11–16]).

containing hematin or related compounds, some strains may produce catalase or even cytochromes [3]. Though aerotolerant, they are a group of bacteria typical of non-aerobic habitats, very demanding from a nutritional point of view and tolerate very low pH values, with acidity tolerance being a variable trait among strains. LAB are present in very diverse environments (e.g., fermented foods and beverages, plants, fruits, soil, wastewater) and are also part of the microflora of the respiratory, intestinal, and genital tracts of man and animals [4, 5].

Lactic acid bacteria (LAB) are naturally part of the microbiota of grapes, musts, and wines. In musts and wines, the LAB species that may be present and isolated are (i) heterofermentative cocci belonging to *Leuconostoc* and *Oenococcus* genera and homofermentative cocci belonging to *Pediococcus* of Streptococcaceae family and (ii) homofermentative, facultative, and strict heterofermentative bacilli belonging to *Lactobacillus* genus of Lactobacillaceae family [6–8]. In wine grapes, from several Australian vineyards, Bae et al. [9] were not able to isolate *Oenoccoccus* strains, but they detected strains of *Enterococcus*, *Lactococcus*, and *Weissella*; LAB more frequently associated to other food matrices. Although *Oenococcus oeni* is the predominant species in the final stage of wine production, it has rarely been isolated from grapes in the vineyard [10]. Recently, in a large survey of LAB isolation in grapes and wines from a Spanish region (Priorat Catalonia), Franqués et al. [11] were able to isolate 53 strains of *Oenococcus oeni* in a total of 254 LAB isolates from grapes. In **Table 1**, a list of LAB species isolated from grapes, musts and wines that undergone spontaneous MLF or from wines with alterations of different regions of the world is shown.

3. LAB metabolism in wine

Either complexity or multiplicity of LAB metabolic activities in wine demonstrates that MLF is more than a simple decarboxylation of L-malic acid into L-lactic acid, and thus this very special and important fermentation may affect positively and/or negatively the quality of wine [17].

Besides the immediate effect of decrease in acidity by the transformation of a dicarboxylic acid (L-malic acid) into a monocarboxylic acid (L-lactic acid), MLF also improves sensorial characteristics and increases wine microbiological stability [18, 19]. Modifications in wine aroma induced by LAB are due to L-lactic acid, less aggressive to palate, and a huge number of other compounds such as diacetyl, acetoin, 2,3-butanediol, ethyl lactate and diethyl succinate esters, and some higher alcohols and aromatic aglycones that become free by the action of LAB β-glucosidases [20–23]. Although produced in lower concentrations, sulfur compounds, particularly 3-methylsulfanyl-propionic acid with chocolate and toasted odors, may contribute to aromatic complexity of wines [24]. Also the activity of taninoacil hydrolase enzyme, commonly termed tannase, reducing wine astringency and turbidity may increase the quality and result in a better and pleasant sensorial perception for consumers [25].

Although not well understood at that time, the knowledge of the negative role of LAB on wine quality comes from the first studies of Pasteur at the beginning of the twentieth century. Some wine defects due to microorganism development were accurately described and LAB were shown to be responsible for wine "diseases" such as "tourne," the degradation of tartaric acid; "bitterness," the degradation of glycerol; and "ropiness," the unacceptable increase in wine viscosity [26]. Although less frequent nowadays, due to better hygienic conditions in wineries and knowledge of microorganisms, these wine "diseases" together with others such as butter aroma due to excessive production of diacetyl, flocculent growth, mannitol taint, and the geranium odor, presented in **Table 2**, still may occur. Also, the formation of volatile phenols (4-ethylguaiacol and 4-ethylphenol) and mousy off-odor by acetamide production of tetrahydropyridines can be produced by some strains of LAB species responsible for malolactic fermentation (MLF). Other compounds, such as ethyl carbamate formed by the degradation of arginine and biogenic amines (histamine, tyramine, and putrescine) from the degradation of amino acids, contribute negatively to wine quality and may affect the consumer's health [18, 29, 30].

3.1. Production of volatile compounds by LAB

The main effect of malolactic fermentation is the decarboxylation of L-malic acid into L-lactic acid, catalyzed by the malolactic enzyme. However, lactic acid bacteria produce several volatile compounds that can significantly influence wine aroma. Acetic acid and acetoinic compounds (C4 compounds) are the major products of citric acid metabolism by LAB. Acetoinic compounds comprise diacetyl, acetoin, and 2,3-butanediol. The biosynthesis of these compounds depends on citric acid metabolism (**Figure 1**).

Deterioration	Compounds	Sensory descriptor	Responsible microorganisms	Aroma threshold
Amertume/bitterness formation of acrolein from the degradation of glycerol	Acrolein	Bitterness	*Lactobacillus cellobiosus* *L. hilgardii* *Leuconostoc* mesenteroides Pediococcus *parvulus*	
Butter aroma due to excessive diacetyl production	2,3-Butanedione (diacetyl)	Buttery, nutty, caramel	*Lactobacillus plantarum* *Oenococcus oeni* *Pediococcus* spp.	0, 1–2 mgl^{-1}
Flocculent growth			*Lactobacillus trichodes*	
"Mannitol taint" manitic fermentation reduction of fructose to mannitol	Mannitol	Viscous, sweet, irritating finish	*Lactobacillus brevis*	
Formation of volatile phenols (4-ethylguaiacol and 4-ethylphenol) by degradation of phenolic acids mainly ferulic acid and *p*-coumaric acid	4-Ethylguaiacol and 4-ethylphenol		*Lactobacillus* plantarum Lactobacillus spp. *Pediococcus* spp.	
Formation of glyoxal and methylglyoxal			*Oenococcus oeni*	
Ropiness production of extracellular polysaccharides that increase the viscosity of wine	β-D-glucan (exopolysaccharide)	Ropy, oily, thick viscous, slimy, texture	*Leuconostoc mesenteroides* *Pediococcus damnosus* *Pediococcus pentosaceus*	
"Geranium odor" reduction of sorbic acid to 2,4-hexadienol which esterifies with ethanol to give 2-ethoxyhexa-3,5-diene, responsible for geranium odor	2-Ethoxy-3,5-hexadiene	Crushed geranium leaves	*Oenococcus oeni, Lactobacillus, Pediococcus*	0.1 μgl^{-1},
Mousiness production of tetrahydropyridines	2-Acetyl-tetrahydropyridine (ACTPY), 2-ethyltetrahydropyridine (ETPY), 2-acetyl-1-pyrroline (ACPY)	Caged mouse	*Lactobacillus* brevis Lactobacillus *cellobiosus* *Lactobacillus hilgardii*	4–5 μgl^{-1}, 2–18 μgl^{-1}; 7–8 μgl^{-1}
Production of biogenic amines (histamine, tyramine, putrescine) by decarboxylation of amino acids	Histamine, tyramine, putrescine		*Lactobacillus brevis* *Lactobacillus hilgardii* *Oenococcus oeni* *Pediococcus damnosus*	
Production of ethyl carbamate precursors	Ethyl carbamate		*Lactobacillus brevis* *Lactobacillus buchneri* *Lactobacillus hilgardii* *Oenococcus oeni*	

Deterioration	Compounds	Sensory descriptor	Responsible microorganisms	Aroma threshold
"Lactic peak" lactic fermentation of sugars, production of D-lactic acid and excessive production of acetic acid involved in the fermentation	Acetic acid		*Lactobacillus brevis* *Lactobacillus kunkeei* *Lactobacillus nagelii* *Oenococcus oeni*	0.2 gl^{-1}
"Tourne disease" tartaric acid degradation	Acetic acid		*Lactobacillus brevis* *Lactobacillus plantarum*	

Table 2. Main spoilage activities in wines caused by LAB (adapted from [12, 27, 28]).

Diacetyl (2,3-butanedione), one of the most important flavor compounds produced by LAB, imparts a distinct buttery or butterscotch aroma to wine. Diacetyl is formed as an intermediate metabolite of the reductive decarboxylation of pyruvate to 2,3-butanediol, associated with citrate metabolism by LAB. The precursor of diacetyl in this pathway is α-acetolactate, which is also an intermediate in the biosynthesis of the amino acids valine and leucine in prototrophic LAB. Pyruvic acid results from the metabolism of sugars and citric acid. To be capable to utilize citrate, LAB must possess the genes encoding permeases for citrate transport and citrate lyase for citrate metabolism [31].

Yeasts are also able to synthesize diacetyl in the course of alcoholic fermentation. However, most of this diacetyl is reduced by yeasts to acetoin and 2,3-butanediol, and only low concentrations of diacetyl remain at the completion of fermentation. Diacetyl reduction is further encouraged by the presence of yeasts or LAB after the conclusion of malolactic fermentation [32].

Salo [33] determined a sensory odor threshold level of 0.0025 mg/L for diacetyl in 9.4% (w/w) ethanolic solution. Yet, Guth [34] calculated 0.1 mg/L for diacetyl odor threshold in water/ethanol (90 + 10, w/w). Moreover, Martineau et al. [35] showed that the diacetyl flavor threshold depends on the wine type. They found that the flavor detection threshold was 0.2 mg/L in a lightly aromatic Chardonnay wine, 0.9 mg/L in a low tannic aromatic Pinot noir wine, and 2.7 mg/L in a full-flavored, full-bodied Cabernet Sauvignon wine. These wines were made without oak contact.

Reports of diacetyl concentration in wine vary from 0.2 to 4.1 mg/L [36]. The final concentration of diacetyl in wine depends on the concentration of sulfur dioxide. Sulfur dioxide combines reversibly with diacetyl in wine, suppressing the buttery note of wine flavor [37].

3.1.1. LAB esterase activity

Wine esters are important contributors to wine aroma. They comprise ethyl esters of organic acids (e.g., ethyl lactate), fatty acids (e.g., ethyl hexanoate, ethyl octanoate, ethyl decanoate), and acetates of higher alcohols (e.g., ethyl acetate, isoamyl acetate). These compounds are not only produced by yeasts during alcoholic fermentation and LAB during MLF but can also be formed by slow chemical esterification between alcohol and acids during wine aging [38]. LAB of the genera *Oenococcus*, *Lactobacillus*, and *Pediococcus* show esterase activity being capable

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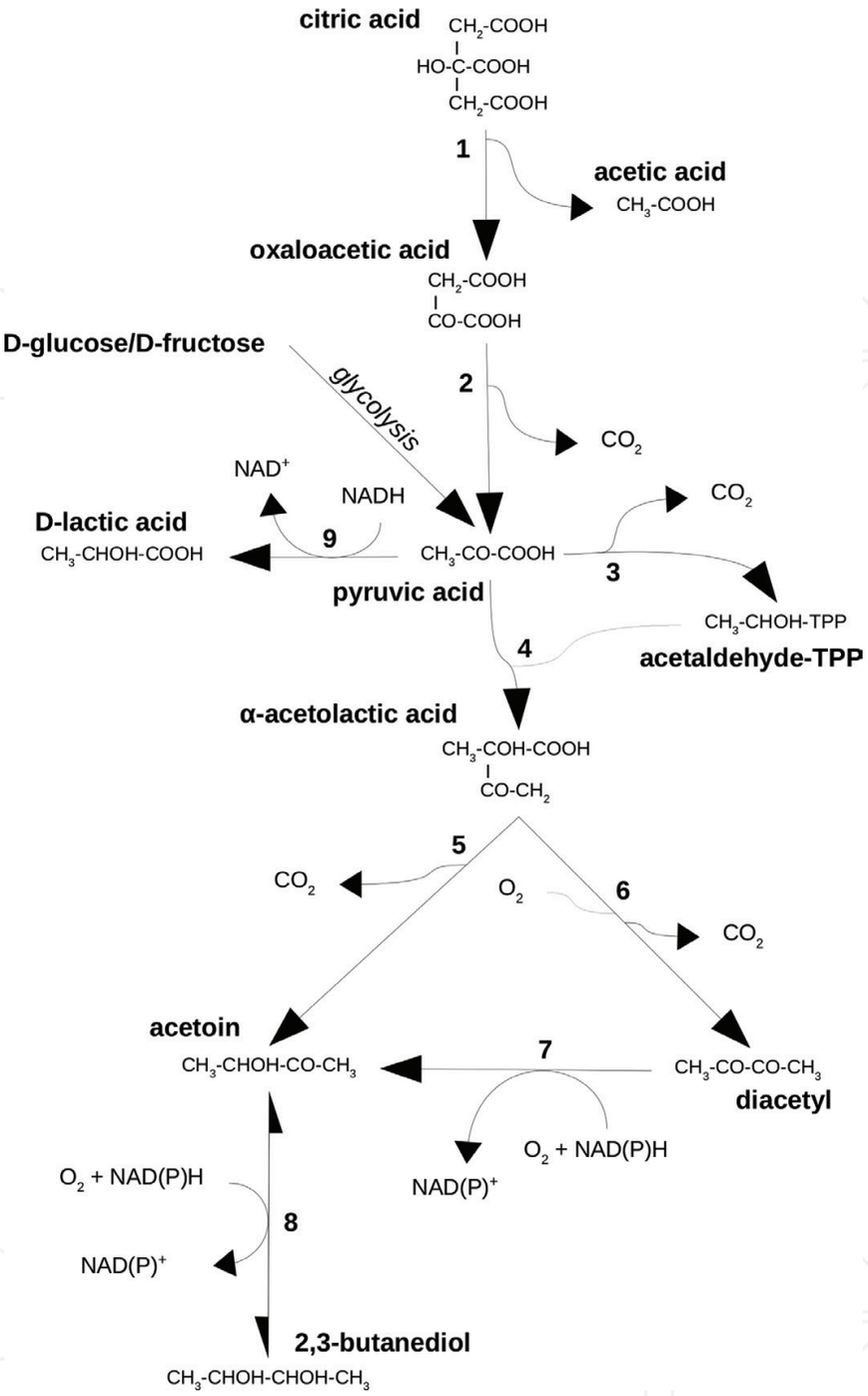

Figure 1. Citric acid metabolism by *O. oeni*. 1, citrate lyase; 2, oxaloacetate decarboxylase; 3, pyruvate decarboxylase; 4, α-acetolactate synthase; 5, α-acetolactate decarboxylase; 6, nonenzymatic oxidative decarboxylation of α-acetolactate; 7, diacetyl reductase; 8, acetoin reductase; 9, lactate dehydrogenase; and TPP, thiamine pyrophosphate.

of hydrolyzing ester substrates, with *O. oeni* showing the highest activity. But responses to pH, temperature, and ethanol concentration were strain-dependent [39]. LAB showed greater esterase activity toward short-chained esters (C2–C8) than long-chained esters (C10–C18). They present the highest esterase activity at a pH close to 6.0, though *Oenococcus oeni* retained appreciable activity even down to a pH of 3.0 and showed an increase in activity up to an

ethanol concentration of 16% v/v [40]. *O. oeni* esterases have the ability to hydrolyze and also to synthesize esters of short-chained fatty acids, the extent of each activity depending on strain and wine composition [23]. In a recent study, the concentrations of acetates and ethyl esters decreased after MLF, whereas levels of branched esters, such as ethyl 2-hydroxy-3-methylbutanoate and ethyl 2-hydroxy-4-methylpentanoate, increased. Moreover, LAB only synthesized the R forms of these two esters [41].

3.1.2. LAB glycosidase activity

Most volatile compounds that make the varietal aroma of wines are present in grapes in the form of glycoconjugated nonvolatile odorless molecules. These glycosides are β-D-glucose and diglycoside conjugates, with the latter consisting of glucose and a second sugar unit of α-L-arabinofuranose, α-L-rhamnopyranose, β-D-xylopyranose, or β-D-apiofuranose [42]. The aglycon moiety of these compounds belongs to different classes of volatiles, including monoterpenes and C_{13}-norisoprenoids. The glycoconjugates can be slowly transformed into free volatile aroma compounds through acidic hydrolysis during wine aging. Yet, a faster enzymatic hydrolysis of these glycosides by wine microorganisms can also occur. The hydrolysis of the disaccharide glucosides requires the action of two enzymes in sequence: first the disaccharide (1 → 6) linkage is cleaved by the appropriate *exo*-glycosidase releasing the outermost sugar molecule and the corresponding β-D-glucoside; subsequently, liberation of the odorous aglycon takes place after action of β-D-glucosidase. Yet, the hydrolysis of monoglucosides only requires the action of a β-D-glucosidase.

Yeasts, mainly non-*Saccharomyces* species found on grapes, possess glycosidase enzymes capable of liberating aroma compounds, particularly volatile terpenes, from their glycosilated precursors. However, in a study by Rosi et al. [43] only one of 153 strains of *Saccharomyces cerevisiae* showed β-glucosidase activity.

O. oeni has the ability to hydrolyze grape-glycoconjugated aroma precursors, but large differences in the extent and specificity of this hydrolysis activity were observed [44].

The β-glucosidase activity of different strains of *O. oeni* was affected by pH, sugar, and ethanol content in variable degree [45]. β-glucosidase activity was optimal at a pH of 5.5 and decreased as pH was reduced: within a pH range of 3.5–4.0, *O. oeni* showed just 12–43% of the maximum activity. The β-glucosidase activity of some strains was strongly inhibited by even a low sugar content (10 g/L), while others were not affected by higher sugar contents (30 g/L). Ethanol concentration up to 10% v/v led to an increased *O. oeni* β-glucosidase activity, and for most strains higher concentrations (up to 14% v/v) did not affect or only slightly decreased this activity [45].

Glycosidic activity is widespread in *O. oeni*, and some strains retain significant hydrolytic activity at pH values between 3.0 and 4.0, residual glucose and fructose contents (up to 20 g/L), and ethanol contents (up to 12%). *O. oeni* not only presented β-D-glucopyranosidase, α-D-glucopyranosidase, and β-D-xylopyranosidase activities but also minimal α-L-rhamnopyranosidase and α-L-arabinofuranosidase activities [46].

Lactobacillus plantarum isolated from Italian wines showed β-glucosidase activity and the ability to release odorant aglycones from odorless glycosidic aroma precursors [47]. *Lactobacillus* spp. and *Pediococcus* spp. possess varying degrees of β-D-glucopyranosidase and α-D-glucopyranosidase activities, influenced differently by ethanol and/or sugar concentration, temperature, and pH. But these activities are approximately one order of magnitude less than those seen for *O. oeni* [48].

3.1.3. Methionine metabolism

LAB isolated from wine (including strains of *O. oeni*, *L. brevis*, *L. hilgardii*, and *L. plantarum*) were able to metabolize methionine during MLF, forming the following volatile sulfur compounds: methanethiol, dimethyl disulfide, 3-(methylsulphanyl)propan-1-ol, and 3-(methylsulphanyl)propionic acid. However, in Merlot wines, only 3-(methylsulphanyl)propionic acid concentration increased significantly. This compound is characterized by chocolate and roasted odors and has a perception threshold in wine of 0.244 mg/L [24]. Moreover, *O. oeni* showed greater capacity to form 3-(methylsulphanyl)propan-1-ol and 3-(methylsulphanyl) propionic acid.

3.1.4. Production of off-flavors by LAB

When sorbic acid ((E,E)-2,4-hexadienoic acid) as potassium sorbate is added as an yeast inhibitor to wines containing residual sugar, LAB can degrade this compound in 2-ethoxyhexa-3,5-diene (2-ethoxy-3,5-hexadiene). 2-Ethoxyhexa-3,5-diene has an offensive crushed geranium leaves odor with a detection threshold of less than 1 ng/L [49, 50]. Sorbic acid inhibits yeast growth, but it does not inhibit LAB growth at the levels allowed in wines for this compound, demonstrating the need for maintaining adequate levels of sulfur dioxide (an effective inhibitor of LAB) in such wines. When used together, sorbate and sulfur dioxide can prevent secondary fermentations and control the growth of LAB in sweet table wines, with a pH of 3.3–3.9, at levels as low as 80 mg/L sorbate and 30 mg/L sulfur dioxide [51].

Various LAB isolated from wine showed the ability to synthesize 4-vinylphenol, by decarboxylation of *p*-coumaric acid. *Lactobacillus plantarum* produced significant quantities of ethylphenols, including 4-ethylphenol, still over 30 times less than the quantities produced by the yeast *Dekkera intermedia* and with no negative impact on wine aroma. *Lactobacillus brevis* and *Pediococcus pentosaceus* produced relatively large quantities of 4-vinylphenol, small quantities of 4-vinylguaiacol, and traces of ethylphenols. *Lactobacillus hilgardii*, *Pediococcus damnosus*, and *O. oenos 8417* produced only small amounts of vinylphenols (a few hundred μg/L) and little or no ethylphenols. *O. oenos* LALL produced very small quantities of volatile phenols [52].

3.2. Production of ethyl carbamate and biogenic amines by LAB

LAB use amino acids both as a strategy of survival particularly in nutrient limiting media and evidently in response to acid stress and as a source of energy. However, this may have implications for the quality and food safety of fermented products [53, 54].

The metabolism of amino acids such as arginine and histidine does not affect taste but creates a problem at consumer's health level by increasing the concentrations of biogenic amine and ethyl carbamate precursors in the wine, which are toxic compounds, thus contributing negatively to wine safety [55].

3.2.1. Degradation of arginine and formation of ethyl carbamate

Arginine is one of the amino acids present in higher concentrations in grape musts and wines. LAB may use this amino acid by arginine deaminase pathway. This pathway involves three enzymes: arginine deiminase (ADI, EC 3.5.3.6), ornithine transcarbamylase (OTC, EC 2.1.3.3), and carbamate kinase (CK; EC 2.7.2.2) [56]. The presence of the three enzymes of the ADI pathway appears to occur in most heterofermentative lactobacilli, leuconostocs, and oenococci, although they have already been detected in homofermentative species of LAB isolated from wine. However, the arginine pathway presence in all species seems to be a strain-dependent phenotype [57]. By this pathway, 1 mole of L-arginine is converted into 1 mole of ornithine and 1 mole of carbon dioxide and 2 moles of NH_3. The intermediate products of this pathway, citrulline and carbamoyl phosphate, are precursors of the ethyl carbamate, a potentially carcinogenic compound. This compound is formed from a spontaneous chemical reaction involving ethanol and precursors including urea, citrulline, carbamoyl phosphate, N-carbamyl, α- and β-amino acids, and allantoin [58]. According to Ough et al. and Kodama et al. [59, 60], the ethanolysis reaction of citrulline and urea for ethyl carbamate formation may occur at normal or elevated storage temperatures. Even though ethyl carbamate is produced in small quantities, its concentration in wine is subjected to international regulation and therefore must be carefully controlled. Maximum level in the European Union and Canada for table wines is 30 μg/L (100 μg/L for fortified wines in Canada), while in the USA the values are more restrictive, being 15 μg/L for table wines and 60 μg/L for dessert wines [55, 60, 61].

Some controversial information about the contribution of LAB for ethyl carbamate production is found in the scientific literature [8]. Tegmo-Larsson et al. [62] reported that malolactic fermentation did not affect the concentrations of ethyl carbamate in wine. However, more recent information suggests that some lactic acid bacteria, specifically *O. oeni* and *L. hilgardii*, can contribute to ethyl carbamate formation [61]. It must also be emphasized that in wine, prolonged contact of viable and viable but not cultivable LAB strains with residual lees from yeast should be considered as a significant risk factor for the increased formation of citrulline and therefore ethyl carbamate [63–65]. Therefore, it is not prudent to use *Oenococcus oeni* strains that excrete citrulline as starter cultures. Some of these authors further suggest that strains that possess only the first pathway enzyme (ADI +, OTC-) or strains that have ADI but low OTC activity should also be excluded in a starter selection process for MLF.

3.2.2. The formation of biogenic amines

Biogenic amines are low molecular weight organic bases, which can be formed and degraded during the normal metabolic activity of animals, plants, and microorganisms [29]. In the human body, these substances may play an important metabolic role, related to growth (polyamines) or to functions of the nervous and circulatory systems (histamine and tyramine). But when ingested in excess, they may be the cause of hypotension, hypertension, heart palpitations (vasoactive

amines), headaches (psychoactive amines), and various allergic reactions [30, 66]. Biogenic amines are fundamentally formed from the decarboxylation of the precursor amino acids by the action of substrate specific enzymes [6, 67, 68]. Thus, the amines histamine, tyramine, tryptamine, serotonin, 2-phenylethylamine, agmatine, and cadaverine are formed from the amino acids histidine, tyrosine, tryptophan, hydroxytryptophan, phenylalanine, arginine, and lysine, respectively [69–71]. Putrescine can be formed from ornithine or agmatine, and spermidine and spermine are formed from putrescine by the binding of aminopropyl groups catalyzed by spermidine synthase and spermine synthase [72]. During the fermentative processes of many raw materials (milk, meat, vegetables, barley, and grapes) to obtain food and beverages, such as cheese, sausages, fermented vegetables, beer, and wine, the formation of biogenic amines by LAB may occur. Many bacteria present decarboxylase activities, which favor their growth and survival in acidic environments, by the increase of pH, as previously mentioned. In wine, several amino acids can be decarboxylated, and consequently, biogenic amines can be found, predominating histamine, tyramine, putrescine, isopentylamine, cadaverine, and α-phenylethylamine [29, 30, 73–81]. However, their content in wine is much lower than that found in other foods [82], although ethanol may potentiate the toxic effect of histamine by inhibiting amino oxidases. Like ethyl carbamate, there are recommendations for the maximum histamine levels allowed in wine. EU countries and Canada recommend histamine levels not exceeding 10 mg/L, except Germany where the limit is 2 mg/L. Some biogenic amines, for example, putrescine and cadaverine, when in high concentrations, besides their toxicity, can confer sensory detectable unpleasant alterations, such as a fruit and rotten flesh odor, respectively. In wine, although biogenic amines may have other sources such as grapes, the metabolic activity of *Saccharomyces* and non-*Saccharomyces* yeasts and of acetic acid bacteria, they usually increase after MLF [30, 76, 79, 83–87]. Among LAB, the decarboxylase activity is strain-specific and is randomly distributed within the different species of *Lactobacillus*, *Pediococcus*, *Leuconostoc*, and *Oenococcus*.

So, the existing content of biogenic amines in wine will depend on the presence of precursor amino acids, LAB strains with decarboxylase activity, and environmental factors that affect the growth of these strains as well as some oenological practices [30, 88, 89]. In general, low pH and high concentrations of SO_2 and ethanol limit the growth of these strains and consequently the production of biogenic amines. On the other hand, factors favoring microbial growth such as high temperatures, availability of nutrients in must and wine (sugars, amino acids, organic acids), and inappropriate hygienic practices increase the probability of high amine concentrations [29]. As referred for the formation of ethyl carbamate, wines stored in prolonged contact with lees show higher levels of biogenic amines, attributed to viable but non cultivable LAB cells [30]. Generally, higher biogenic amine contents are found in red wines comparing to rosé, white, and fortified wines [86, 90, 91].

4. Conclusions

The contribution of LAB to wine flavor and composition has been described in this review. The difficulties in controlling and anticipating the effects of malolactic fermentation (MLF) on wine quality, given ample species and strain-dependent behavior, remark the importance of strain selection to explore the genomic diversity of LAB.

Selection of starter cultures for MLF should target good adaptation to the harsh wine conditions and potential for the production of flavor compounds, emphasizing in particular glycosidase and esterase activities. Also, the absence of arginine deaminase pathway and amino acid decarboxylases and ability to detoxify mycotoxins such as ochratoxin [92] and biogenic amine degradation [93, 94] should be considered as criteria for LAB strain selection for using as starter cultures.

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