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Review

Lactobacillus plantarum as a malolactic starter culture in winemaking: A new (old) player?

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ABSTRACT

Malolactic fermentation (MLF) is a process in winemaking responsible for the conversion of L-malic acid to L-lactic acid and CO_2, which reduces the total acidity, improves the biological stability, and modifies the aroma profile of wine. MLF takes place during or after alcoholic fermentation and is carried out by one or more species of lactic acid bacteria (LAB), which are either present in grapes and cellars or inoculated with malolactic starters during the winemaking process. Although the main bacterium among LAB used in commercial starter cultures for MLF has traditionally been *Oenococcus oeni*, in the last decade, *Lactobacillus plantarum* has also been reported as a malolactic starter, and many works have shown that this species can survive and even grow under harsh conditions of wine (i.e., high ethanol content and low pH values). Furthermore, it has been proved that some strains of *L. plantarum* are able to conduct MLF just as efficiently as *O. oeni*. In addition, *L. plantarum* exhibits a more diverse enzymatic profile than *O. oeni*, which could play an important role in the modification of the wine aroma profile. This enzymatic diversity allows obtaining several starter cultures composed of different *L. plantarum* biotypes, which could result in distinctive wines. In this context, this review focuses on showing the relevance of *L. plantarum* as a MLF starter culture in winemaking.
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1. Introduction

1.1. Malolactic fermentation (MLF) in wine production

Winemaking is a complex microbial process in which yeasts, mainly *Saccharomyces cerevisiae*, consume the sugars present in the grape to yield ethanol, a process known as alcoholic fermentation, which leads to the transformation of must into wine. During alcoholic fermentation, the natural development of lactic acid bacteria (LAB) correlates with their sensitivity to increasing ethanol concentrations and resistance to low pH values. After the completion of alcoholic fermentation, yeast activity diminishes and wine LAB are able to grow under the stimulation of the yeast lysis products, although wine conditions are quite restrictive and only a few species are able to survive [1]. The survival of LAB plays a significant role in winemaking, thus guiding a secondary biological process known as malolactic fermentation (MLF). This process converts L-malic acid to L-lactic acid and CO_2 and is carried out by one or more LAB species. MLF produces the deacidification of wine, with a concomitant increase in the pH, which is a particularly desirable effect in wines with high acidity. MLF also improves the microbial stability of wine, by the removal of L-malic acid as a possible carbon substrate, and leads to the modification of the wine aroma profile, which is linked to different enzymatic activities [2,3,4,5]. MLF could take place either spontaneously or by the addition of malolactic starter cultures [6,7,8,9]. The wine LAB that are naturally present in the must can perform MLF spontaneously after growing up to a critical population that is necessary to start and achieve malic acid degradation. Spontaneous MLF is the result of different LAB populations growing in the must and depends on both the grape sanitary conditions and the physicochemical characteristics of the wine [10]. Similarly, spontaneous MLF could have unpredictable results such as a considerable increase in the volatile acidity, the consumption of residual sugars, and the formation of undesirable metabolites including biogenic amines [11]. For these reasons, the use of starter cultures in winemaking is a common practice because of the technological advantages such as the reduction of time to complete MLF and the reduction of spoilage risks of wine [12]. In the last decades, the commercial availability of several starter cultures has allowed the widespread use of this practice among wineries.

Oenococcus oeni is probably or popularly the main species of LAB best adapted to overcome the harsh environmental wine conditions and is therefore present in most of the commercial MLF starter cultures. Nevertheless, *Lactobacillus plantarum* is also widely used in food biotechnology of fermented products and has begun to have relevance in the winemaking process. Like other *Lactobacillus*, *L. plantarum* is able to survive under harsh conditions of the wine [9,11,13,14] and, as mentioned below (see Section 6), some commercial starter cultures of *L. plantarum* strains have been released in the last decade.

1.2. L. plantarum and its presence in wine

The genus *Lactobacillus*, which belongs to the phylum Firmicutes, class Bacilli, order Lactobacillales, and family Lactobacillaceae [15], contains a large number of species and strains that exhibit important properties in an applied context, especially in fields of food and probiotics [16]. In particular, several *Lactobacillus* spp. have been identified in wine. These include *L. plantarum*, *Lactobacillus brevis*, *Lactobacillus rhamnosus*, *Lactobacillus buchneri*, *Lactobacillus collinoides*, *Lactobacillus paracasei*, *Lactobacillus fermentum*, *Lactobacillus casei*, *Lactobacillus guizhouensis*, *Lactobacillus kunkeei*, *Lactobacillus lactis*, *Lactobacillus delbrueckii*, *Lactobacillus sakei*, *Lactobacillus mali*, *Lactobacillus curvatus*, and *Lactobacillus lindneri*, among others [8,9, 17,18]. *Lactobacillus* spp. possess fermentative metabolisms and can be divided into three main metabolic groups according to their metabolite production from glucose/pentose: obligatory homofermentative, facultative heterofermentative, and obligatory heterofermentative [19,20]. *L. plantarum* is homofermentative for hexose and heterofermentative for pentose [20,21], and given that wine is usually composed of a range of monosaccharides and disaccharides, such as arabinose, glucose, fructose, and trehalose [22], the main sugars used by this species in the fermentation are glucose, fructose, and arabinose [20,21].

The classification of *Streptobacterium plantarum* [23], currently called *L. plantarum*, was originally applied to a series of bacteria widely distributed in fermenting plants and animal products isolated from butter, milk, cheese, fermenting potatoes, beets, cabbage, and dough [24] and also normally found in high-acid ciders [25] and wines [8,9,17,18]. Valdés La Hens et al. [9] showed that *L. plantarum* is present at all stages of MLF, together with *O. oeni*. Moreover, *L. plantarum* is widely used in industrial fermentation and processing of raw foods and "generally recognized as safe" (GRAS), and it has a qualified presumption of safety (QPS) status [15].

Regarding winemaking, *L. plantarum* has been repeatedly isolated from certain wines (Table 1), especially owing to its ability to tolerate low pH and high alcohol content [21,26]. In the beginning of winemaking, the identification of the LAB present in wine was based on phenotypic and biochemical tests; nevertheless, the development of molecular and genetic characterization tools, such as RAPD-PCR [9,17,27] or pulsed-field gel electrophoresis (PFGE) [28,29], has greatly increased the quality of identification, thereby allowing a better discrimination of *L. plantarum* from other LAB species that are genetically similar [7,18].

2. *L. plantarum* strains: Technological advantages as malolactic starter cultures

2.1. Tolerance to wine-like stress conditions

One of the main stress factors of wine is its low pH because it affects the metabolism of sugars and has a selective effect on LAB species. Although most studies agree that the response of *L. plantarum* to stress factors is variable and strain dependent, several studies have shown the ability of *L. plantarum* to efficiently grow at low pH [11,14, 30,31,32,33]. For example, G-Alegría et al. [33] described that several *L. plantarum* strains from Spanish Rioja red wines were able to successfully grow at pH 3.2 on MLO medium and reach population values similar to those of *O. oeni* strains. In addition, Berbegal et al. [34] showed that 62 *L. plantarum* strains isolated from Nero di Troia wines were able to grow in MRS medium at pH 3.5 under different conditions (combined with ethanol 8–12% (v/v), supplemented with glucose, fructose, and L-malic acid). In a recent work, Lucio et al. [35] studied the consequences of the interactions of different combinations of *L. plantarum* and *S. cerevisiae* during white grape must fermentation and demonstrated that managing wine acidity (which changes as a

Table 1
Isolation of *L. plantarum* from wine.

Isolation source	Identification technique	Country	Reference
Bitter wine and cider	Traditional microbiology, biochemical tests	Denmark	[115]
Wine and grape must	Traditional microbiology, biochemical tests	USA	[116]
Ciders	Traditional microbiology, biochemical tests	England	[25]
Wines	Traditional microbiology, biochemical tests	Australia	[117]
Red wine: Carignan and Cabernet Sauvignon	Traditional microbiology, biochemical tests	Israel	[118]
Cinsaut wine	Traditional microbiology, biochemical tests	South Africa	[119]
Cabernet Sauvignon wine and Cabernet grapes, Colombard and Ugni Blanc grapes	Traditional microbiology, biochemical tests	France	[120]
Wines: Merlot and Cabernet	Colony hybridization	France	[121]
Red wine	16S rDNA-ARDRA	Japan	[122]
Nero di Troia wine	recA and 16S rRNA gene sequencing	Italy	[123]
Wine must	API 50CH, PCR species specific for the recA gene	Italy	[124]
Red wines	16S rRNA gene sequencing	Italy	[94]
Red wine: Tempranillo	API 50 CHL system and species-specific PCR, Pulsed-Field Gel Electrophoresis (PFGE).	Spain	[33]
Brandy	16S rRNA gene sequencing	South Africa	[30]
Red wine: Cencibel	PFGE	Spain	[125]
Red wine: Cabernet Sauvignon grape berries	Sequence of segments of the 16S rDNA	Australia	[8]
Wines	Multilocus sequence typing, ribotyping, and RFLP of PCR 16S-23S rDNA (ISR)	Spain	[126]
Red wine: Merlot, Cabernet Sauvignon, Cabernet Franc, and Petit Verdot. White wine: Sémillon and Sauvignon Blanc	PCR-DGGE *rpo*B gene	France	[127]
Red wine: Tempranillo	Species-specific PCR	Spain	[11]
Grape musts and wines	Chromosomal DNA digestion and PFGE	Spain	[109]
Wine: Pinotage	Species-specific PCR	South Africa	[61]
Red wine: Mavroliatis and Sefka	DGGE-PCR *16S rRNA*	Greece	[128]
Mencia musts and wines	*16S rRNA* sequencing and *16S rDNA*-ARDRA	Spain	[129]
Red wine: Nero di Troia	*16S rRNA* and rec A gene sequencing	Italy	[83]
Palm wine	*16S rRNA* and gyrB genes	Burkina Faso	[130]
Tempranillo Wine	Species-specific PCR-*16S rRNA* sequencing	Spain	[28]
Wines: Montepulciano; Piedirosso, Pentro d'Isernia, AglianicoTaurasi, Tintilia	PCR-RFLP *16S rRNA* gene sequencing	Italy	[131]
Wines and Greek grapevine: Vilana, Mandilaria, and Kotsifali Grapes of the Agiorgitiko (red variety)	*16S rRNA* region (ARDRA)	Greece	[128]
Wines: Pinot noir and Merlot	RFLP-PCR of the *rpo*B gene and PCR-*16S rRNA* gene	Argentina	[9]
Wine: Nero di Troia	Genome sequencing (Illumina GAIIx platform)	Italy	[132]
Wine: Nero di Troia	PCR-*16S rRNA* gene	Italy	[34]
Rice wines	Metagenomics (MiSeq_System)	India	[133]
Must: Cabernet Sauvignon, Tempranillo, Syrah, Macabeo, Grenache, Carignan, Syrah, and Nebbiolo	Multiplex PCR	Mexico	[134]
Wines	PCR-DGGE and 16S rRNA gene sequencing	Italy	[41]
Cherry wines	16S rRNA sequencing and species-specific identification	China	[135]
Wines: Grenache and Carignan	16S rDNA-ARDRA	Spain	[136]
Pinot noir wine	16S rRNA region (ARDRA) and sequencing of the *16S rRNA* gene	Argentina	[27]

result of climatic change) is possible by co-inoculating *L. plantarum* and *S. cerevisiae*. However, they also found that the growth of LAB strains was severely limited after yeast inoculation [35]. Finally, Bravo-Ferrada et al. [17] found that eight *L. plantarum* strains from Patagonian wines were able to grow in MRS medium with a pH ranging from 3.5 to 3.8.

Another stress factor for the survival of LAB in wine is the presence of ethanol. Ethanol is the main metabolite produced by yeasts during alcoholic fermentation, which can reach a concentration higher than 12% v/v and, in certain climates, exceed 16% v/v [17,33,36]. Ethanol can interact with the polar head group of membrane lipids, thereby inducing membrane disorganization and affecting several biochemical processes such as proton motive force, all of which leads to the loss of intracellular compounds and, eventually, bacterial death [37,38].

For this reason, one of the first steps to select the best bacterial strain for winemaking is to determine its ability to grow in MRS medium containing ethanol [17,34,39]. Berbegal et al. [34] and Bravo-Ferrada et al. [17] showed that different strains isolated from the same wine but in the presence of different ethanol concentrations have a distinct growth rate. In the same way, a recent study conducted with 42 enological strains of *L. plantarum* isolated from red wines showed that the limit growth value for 10 selected strains was pH 3.5 and 8% ethanol [40]. Interestingly, these results are in agreement with those obtained by several authors [34,39] but in opposition with those of others [17,41], who reported that some strains of *L. plantarum* are able to grow not only in the presence of 13% ethanol but also at pH values ranging from 3.2 to 3.5. All these data confirm that ethanol resistance is a strain-dependent feature.

Finally, regarding other stress factors, Bravo-Ferrada et al. [17] also showed that several strains of *L. plantarum* are able to tolerate the presence of sulfite and lysozyme (two compounds usually applied as antimicrobial agents in the wine industry) in the concentration range used in winemaking.

2.2. Wine inoculation and acclimation

In addition to the natural ability of bacterial strains to tolerate the harsh wine conditions, some practices such as culture acclimation could improve their viability and enological properties. Several acclimation media have been described for malolactic LAB strains by supplementation of MRS medium with different ethanol concentrations (from 4 to 10% v/v), low pH (3 to 5) [40] or by the synergistic effect of ethanol and low pH [12,42,43]. For *L. plantarum* in particular, acclimation in ethanol 6% and 10% v/v, pH 4.5, in the presence of a high glucose and fructose concentration has been described as a favorable medium for the preadaptation of several strains of this species, with positive effects on the subsequent survival and L-malic acid consumption under wine conditions [27,44,45,46].

Bravo-Ferrada et al. [44] studied the effect of ethanol content during acclimation of Patagonian *L. plantarum* enological strains and found that direct inoculation of the *L. plantarum* strains tested in a wine-like medium (14% v/v ethanol, pH 3.5) induced a rapid disruption of the

membrane integrity and a decrease in the cell viability of more than six orders of magnitude in 24 h. However, when cells were previously acclimated in the presence of 6% and 10% v/v ethanol, their membrane showed lower damage after wine inoculation, and consequently, the strains showed an improvement in their viability and L-malic acid consumption after 15 d of incubation.

Bravo-Ferrada et al. [17] also found a higher decrease in the unsaturated/saturated (U/S) fatty acid ratio after acclimation, which was more drastic at higher ethanol concentrations. This decrease in the U/S ratio was concomitant with a decrease in the hydrocarbon chain lengths. Furthermore, the increase in L-malic acid consumption was correlated with the decrease in the U/S ratio and the decrease in the chain length. Nevertheless, the percentage of L-malic acid consumption was strain specific [13].

In this context, it is important to emphasize that the nutritional requirements of *L. plantarum* are lower than those of *O. oeni*. Further, the growth kinetics of *L. plantarum* is faster than that of *O. oeni*. Supporting these facts, Brizuela et al. [27] found that some *L. plantarum* strains isolated from Patagonian wines were able to conduct MLF with lower inoculum sizes than *O. oeni* strains and without the need for a previous acclimation treatment, which is technologically relevant for biomass production at low cost.

3. *L. plantarum* strains: Enological advantages as malolactic starter cultures

L. plantarum has a diverse array of enzymes that could have positive effects on the organoleptic properties of wine [21,47]. In addition to the malolactic enzyme itself, some of the most interesting enzymes that influence wine flavor include glycosidases, β-glucosidases, esterases, phenolic acid decarboxylases, and citrate lyases [48,49,50,51]. Enzymes are also involved in improving color in red wines and can solve problems associated with wine filtration such as tannase activities. Therefore, in enological *L. plantarum* strains, it is crucial to analyze their potential to influence wine composition and hence the processing, organoleptic properties, and the quality of the wine.

3.1. Malolactic activity

As already pointed out above, the main role of LAB in wine is MLF. From the metabolic point of view, MLF is only a decarboxylation process where the only apparent benefit to the cell would be the increase in the external pH. However, from an enological point of view, this deacidification leads to an improvement in wine quality, thus reducing the astringent taste of malic acid [52].

The gene coding for the malolactic enzyme seems to respond differently for *L. plantarum* [14] and *O. oeni* [53], depending on the stress conditions in the medium. Miller et al. [14] investigated the influence of pH and ethanol on the expression of the structural malolactic enzyme gene from *L. plantarum* in a synthetic wine medium and found that the expression of this gene was inducible by the presence of malic acid, with an increased expression in the middle of MLF. The expression of the malolactic enzyme was also increased at low pH values and decreased in the presence of ethanol.

Bravo-Ferrada et al. [17] evaluated the malolactic enzyme activity directly in a wine-like medium by inoculation of selected strains and analyzed the levels of malic acid consumed. They found that eight *L. plantarum* isolates were able to consume almost all the malic acid present after only 4 d of incubation. du Toit et al. [21] found similar results, where three of seven *L. plantarum* isolates were able to complete MLF (i.e., consume all the malic acid present) in the synthetic wine medium, in 44 d. Finally, Brizuela et al. [27,54] showed that some *L. plantarum* strains isolated from red wines exhibit a higher ability to consume malic acid than *O. oeni*, even without any preacclimation treatment, with the consequent economic advantages regarding the putative production of the starter cultures.

3.2. Glycosidases

Odorless nonvolatile glycosides are an important pool of compounds found in grapes and wine that can contribute to wine aroma [55,56]. Most commercial glycosidase preparations are crude extracts prepared from fungi rather than from bacteria. Glycosidase activities that can affect wine aroma have been detected in *Oenococcus*, *Lactobacillus*, and *Pediococcus* [48,49,57]. Researchers who investigated the effects of glycosidase activities of *L. plantarum* concluded that this activity is influenced by some environmental factors such as pH, temperature, and the presence of sugars and ethanol [48,57]. Bravo-Ferrada et al. [17] analyzed the glycosidase activity in eight selected Patagonian *L. plantarum* strains and found that all of them were positive for this activity, although with quantitative differences among the strains.

3.3. Esterases

Esters are a group of volatile compounds that can positively contribute to wine flavor, and changes in their concentration have the potential to influence wine quality [58]. The esterase activities in *L. plantarum* were described for the first time by Gobbetti et al. [59]. Later, studies performed by Mtshali et al. [60] on *Lactobacillus* strains isolated from South African grape and wine samples demonstrated that 60% of the strains tested possessed genes coding for esterases. In particular, all *L. plantarum* species studied were positive for some of the genes that codify this activity. Similar results were reported by Lerm et al. [61], who focused on the study of *L. plantarum* strains also isolated from a South African wine. At the end of the study, the authors selected a total of six *L. plantarum* strains, all of which were positive for a putative esterase gene.

The content of some ethyl esters analyzed in some studies showed significant difference among wines fermented by *L. plantarum* and *O. oeni* strains [32,62]. In addition, alcohol acyltransferase activity has also been recently identified in *L. plantarum* as a mechanism to increase ester concentrations and subsequently impact the fruity aromas of red wine [63].

3.4. Metabolism of amino acids and other compounds related to flavor

The catabolism of amino acids by wine LAB is expected to have a significant impact on wine quality, given that a range of compounds such as aldehydes, alcohols, and acids, in addition to amines, can be produced. Few studies have been conducted on the catabolism of amino acids by enological *L. plantarum*.

The main amino acid present in wine is arginine. The concentration of arginine in grape juice ranges from a few hundred mg L^{-1} to 2.4 g L^{-1}. Liu and Pilone [64] studied the catabolism of arginine by wine LAB and its practical significance in detail and found that arginine-degrading wine LAB catabolize arginine through the arginine deiminase pathway (ADI) [65]. One of the main concerns about arginine metabolism by wine LAB is the formation of ethyl carbamate precursors because ethyl carbamate, also referred to as urethane, is a known animal carcinogen found in fermented foods and beverages, including wine [64] (see Section 4.2).

Liu [50] also observed that *L. plantarum* also uses tyrosine and phenylalanine during MLF. Although the metabolic pathway of the two amino acids in this species of *Lactobacillus* is not known, it is possible that they are decarboxylated to form the corresponding amines, i.e., tyramine and phenylethylamine [50], given the prevalence of the two amines associated with *lactobacilli* in wine (see below).

Pozo-Bayón et al. [32] analyzed the changes in 21 amino acids during the MLF carried out by strains of *O. oeni* and *L. plantarum* in a Tempranillo red wine and observed that methionine, tryptophan, and threonine were degraded by *L. plantarum* but not by *O. oeni*. These results suggest a degree of metabolic diversity in both LAB groups because wines showed specific characteristics depending on

the LAB strain. This suggests that the metabolism of these compounds is strain dependent, thus showing high variability among species.

Regarding other compounds related to wine flavor, sulfur compounds show different sensory properties depending on their concentration and the sulfur atom molecular position; some of them contribute negatively to the wine quality, whereas some others have a positive effect on the aromatic properties of wines. The presence of these compounds in wines has two main origins: (1) nonenzymatic processes such as the chemical reactions of sulfur compounds during winemaking processes and storage and (2) enzymatic processes including the degradation of sulfur contained in amino acids during fermentation by yeasts and LAB. The two main amino acids involved in the production of volatile sulfur compounds with a negative impact on wine quality are methionine and cysteine. Grape juice is usually deficient in these two amino acids [66]. However, LAB and yeasts are able to synthesize methionine and cysteine from inorganic sulfate or sulfite sources [67], thus making them accessible for LAB metabolism [66,68].

Regarding wine aroma, diacetyl is the most important aroma compound from LAB, and its production and modulation during MLF have been well studied [69]. The buttery character in both red and white wines is due to the formation of diacetyl through the metabolism of citrate, a finding first reported by Guymon and Crowell [70]. The diacetyl content in wine can be influenced by several factors such as the strain of malolactic bacteria, inoculation rate, wine type, pH, aeration, and SO_2 addition [69,71]. Unfortunately, when this compound is present in wine at high concentrations, it can also be considered as an off-flavor. This suggests that wines that undergo MLF dominated by strains with or without low transcriptional levels of citrate lyase will have very low diacetyl concentrations, and therefore better organoleptic characteristics. In this context, it has been reported that some strains of *L. plantarum* and other *Lactobacillus* spp. do not possess citrate lyase complex genes [60,72]. Thus, future studies are needed to elucidate the concentrations of citrate metabolism products necessary to obtain a wine of high aromatic quality.

Other compounds related to wine aroma are phenolic acids, which are important aromatic acids and natural constituents of plant cell walls. Some volatile phenols, particularly vinyl and ethyl guaiacol (generated from ferulic acid), naturally contribute to the aroma in wines [73]. Depending on their concentration, these compounds can contribute to wine aroma either positively or negatively, owing to their low detection thresholds and their distinct flavor.

The production of volatile phenols in wine is usually associated with the spoilage caused by the yeast *Dekkera bruxellensis* [74]. By using PCR enzyme-specific primers for the *pad* (phenolic acid decarboxylase) gene, Mtshali et al. [60] screened 120 South African *Lactobacillus* strains (including *L. plantarum*) and found that more than 70% of the strains studied possessed the gene. Lerm et al. [61] also reported the presence of a gene coding for PAD in *L. plantarum* strains isolated from South African wine and also found that *L. plantarum* strains might have an added beneficial influence on the wine aroma profile to a larger extent than *O. oeni* because of the cache of enzymes (serine protease, esterase phenolic acid decarboxylase, β-glucosidase, and citrate lyase). As far as we know, the metabolism of phenolic acids by *L. plantarum* in wine has not been characterized and thus warrants further studies.

4. Other metabolic actions that produce undesirable compounds for wine quality

In some cases, the development of LAB can have negative consequences on the quality of wines. Here, we will focus on two groups of substances released by LAB during and after winemaking, which are undesirable for the health of the wine consumer: biogenic amines and ethyl carbamate precursors [75].

4.1. Biogenic amines

Biogenic amines are basic nitrogenous compounds formed mainly by the decarboxylation of the corresponding amino acid through substrate-specific enzymes present in microorganisms [76]. High concentrations of biogenic amines can cause undesirable physiological effects in sensitive humans, especially when alcohol and acetaldehyde are present [77].

Although food-fermenting LAB are generally considered to be nontoxinogenic or pathogenic, some can produce biogenic amines [78]. Currently, there is a growing concern regarding the limits of biogenic amines in wines because of their potential health implications [79]. Although not regulated uniformly worldwide, biogenic amines are generally confronted under regulations similar to those for allergens. As a matter of fact, wines containing high amounts of histamine are rejected in certain markets owing to the recommended or suggested limits of this compound [80].

The concentrations of biogenic amines in wine may be influenced by their presence in grapes, which is in turn determined by factors such as soil potassium deficiencies, grape variety, geographical region, and vintage. The concentrations of precursor amino acids are influenced by winemaking practices such as grape skin maceration. The formation of biogenic amines is also determined by wine parameters and components, of which pH, ethanol, SO_2, and pyridoxal 5′-phosphate have the most important effect on the diversity of microorganisms, decarboxylase enzyme activity, and decarboxylase gene expression. The concentration of biogenic amines is dependent on the wine type and style, but the presence of biogenic amines seems to be attributed, in all cases, to the presence of LAB [80].

In this context, for any strain being considered for use as a starter culture, the inability to produce biogenic amines is an important characteristic. Several species of LAB have been characterized as biogenic amine producers in wine directives worldwide.

Bauza et al. [81] and Landete et al. [82] screened five *L. plantarum* strains from Spanish red wines for their ability to form tyramine and phenylethylamine by different methods (plate medium, HPLC, and PCR) and found that all strains were negative for these amines. In addition, these authors demonstrated that the ability to degrade biogenic amines is a species-specific feature. Capozzi et al. [83] selected two *L. plantarum* strains (namely, NDT 09 and NDT 16) from an Italian red wine undergoing MLF and showed that in addition to not producing biogenic amines, they were able to degrade biogenic amines such as putrescine and tyramine. Similarly, Xia et al. [84] showed that the co-inoculation of strains of *L. plantarum* and *Staphylococcus xylosus* induced a significant reduction in putrescine, tyramine, and histamine. These results show that inhibiting the growth of indigenous LAB and inoculating commercial selected strains unable to produce biogenic amines may be a potential alternative in winemaking [85].

Additionally, it is usually accepted that *L. plantarum* does not secrete enzymes responsible for the production of the most common amines in wines [41,61,79,83,86,87,88]. Arena et al. [89] reported that a strain of *L. plantarum* isolated from wine and harboring the *tdc* gene was able to produce tyramine in wine. However, these authors also claimed that the ability of the tyramine-producer *L. plantarum* is not widespread in fermented food and is confined only to *L. plantarum* strains harboring the *tdc* gene [89], thus reinforcing the idea that a screening for this gene is mandatory for strains considered as putative MLF starters.

4.2. Ethyl carbamate

Ethyl carbamate, also referred to as urethane, is a genotoxic compound both in vitro and in vivo; it binds covalently to DNA and is an animal carcinogen. This compound is formed by the reaction between ethanol and N-carbamyl compounds such as urea, citrulline,

and carbamyl phosphate, at acidic pH, and its formation is dependent on the concentration of the reactant. This reaction is favored by increasing temperature and acidic pH. The content of ethyl carbamate is therefore higher in wines that have been stored for a long time and in which temperature has not been well controlled [75,90]. In some wines, ethyl carbamate has been detected at very low concentrations (approximately 20 μg L^{-1}); therefore, it is important to keep the level of ethyl carbamate in wine as low as possible.

Arginine degradation could conduce to the production of citrulline and the potential formation of ethyl carbamate. In this context, several authors have reported the ability of some *L. plantarum* strains to degrade arginine in various biological systems such as fish [91] and orange juice [92], particularly in wine [93]. *arc* genes, which encode the three enzymes of this pathway in LAB, are clustered in an operon-like structure: arcA (ADI), arcB (OTC), and arcC (CK) [71]; their presence has been demonstrated in *L. plantarum* in different reports [61,94]. Romero et al. [90] also studied the degradation of arginine and the production of citrulline and the potential formation of ethyl carbamate in *O. oeni* and *L. plantarum* and found that in the case of the *L. plantarum* strain CECT 5671 isolated from a Tempranillo wine, arginine was not degraded and citrulline was not produced; interestingly, the potential ethyl carbamate obtained was comparable to that obtained using the *Oenococcus* strains studied, which are able to degrade arginine and produce citrulline. These results suggest that the degradation of arginine in *L. plantarum* is probably strain dependent as already reported for some strains of *O. oeni* [93].

4.3. Production of other compounds that may impart undesirable characteristics to wine

Acetic acid imparts an unpleasant odor and taste to the wine, thus resulting in highly poor-quality wine. In this context, as pointed out above, because of its homofermentative metabolism, *L. plantarum* (through the Embden–Meyerhof pathway) produces primarily lactic acid but not acetic acid during the consumption of hexoses. However, some acetic acid can be produced during the consumption of pentoses [95]. Despite this fact, *L. plantarum* is preferred to *O. oeni* because of the heterofermentative pathway of the *Oeni* ferment hexoses (the main carbon source in the must [59]) not only in lactic acid but also in acetic acid.

5. Preservation processes

In addition to the ability of a bacterial strain to survive the conditions of wine, the preservation of a strain is an important technological property when choosing a new malolactic starter culture. The most used methods for small- and large-scale storage of *L. plantarum* for long periods are freezing and freeze-drying.

The preservation of probiotic *L. plantarum* strains has been widely studied. This species has been found to be highly resistant to the dehydration process [96,97,98,99], as well as highly resistant to the freeze-drying process [33]. However, the effects of the preservation process of *L. plantarum* and its posterior inoculation in the wine medium have been poorly studied. The main difficulty in freeze-drying and subsequent inoculation is the conservation of the membrane properties of the bacteria because the membrane is the first object of damage after drying. Maintaining the integrity of the membrane in a medium with high ethanol content (such as wine) is mandatory for bacterial survival.

For this purpose, several agents such as sugars or amino acids are added to the drying medium to protect cells. Among these, trehalose, sucrose and glutamate are extensively used to preserve *Lactobacillus* and *O. oeni* strains [100,101,102,103]. These compounds can form hydrogen bonds with the polar groups of the lipid membranes and proteins, thus maintaining their structure by the water replacement hypothesis [104].

Bravo-Ferrada et al. [13] studied the effect of trehalose, sucrose, and glutamate as protective agents and the effect of acclimation treatments on freezing and freeze-drying of three *L. plantarum* strains. They found that the survival of preserved *L. plantarum* strains in synthetic wine was strain and process dependent, with freeze-drying being the most drastic process, with a higher percentage of damaged membranes. Acclimation in the presence of low ethanol concentration improves the viability after the freeze-drying process. Similar results have been reported for *O. oeni* strains [105,106]. On the other hand, freezing temperatures affect the resistance after wine inoculation and the viability of *L. plantarum* (previously acclimated) frozen at −80°C, without showing any significant differences with control cells and that the acclimation process remarkably improves survival under wine inoculation of cells frozen at −20°C and freeze-dried cells [44]. In all the conditions assayed, the increase in the ethanol concentration present in the wine had a strong impact on the survival of *L. plantarum*, the impact being significantly lower at 14% than at 13%.

However, acclimation at high ethanol concentrations of some *L. plantarum* strains was detrimental to freeze-drying. The atomic force microscopy results showed that acclimation with high ethanol concentrations leads to changes in the bacterial surface (an increase in the zeta potential), thereby making cells more susceptible to surface damage after freeze-drying [45].

In conclusion, preservation studies indicate that the best conditions for long-term storage of *L. plantarum* starters for direct inoculation and for the success of MLF must be previously optimized for each strain.

6. Commercial starter cultures of *L. plantarum*

As pointed out above, inoculation with starter cultures reduces the potential of spoilage by other LAB and/or bacteriophages, ensures a rapid onset of MLF, and provides better control over the production of aromatic compounds and therefore of the wine flavor [2,107]. Most starter cultures commercially available for MLF are made using strains of *O. oeni* for the simple reason that it was believed that this LAB was the most reliable bacterium for the completion of MLF. However, as mentioned, some *Lactobacillus* species have many favorable characteristics that would make them suitable candidates for their use as malolactic starters [61]. Among them, *L. plantarum* has been shown to be the best candidate for its use in winemaking processes. As shown in previous sections of this review, *L. plantarum* possesses several characteristics that make it the possible next generation of MLF starter culture, not only because of its resistance to wine harsh conditions (see Sections 3 and 4) [21] but also because it does not produce acetic acid from carbohydrates, it has a more diverse array of enzymes that could lead to more complex production of aroma compounds (see Section 4) [60,62], and it can produce bacteriocins (plantaricins) that can reduce the participation of other LAB during MLF [108,109]. Moreover, some *L. plantarum* strains are able to inhibit spoilage by bacteria, degrade biogenic amines, grow in less time with less nutritional requirements, and show greater resistance to preservation [21,83,110]. Interestingly, the application of a *Lactobacillus* spp. as a starter culture is not particularly novel. Indeed, the *Lactobacillus* strain ML-30 was successfully used in inoculation timing trials in Pinot Noir in the early 1960s [111], and a commercial *L. plantarum* strain (Viniflora plantarum, CHR Hansen) was promoted in the late 1980s [112] for inoculation before alcoholic fermentation [113].

In the last decade, four commercial malolactic starters using *L. plantarum* have been released in the market, namely, Lallemand® culture V22, ML Prime™, Anchor NT 202 Co-Inoculant, and CHR Hansen Viniflora ® Nova™. The Lallemand® culture V22 is a pure *L. plantarum* culture of European origin, which can be used both for co-inoculation during alcoholic fermentation and for sequential inoculation after alcoholic fermentation [26]. The culture named ML Prime™, also released by Lallemand, is made from a pure *Lactobacillus*

culture with facultative heterofermentative metabolism. The manufacturer claims that the selected strains convert glucose or fructose only to lactic acid but not to acetic acid, therefore preventing an increased production of volatile acidity during MLF. This starter is recommended for fast and reliable MLF in wines of acidic pH (pH ≥3.4) (http://www.lallemandwine.com/wp-content/uploads/2015/08/2015-ML-Prime-east.pdf). The Oenobrands® product, which is marketed under the Anchor brand and named Anchor NT 202 Co-Inoculant, is a blend of selected *O. oeni* and *L. plantarum* strains from South Africa [61]. Finally, in 2014, CHR Hansen released Viniflora® Nova™, a *L. plantarum* strain that Saerens et al. [114] isolated from a screening undertaken in collaboration with Professor du Toit at Stellenbosch University in South Africa (http://www.chr-hansen.com). As with their previous *L. plantarum* product (Viniflora plantarum), the manufacturers recommended that this starter culture should be inoculated into grape must before alcoholic fermentation, meaning that MLF takes place before and during alcoholic fermentation, in an approach called "*reverse malolactic fermentation*."

The fact that four new *L. plantarum* starters have been released in the last decade reinforces the idea that this bacterium could play an important role in the wine making industry.

7. Conclusion and perspectives

This review focuses on the potential of *L. plantarum* as a MLF starter culture in winemaking. The shorter incubation time and better viability conditions found in some strains of *L. plantarum* make this species an economic and easy alternative to produce malolactic starter cultures with special potential applications in red wines.

In addition to the ability of LAB to consume L-malic acid, other enzymatic activities of LAB related to the aroma are gaining relevance. In this context, the genetic potential of *L. plantarum* to produce metabolites that are important in wine aroma, i.e., wine aroma-related enzyme genes, allows us to conclude that *L. plantarum* has an excellent potential that would make it suitable in the future to be a major player in the development of MLF starter cultures. It should be pointed out that all commercial starter cultures have an aromatic potential associated with the presence of *L. plantarum*. The fact that there are only a few cultures available as commercial starters, in addition to the increasing scientific data that support the role of *L. plantarum* both in the conversion of L-malic acid into L-lactic acid and in the formation of wine aroma, confirms that the full potential of *L. plantarum* is only starting to show.

Conflict of interest

Authors state that there are no conflicts of interest that might bias this work.

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