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# Malolactic Fermentation—Theoretical Advances and Practical Considerations

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**Abstract:** There are two main fermentations associated with the vinification process. Alcoholic fermentation (AF), which is conducted by yeasts and malolactic fermentation (MLF), which takes place as a result of the metabolic activity of lactic acid bacteria (LAB) of the genera *Oenococcus*, former-*Lactobacillus*, *Pediococcus* and *Leuconostoc*. MLF is defined as the biotransformation of L-malic acid to L-lactic acid and carbon dioxide and in addition to deacidification, contributes significantly to microbial stability and often to the improvement of the sensory profile of wines. Therefore, the abiotic and biotic factors that affect MLF, along with its correlation with quality characteristics, has been in the epicenter of intensive research. In addition, practical issues that accompany MLF have also been considered and adequately assessed. The aim of the present review was to explore and critically discuss MLF from both theoretical and practical perspectives.

**Keywords:** malolactic fermentation; bacterial metabolites; wine quality; lactic acid bacteria; *Oenococcus oeni*



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## 1. Introduction

In winemaking, alcoholic fermentation (AF) is traditionally considered as the key determinant. Wine yeasts, through their primary and secondary metabolism, direct the sensory profile of the final product. Malolactic fermentation (MLF), a secondary fermentation that usually follows AF, seems to be equally important, especially in the case of red wines and specific wines, such as Chardonnay [1]. Malolactic fermentation, namely the bioconversion of L-malic acid to L-lactic acid and carbon dioxide, is performed by lactic acid bacteria (LAB) of the genera *Oenococcus*, former-*Lactobacillus*, *Pediococcus*, and *Leuconostoc* and results in significant physicochemical and organoleptic modifications. Substitution of the dicarboxylic L-malic acid, which is characterized by a harsh taste, with the milder monocarboxylic L-lactic acid, results in deacidification of the wine with concomitant modification of its gustatory and olfactory perception [2]. In addition, removal of L-malic acid, a potential carbon source for some spoilage yeasts [3], enhances the stability of the final product. Finally, a series of modifications are also likely to take place depending on the grape cultivar, the metabolic capacity of the strain(s) driving MLF, and technological parameters [4,5].

The aforementioned reasons triggered intensive research on the nature of MLF, through the elucidation of the genetic and transcriptional organization of MLF, the biotic and abiotic parameters that affect MLF as well as the correlation between growth of malolactic bacteria with wine quality characteristics. At the same time, a number of practical considerations arose, mainly regarding the inoculation protocol and more specifically the temporal relationship between AF and MLF and the compatibility between the microbial strains employed. The recent technological and conceptual advances have improved our knowledge and

understanding of the physiology of malolactic bacteria, have provided valuable insights, and have enabled evaluation of their effect beyond the narrow limits of MLF. The aim of the present review was to collect, connect, and comprehensively present all available data regarding the theoretical advances and practical considerations of MLF.

## 2. Genetic and Transcriptomic Organization of MLF

Malolactic fermentation consists of three steps:

I. L-malate import to the cell,
II. L-malate decarboxylation to L-lactate, and
III. L-lactate release to the growth environment.

In *Oenococcus oeni*, importing of the L-malate into the cell is driven by a concentration gradient and takes place through a L-malateH- uniport, but only at pH values 3.0–5.6 and L-malate concentrations below 1 mM. At L-malate concentrations above 1 mM, passive diffusion may also take place [6]. Other mechanisms for L-malate transport have also been described, e.g., the malate/lactate antiporter in *Lactococcus lactis* [7] and the L-malate:proton symport of *Lactiplantibacillus plantarum* [8]. Once inside, L-malate may be decarboxylated to L-lactate or converted to pyruvate directly or through oxaloacetate, according to the cell needs and the capacity of the strain (Figure 1).

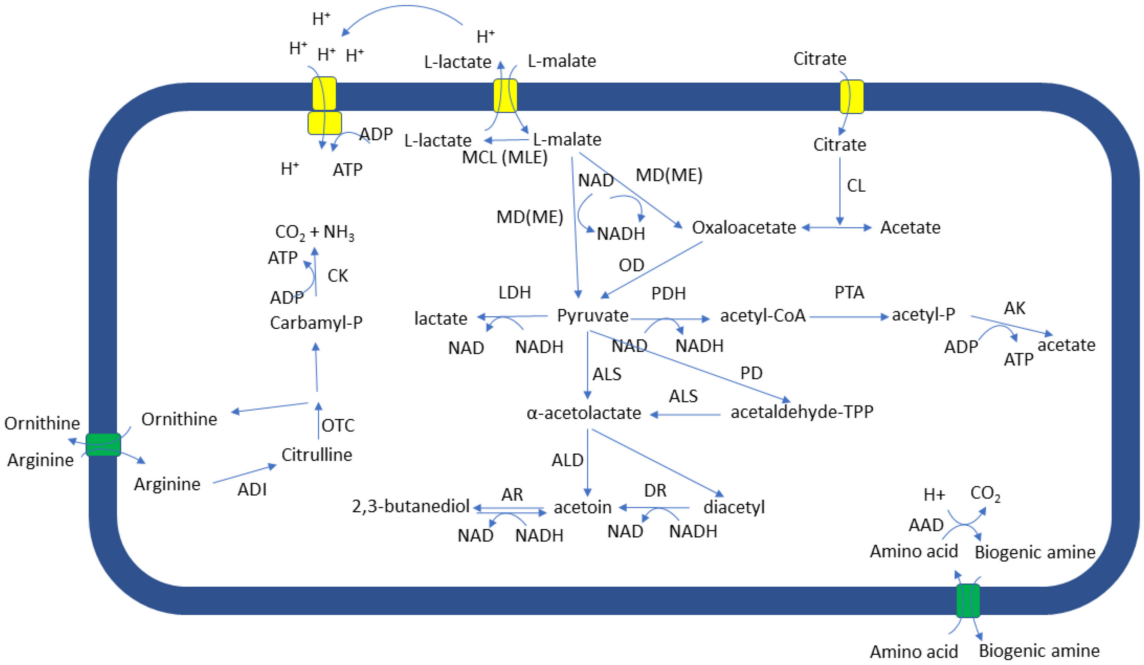


**Figure 1.** Pathways of malate, citrate, and arginine metabolism as well as formation of biogenic amines by LAB. AAD: amino acid decarboxylase; ADI: arginine deiminase; AK: acetate kinase, ALD: α-acetolactate decarboxylase, ALS: α-acetolactate synthase, AR: acetoin reductase; CK: carbamate kinase; CL: citrate lyase; DR: diacetyl reductase; LDH: lactate dehydrogenase; MCL (MLE): malate carboxy lyase (malolactic enzyme); MD(ME): malate dehydrogenase (malic enzyme); OD: oxaloacetate decarboxylase; OTC: ornithine transcarboxylase; PD: pyruvate decarboxylase; PDH: pyruvate dehydrogenase; PTA: phosphotransacetylase.

The fate of L-malate is directed by the energetic needs of the cell. Conversion to pyruvate is performed with $NAD^+$ or $NADP^+$ as cofactors. Pyruvate may be further used in catabolic or biosynthetic reactions. Indeed, Qi et al. [9] reported pyruvate accumulation under acid stress and increased flux towards acetyl phosphate, acetoin, and 2,3-butanediol. On the other hand, decarboxylation to lactate consumes a proton; in *O. oeni*, lactate is released to the growth environment through passive diffusion. This proton translocation across the cell membrane generates or, in the case of wine, sustains the pH difference (ΔpH)

as well as the electrical potential ($\Delta\Psi$) across the cell membrane. Thus, proton motive force is also sustained, and used by membrane ATPases to generate energy in the form of ATP [10]. Conversion of L-malate to L-lactate is facilitated by acid stress and the flux towards pyruvate seems decreased; however, L-lactate dehydrogenase activity seems to complement the pyruvate pool [9].

The genes that encode for the enzymes that are necessary for MLF are located in the *mle* operon. This operon consists of three genes. Genes *mleA* and *mleP* are 1626 bp and 945 bp long and encode the malolactic enzyme and the malate uniporter, respectively. They are transcribed in one bicistronic message. The gene *mleR* is transcribed in the opposite direction and encodes a positive regulator protein of the LysR-type, the expression of which, at least in *Lc. lactis*, is necessary for MLF induction [11,12].

The effect of vinification parameters, namely pH, ethanol, and $SO_2$, on the transcription of the *mle* operon, has been studied to some extent. In *O. oeni*, increase of ethanol concentration resulted in upregulation of *mleA*, *mleP*, and *mleR* [13,14]. Lowering of the pH value also resulted in *mleP* upregulation, but only in the presence of L-malate [15]. Presence of L-malate was also necessary for *mleP* upregulation during rehydration of the starter before inoculation [16]. As far as the effect of $SO_2$ was concerned, upregulation of *mleA* and *mleP* was reported in CCOo medium supplemented with 5 mg/L $SO_2$, but only after 4 h growth at 22 °C and not after 30 min of growth [17]. Similarly, no regulation was observed when the medium was supplemented with 10 mg/L of $SO_2$ [17]. Regarding *Lp. plantarum*, Miller et al. [18] reported that low pH positively affected the transcription of *mleA*, while ethanol affected it negatively; on the other hand, Binati et al. [19] reported no differential transcription of the genes associated with MLF during growth in synthetic grape juice medium at 25 °C for 72 h under different conditions of aeration and nitrogen availability.

## 3. Biotic and Abiotic Parameters Affecting MLF

A series of biotic and abiotic factors may interfere with MLF. These include the pH value, temperature, grapevine cultivar, $SO_2$, organic acids, and the interactions with yeasts. Their individual as well as their combined effect on MLF has been extensively assessed. In the majority of the cases, they affect MLF indirectly, by affecting growth of the LAB that perform it. However, the susceptibility to these factors is a strain-dependent characteristic. Therefore, generalization to species level may be inaccurate or even misleading. In the next paragraphs, the effect that these factors may have on MLF is discussed.

### *3.1. pH Value*

Most wines are characterized by pH values ranging between 3 and 3.8. Therefore, the environment in which LAB will carry out MLF is highly protonated. Given that the cell membrane is highly impermeable to protons, this gradient across the membrane is utilized for energy production [20]. However, organic acids naturally present in grape juice or produced through yeast and LAB catabolic activities, may also be protonated, depending on their pKa value. Undissociated organic acids become more lipophilic and may diffuse through the cell membrane, facilitated by ethanol presence [21]. Once inside the cell, the organic acid is dissociated, triggering acidification of the cytoplasm and accumulation of the anion. Such a condition may be lethal, unless properly addressed by the cell.

In general, at pH values below 3.5, MLF is performed by *O. oeni* strains while at values above 3.5, other lactobacilli, such as *Lp. plantarum* or *Pediococcus parvulus* strains may contribute [22–25]. Apart from the initial pH value, the evolution of pH value during MLF is equally important and should be taken into consideration for effective MLF. However, this is not adequately studied and the evolution of the pH value during MLF is characterized as rather unpredictable [26].

### *3.2. Temperature*

Temperature affects MLF by controlling microbial growth and the antimicrobial potential of ethanol. Regarding microbial growth, decrease of temperature results in prolongation

of lag phase and reduction of specific growth rate and biomass production [27]. On the other hand, increase of temperature enhances ethanol toxicity. As a result, the optimum temperature for MLF seems to range between 15 and 18 °C, depending on the capacity of the microbial strain that performs it [23,28]. However, MLF may also take place at higher temperatures; the impact on the sensorial outcome seems to be dependent upon the temporal relationship between AF and MFL, must composition, and the capacity of each strain [29,30]. More specifically, Sereni et al. [29] reported that the wines produced at 15 and 21 °C presented significant sensorial differences but only when MLF followed AF and not when both fermentations took place concurrently. The wine fermented at the lower temperature was characterized by a greater number of aroma compounds, including ethyl esters, 1-hexanol, and gamma-terpinene. On the contrary, the wine fermented at higher temperature was characterized by diethyl succinate, 2-methylbutanoic acid, isobutyric acid, isopentyl hexanoate, and phenethyl alcohol [29]. Guzzon et al. [30] provided an alternative insight, presenting that even in concurrent AF and MLF, the sensorial outcome may be different under the influence of must composition and microbial strain metabolic capacity.

### *3.3. Grapevine Cultivar*

The grapevine cultivar may affect MLF through the effect that phenolic compounds and organic acids may have on LAB growth. Grape and wine polyphenolic content are largely dependent on grapevine variety and viticultural conditions [31–42]. The effect of hydroxybenzoic acids and esters (e.g., 4-hydroxybenzoic acid, ellagic acid, ethylgallate, gallic acid, methylgallate, syringic acid, vanillic acid), hydroxycinnamic acids (e.g., p-coumaric acid, caffeic acid, ferulic acid, sinapic acid), phenolic alcohols (e.g., tryptophol, tyrosol), stilbenes (e.g., ε-viniferin, ampelopsin A, cis-resveratrol, trans-resveratrol, trans-resveratrol-3-O-glucoside, r-viniferin, r2-viniferin), flavan-3-ols (e.g., (+)-catechin, (−)-epicatechin), flavonols (e.g., isorhamnetin, kaempferol, morin, myricetin, quercetin) may have on LAB of enological significance, namely *P. pentosaceus*, *P. parvulus*, *Lentilactobacillus hilgardii*, *Lp. plantarum*, and *O. oeni*, has been extensively studied [43–47]. The effect that these compounds may have on the growth of LAB and MLF depends on the nature of the phenolic compound, their concentration, and the capacity of the bacterial strain [43,45,48].

The mode by which phenolic compounds affect the growth of LAB has been in the epicenter of intensive research over the last decade. Changes in the cellular membrane structure and function have been identified as the first key features that determine the fate of LAB and MLF. Indeed, Sirk et al. [49] reported that catechins, and preferably non-galloylated ones, are absorbed into the membrane increasing its fluidity and concomitantly its permeability. The capacity of the strain to reduce membrane fluidity by increasing the saturation degree, by mechanisms such as cyclation of fatty acyl chains or altering the fatty acid composition [50,51], will determine its fate and the degree of adaptation. Another effect that may interfere with energy production and concomitantly bacterial growth is through the inhibition of the arginine deiminase pathway. This pathway may be an important energy source for bacterial growth. On the other hand, intermediate products, namely citrulline and carbamyl phosphate, contain carbamyl groups that react with ethanol and yield ethyl carbamate, a known carcinogen. Alberto et al. [52] demonstrated that gallic and protocatechuic acids may inhibit arginine deiminase pathway depriving energy and reducing the amount of ethyl carbamate precursors. On the other hand, vanillic acid, caffeic acid, rutin, quercetin, and catechin did not seem to have such an effect.

The second key feature that determines the fate of LAB, and concomitantly MLF, is the capacity of the LAB to utilize these compounds and gain energy. The ability of some *Lv. brevis* strains to decarboxylate hydroxycinnamic acids to their respective vinyl derivatives has been tested [53–56]. In addition, some strains exhibited the capacity to further reduce these vinyl derivatives to their respective ethyl phenols [55,57]. In the majority of the cases, p-coumaric, ferulic, and caffeic acids were more or less efficiently decarboxylated to vinyl phenol, vinyl guaiacol, and vinyl catechol, respectively. No such activity has been reported for o-coumaric, m-coumaric, cinnamic, and sinapic acids. Similarly, Rodriguez

et al. [58] demonstrated the capacity of *Lp. plantarum* strain CECT 748$^T$ to decarboxylate and further reduce p-coumaric, caffeic, and ferulic acids to their respective vinyl and ethyl derivatives. Decarboxylation of gallic and protocatechuic acids as well as reduction of m-coumaric acid were also reported. On the contrary, no such activity was found on phloretic, chlorogenic, ellagic, o-coumaric, cinnamic, sinapic, syringic, salicylic, benzoic, gentisic, veratric, p-hydroxybenzoic, and vanillic acids. Similarly, *Lp. plantarum* strain 299v degraded caffeic acid to 4-ethylcatechol and ferulic acid to dihydro ferulic acid [59]. The aforementioned capacity may be preceded by tannins degradation through tannase activity. Indeed, several *Lp. plantarum* strains have been reported to degrade tannins into derivatives that can be further utilized as already described [60–62].

On the contrary, metabolism of phenolic compounds by *O. oeni* has not been adequately studied. The positive effect of some phenolic compounds on some *O. oeni* strains has been reported [63–65] which can probably be assigned to their ability to utilize them.

### *3.4. Interactions with Yeasts*

Yeasts may affect MLF by directly or indirectly interfering with the growth of the bacteria that perform it. This effect may be direct when MLF and AF are simultaneous, and indirect when MLF follows AF. In the first case, it may be attributed to the antagonism for nutrients as well as the toxicity of the metabolites. The yeast metabolites that may affect LAB growth are ethanol, $SO_2$, organic acids, medium chain fatty acids, as well as antimicrobial peptides. The antimicrobial activity of ethanol is well known and has been attributed to membrane damage and protein denaturation; it has been reported to be optimal in water solutions within the range of 60 and 90% [66]. In general, lactobacilli and pediococci seem to be less sensitive to ethanol than *O. oeni* in synthetic media [22,28]. Recently, genes candidates implicated to ethanol resistance of *O. oeni* have been studied through heterologous expression to other bacterial species, revealing a complex cell mechanism [67,68]. Regarding ethanol tolerance, the effect of temperature and the wine matrix has also been highlighted [69,70].

The antimicrobial activity of sulfur dioxide is also well known. Molecular sulfur dioxide enters the cell through the cell membrane due to its small size and absence of net charge. Once inside the cell, it yields bisulfite and sulfite, depending on the pH value, and interacts with many cellular components, including proteins, ATP, and cofactors such as $NAD^+$, $FAD^+$, and thiamin, disrupting cell homeostasis [71]. The amount of $SO_2$ needed to prevent bacterial growth depends upon nearly all factors associated with vinification, such as temperature, pH value, ethanol concentration, microbial population, growth stage etc. [71]. Regarding the relevant tolerance of lactobacilli, pediococci, and oenococci, contradictory results are available in the literature [72,73].

Yeasts may also produce peptides with antimicrobial activity [74,75]. Their mode of action includes a variety of effects, including interference with membrane permeability, protein and cell-wall synthesis, enzyme activity, etc. [76]. Several authors have reported the production of such peptides by *Saccharomyces cerevisiae* and their inhibitory activity against *O. oeni* and in some cases non-*Saccharomyces* yeasts [77–82].

Organic acids may also affect the growth of the LAB conducting MLF. It has been estimated that organic acids may account for as much as approximately 1% of grape juice solids. L-tartaric acid is the most abundant and may reach 10 g/L. L-malic acid is also present at concentration that may reach 6.5 g/L, whereas citric and ascorbic acids may also be present at concentrations less than 1 g/L. After alcoholic fermentation by *S. cerevisiae*, L-tartaric and citric acid concentration reduction is very unlikely to occur, but degradation of L-malic acid is possible. However, in the presence of other yeast species, degradation of these organic acids may occur. After AF, production of acetic acid, succinic acid, pyruvic acid, traces of D-lactic acid as well as medium chain fatty acids, is very likely to occur [3]. The effect that these organic acids may have on LAB growth and MLF has been studied to some extent. The stimulatory effect that L-malic acid may have at 2 and 4 g/L, during growth at 20 °C, in a growth medium with pH value 3.5, supplemented with 10% ethanol, has been reported by Fahimi et al. [83]. Regarding MCFA, the effect is type and

concentration dependent. Indeed, Capucho and San Ramao [84] reported that decanoic and dodecanoic concentrations below 12.5 and 2.5 mg/L, respectively, had stimulatory effects on *O. oeni* growth. On the contrary, if the concentration exceeded these limits, an inhibitory effect was noticed.

The effect that yeasts may have on MLF is completely different when MLF follows AF. In that case, there is no antagonism for nutrients. However, LAB have to tolerate the harsh environment that the yeasts' metabolic activities have created. On the other hand, yeast autolysis, which takes place mostly at the end of alcoholic fermentation, may assist proliferation of LAB. During yeast autolysis, yeast cell walls are becoming available to the microorganisms that can decompose them and utilize their building blocks. Yeast cell walls consist of covalently linked β-1,3 glucan, β-1,6 glucan, chitin, and mannoproteins [85]. Mannoproteins are highly glycosylated polypeptides, the carbohydrate content of which, mannose and glucose in the majority of the cases, may reach 95% of the total mannoprotein weight [86]. *Oenococcus oeni* has been reported to possess glucosidase and peptidase activities, through which carbohydrates and amino acids are released, providing the necessary carbon, nitrogen, and energy sources [87]. These enzymatic activities are strain-dependent; the importance of mannoprotein utilization for effective MLF has been recently highlighted by Balmaseda et al. [88]. In this study, the *O. oeni* strain with the lowest mannoprotein utilization capacity exhibited the worst MLF performance among the strains tested. Qualitative and quantitative differences in the mannoproteins provided to *O. oeni* strains could not be correlated with MLF duration [88,89]. Interestingly, the effect that autolysis has on MLF, may also depend upon the yeast that undergoes autolysis. Indeed, Balmaseda et al. [88] reported that supplementation with lees from different *Torulaspora delbrueckii*, *S. cerevisiae*, and *Metschnikowia pulcherrima* strains, had different effect on MLF performance by *O. oeni* strains.

## 4. Correlation between MLF and Wine Quality Characteristics

During malolactic fermentation, a series of bioconversions takes place, which affects the organoleptic characteristics as well as safety of the wine. These depend on the capacity of the strain(s) that drive MLF. In the next paragraphs, the most important activities are summarized.

### *4.1. Glycosidase Activity*

Glycosidase activity may affect the sensorial properties and color stability of the wine. Color stability is largely dependent on monoglucoside anthocyanins. Hydrolysis of these glycoconjugates releases anthocyanidins that may be subsequently spontaneously converted to colorless derivatives [90]. Regarding the sensorial properties, when released from their glycosides, some benzene derivatives, monoterpenes, and C13-norisoprenoids affect aroma, while ethyl esters, carboxylic acids, aliphatic alcohols, and lactones affect taste [91]. Thus, hydrolysis of their glucoconjugates releases them and concomitantly increases the organoleptic complexity of the wine. This hydrolysis is catalyzed by glucosidases specific to the carbohydrate moiety. In the case of monosaccharides, this carbohydrate moiety may be β-D-apiofuranoside, β-L-arabinofuranoside, β-D-glucopyranoside, β-L-rhamnopyranoside, or β-D-xylopyranoside. In addition, β-D-glucopyranosidase activity is required in the case of dissacharides, in order to remove the additional carbohydrate, which is β-D-glucopyranoside [91].

Several *O. oeni*, *Lp. plantarum*, *Levilactobacillus brevis*, and *Pediococcus* spp. strains have been reported to possess the aforementioned enzyme activities [92–105]. Growth stage, ethanol content, residual glucose and fructose concentrations, molecular sulfur dioxide, pH value, and temperature have been reported to affect glucosidase activity, in a strain-dependent manner [92–94,102,105].

Novel insights were provided by Spano et al. [99], Olguin et al. [106], and the studies of Li et al. [103] on the transcriptomic response of β-glucosidase genes to oenologically relevant stresses. Spano et al. [99] reported that the presence of $K_2S_2O_5$, ethanol and low pH

value (3.5) repressed the transcription of the *Lp. plantarum* strain Lp90 β-glucosidase gene. Olguin et al. [106] reported that the transcription of a β-glucosidase gene of four *O. oeni* strains revealed a strain-dependent response to culture conditions. However, no correlation with measured β-glucosidase activity could be established. On the contrary, Li et al. [103] managed to establish a correlation between the transcription levels of β-glucosidase genes OEOE-0224 and OEOE-1210 with the measured β-glucosidase activity of whole cells of *O. oeni* strain SD-2a and the transcription levels of β-glucosidase gene OEOE-1569 with the measured β-glucosidase activity of the disrupted lysate of the strain, suggesting a possible causal relationship.

### *4.2. Esterase Activity*

Microbial esterases are involved in both biosynthetic and hydrolytic reactions, affecting quantitatively and qualitatively the ester content and concomitantly the wine aroma [107]. Although most esters are produced by yeasts during alcoholic fermentation [91], modification of their concentration has been reported after MLF [105,108–115], indicating that the LAB that drive MLF may possess such activity. Indeed, strain dependent esterase activity of 23 *O. oeni*, 16 *Lactobacillus* spp., and 11 *Pediococcus* spp. strains against pNP-acetate, pNP-butyrate, and pNP-octanoate was reported by Matthews et al. [116]. The widespread nature of esterase occurrence among LAB and the strain dependent activity was further verified by Perez-Martin et al. [117] and Diez-Ozaeta et al. [118] against pNP-octanoate in the first study and pNP-acetate and pNP-octanoate in the second. Finally, Gammacurta et al. [119] thoroughly studied the effect of yeast strain and cultivar on ester metabolism by LAB and concluded that only ethyl 2-hydroxy-3-methylbutanoate and ethyl 2-hydroxy-4-methylpentanoate were strongly influenced by the LAB strain, irrespective the yeast strain that carried out the alcoholic fermentation and the grapevine cultivar.

Esterase activity has been reported to be affected by pH, ethanol, and temperature either as single stresses or in combination, in a strain-dependent manner [117,118,120].

Cinnamoyl esterases have drawn specific attention since they are involved in the release of hydroxycinnamic acids from their esters. Unbound hydroxycinnamic acids may then serve as substrates for conversion to volatile phenols by *Brettanomyces/Dekkera bruxellensis* and some wine LAB [121]. Occurrence of cinnamoyl esterases has been reported so far in some *O. oeni* strains [122–124] and their activity has been characterized as strain-dependent [121].

### *4.3. Citrate Metabolism*

The ability of the bacterial strain that performs MLF to degrade citrate is particularly important due to the higher amounts of lactate, acetate, diacetyl, and acetoin that may be produced. Citrate is transported into the cell via citrate or malate permease and converted to acetate and oxaloacetate through the action of citrate lyase (Figure 1). Acetate is excreted from the cell while the oxaloacetate is decarboxylated to pyruvate through oxaloacetate decarboxylase. Pyruvate may be then further utilized through a number of anabolic and catabolic processes, including the ones leading to the production of lactate, acetate, diacetyl, and acetoin. Phenolic compounds, carbohydrate type, and concentration as well as pH value, seem to have a pronounced effect on citrate catabolism. Rozes et al. [125] reported that phenolic compounds reduced glucose and fructose catabolism rate by *O. oeni* and enhanced citrate catabolism, leading to increased acetic acid production. Glucose seems to suppress citrate permease and citrate lyase and thus citrate metabolism [126–128]. On the contrary, fructose may lead to the production of high concentrations of diacetyl and acetoin by both *O. oeni* and *Lp. plantarum* [128]. Regarding the effect of pH value, more citrate was metabolized by *O. oeni* at low pH values (3.0 and 3.5) whereas *Lp. plantarum* seemed to prefer high pH values (4.0 and 5.0) [128].

### *4.4. Production of Exopolysaccharides*

Lactic acid bacteria may produce exopolysaccharides (EPS), which are extracellular polymers with variable composition, size, and degree of branching. Therefore, their spatial arrangement, charge, and capacity to interact with other molecules, such as proteins, alcohols, esters etc., may vary [129]. The fact that the LAB of wine are all capable of producing various EPS derived from several biosynthetic pathways, while the implicated genes, either organized in clusters or isolated, are well conserved between the bacterial species, indicating their importance for the bacteria cell. Although their exact physiological role has not yet been thoroughly understood, they assist in survival of harsh wine environments and in their persistence during the winemaking process [130].

From an enological perspective, it seems that both structure and EPS localization, capsular or free, should be taken into consideration. For instance, the production of β-1,3-glucans can not only cause wine spoilage and economic loss, but at the same time helps the bacteria to adhere on biotic and abiotic surfaces [130–132]. In that case, the solution for the winemaker is the simultaneous enzymatic action of β-glucanase and lysozyme, as recommended by Coulon et al. [133]. On the other hand, possible positive roles in sensorial perception and lyoprotective ability to freeze drying are currently under scrutiny [134].

### *4.5. Biogenic Amines Production*

Biogenic amine production is another strain-dependent characteristic and may take place by both yeasts and LAB. They are produced as a response to harsh environmental conditions, in an attempt to deacidify the cytosol. This is achieved through the coordinated action of a membrane antiport and specific amino acid decarboxylases (Figure 1). Each amino acid decarboxylation consumes one proton, and biogenic amine excretion drives ATP synthesis through proton motive force [135,136]. Such systems have been described for histidine/histamine, tyrosine/tyramine, ornithine/putrescine, and lysine/cadaverine [135,137,138], with the first three being the ones mostly produced during MLF [139]. Interestingly, the capacity of many strains to degrade biogenic amines through monoamino-oxidases or multicopper oxidases has been reported [140,141], providing with new insights into biogenic amine accumulation and additional strategies for their removal. Several factors have been reported to affect biogenic amine accumulation. These include agricultural practices, through their effect on the concentration of the amino acid precursors and technological parameters, including storage conditions, mostly through their effect on the biodiversity of the microecosystem [142].

A very interesting insight was provided by Landete et al. [143]. In that study, the effect of enological factors on the activity of histidine decarboxylase enzyme of *Le. hilgardii*, *P. parvulus* and *O. oeni* as well as the transcription levels of the histidine decarboxylase gene (*hdc*) of *Le. hilgardii* were assessed. It was reported that increases of pH value, temperature, lactic acid, tartaric acid, ethanol, and $SO_2$ concentration had no effect on the activity of the enzyme of preadapted cultures of the strains assessed. On the contrary, the activity was reduced upon increase of malic acid, citric acid, and glucose concentration. These results were in concordance with the transcriptomic response of *hdc*.

### *4.6. Ethyl Carbamate (Urethane) Production*

Ethyl carbamate is produced through the reaction of ethanol with carbamyl compounds. Such compounds may arise from arginine catabolism by yeasts and LAB (Figure 1). In the case of the LAB, arginine is usually catabolized through the arginine deiminase pathway which results in the production of one molecule of ornithine, carbamyl phosphate, and ATP per arginine molecule. Both catabolic products contain carbamoyl groups and thus may react with ethanol. The factors that affect ethyl carbamate production include the concentration of the reactants, as well as storage temperature and time; pH value does not seem to affect it significantly [144,145].

## 5. Practical Considerations of MLF

Malolactic fermentation (MLF) can be spontaneous or can be induced by wine inoculation with selected LAB starter cultures. The process of spontaneous MLF is manifested by the growth and metabolism of indigenous LAB, with dominant species *O. oeni*, which are perfectly adapted to the environmental conditions of each medium and space [131]. However, in this case, the bioconversion of malic acid into lactic acid can be slow or incomplete, while undesirable compounds, such as volatile phenols and diacetyl overproduction as well as potentially hazardous compounds, such as biogenic amines can be produced as previously discussed. Certainly, the use of selected LAB starters can help minimize these risks while the moment of inoculation seems to be crucial for the winemaking process.

### *5.1. Malolactic Starters*

In addition to *O. oeni*, there are several LAB that have been used as MLF starters belonging to the species *Lp. plantarum*, *Le. hilgardii*, *Lv. brevis*, *Lacticaseibacillus casei*, and *Pediococcus* spp. [146]. Each has demonstrated different properties with significant strain dependence. Under high pH conditions, *Lp. plantarum* strains have shown particularly interesting results [147], not only for their ability to induce MLF, but also for their homofermentative catabolism of hexoses, which minimizes the risk of acetic acid production [148]. Furthermore, *Lp. plantarum* has been found to possess a complex enzymatic system, such as β-glucosidases, proteases, esterases, and decarboxylases, which could play a significant role in modifying wine organoleptic properties [24,86,149]. Regarding the genus *Pediococcus*, it is generally considered a wine spoilage microorganism [150]. However, some findings have indicated that the presence of certain strains of *Pediococcus* spp. may contribute positively to a wine's sensory profile [150–152]. In recent years, mixed inoculation strategies have also been employed. The use of blended cultures of *Lp. plantarum* and *O. oeni* as MLF starters, can facilitate the rapid consumption of malic acid, while contributing significantly to the volatile profile of wine [153].

### *5.2. Inoculation Protocol*

The yeast and bacteria species and strains as well as vinification parameters should be taken into consideration when designing an inoculation protocol. The interplay between these factors affects growth and metabolic activity of the microbial starters employed and concomitantly wine quality (Figure 2). Selection of the yeast strains should not be solely based on their ethanol production capacity, factors that should also be taken into consideration include the release of antimicrobial peptides, medium-chain fatty acids and mannoproteins. Similarly, lactic acid bacteria population and growth phase should also be considered for effective MLF. A bidirectional interaction between these and vinification parameters, such as $SO_2$, oxygen, temperature, pH and cultivar exists and define the inoculation protocol that should be employed.

Temporal relationship between AF and MLF is a major practical issue. Theoretically, MLF can precede, follow, or take place simultaneously with AF [69,71,146,154,155]. The effect that yeast and LAB metabolic coexistence or succession may have on wine quality has been extensively studied. The option to conduct MLF before AF, although promising [155], is rarely used since oxygen availability may result in increased acetic acid production. This is also the case regarding simultaneous MLF and AF; therefore, LAB are inoculated usually 24 h after yeast inoculation, since oxygen needs to be depleted before LAB become metabolically active. Metabolic coexistence of yeasts and LAB will result in antagonism for the available nutrients and energy sources. This, along with the metabolites produced may result in growth inhibition of either microorganism [156,157]. In Table 1, studies that comparatively assess the outcome of simultaneous and sequential MLF and AF are presented. In only a couple of cases, co-inoculation had a negative effect on the viability of the yeast or the LAB strains employed. It is generally accepted that simultaneous MLF and AF significantly reduces the overall winemaking time, and thus the risk for microbial spoilage, since sulfuring takes place earlier. In addition, ethanol content is not affected

by co-inoculation. However, modification of wine composition and sensorial properties may take place. More accurately, increase of volatile acidity, decrease of color intensity and tonality, and enhancement of floral, vegetable, red, and ripe fruit tones, have been recorded. However, this effect seems to be winery, cultivar, vintage, fermentation temperature, and microbial strain dependent. Therefore, proper arrangement of the aforementioned parameters is necessary for successful simultaneous MLF and AF fermentation.

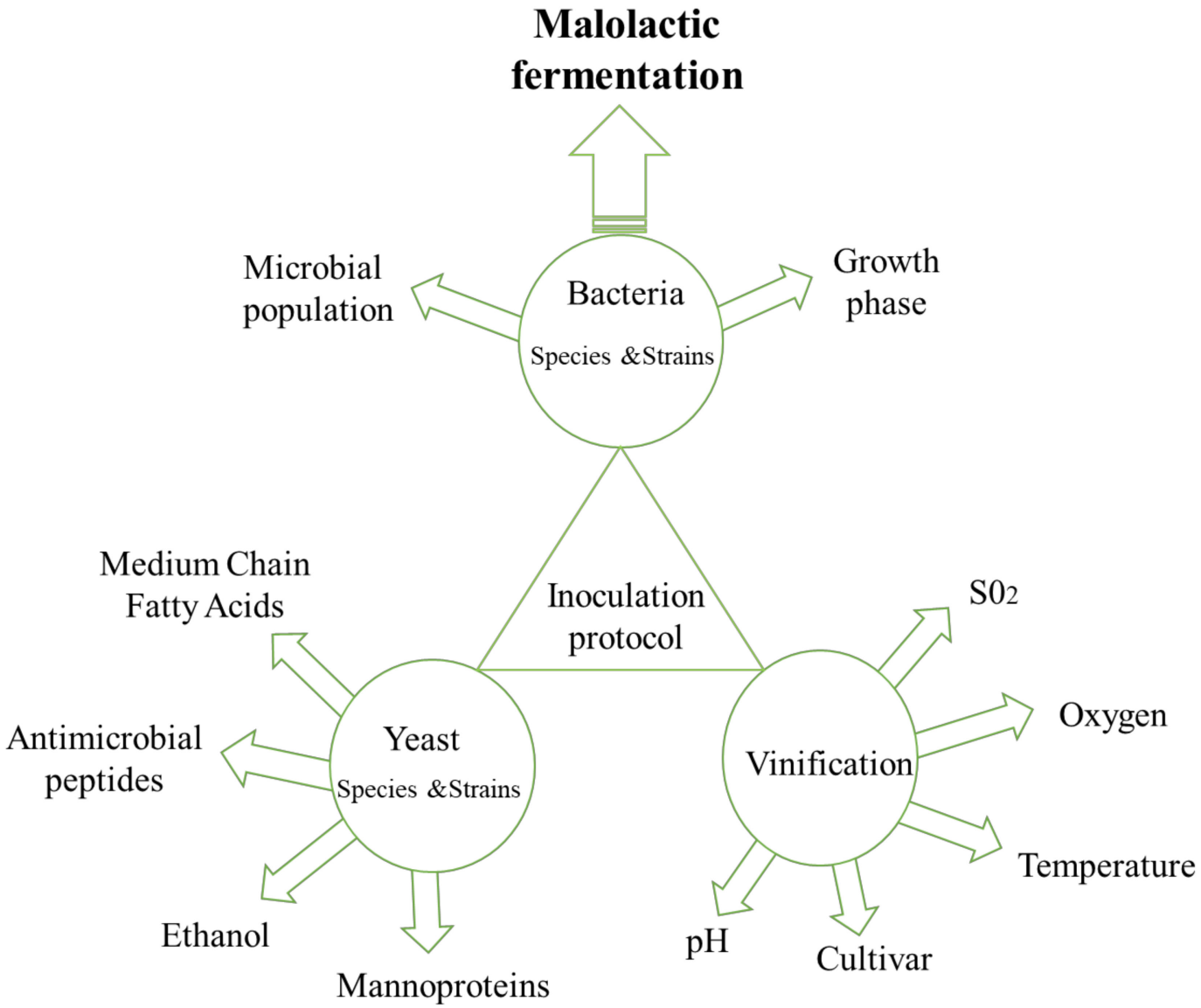


**Figure 2.** Biotic and abiotic factors affecting MLF.

**Table 1.** Studies that assess the effect of different inoculation strategy on wine quality.

| Cultivar | Yeasts/LAB | Inoculation Strategy | Comment | Reference |
|---|---|---|---|---|
| Cabernet Franc | *S. cerevisiae* Uvaferm VN®; *O. oeni* C22L9 | 1. LAB inoculation after AF<br>2. LAB inoculation 24 h after yeast inoculation | Inoculation strategy had no effect on yeast growth, ethanol content, color intensity, total and volatile acidity. Simultaneous inoculation reduced color tonality and increased free and polymerized anthocyanins. Simultaneous fermentation resulted in increased propanol, ethyl acetate, hexyl acetate, ethyl lactate, ethyl butyrate, ethyl hexanoate, ethyl octanoate, diethyl succinate, valeric acid, acetaldehyde, and 2-methyl-tetrahydrothiophene-3-one and decreased 1-octen-3-ol, 2-phenylethanol, tyrosol, 2-phenylethyl acetate, ethyl dodecanoate, 2-phenylethyl succinate, diethyl malate, phenylacetic acid, furfural, hydroxymethyl furfural, 4-vinyl-guaiacol, 4-vinylphenol, 3-oxo-α-ionol, dihydro-α-ionone, 3-oxo-7,8-dihydro-α-ionol, vanillin, zingerone, homovanillyl alcohol, and siringol concentration. Simultaneous inoculation resulted in wines with increased aromatic intensity, floral, and vegetable aroma. Sequential inoculation produced more intense spicy tones and longer aftertaste intensity and body in wine. | [158] |
| Cabernet Franc | *S. cerevisiae* NT-202; *O. oeni* and *Lp. plantarum* NT-202 co-inoculant | 1. LAB inoculation after AF<br>2. LAB mixture inoculation after 3 days of AF (specific gravity of ca. 1040) | Simultaneous fermentation had no effect on ethanol, total acidity, and total phenolic content. However, volatile acidity increased, while glycerol, color intensity, and tonality decreased. The volatile compounds with more pronounced increase were isobutyl alcohol, 3-etoxy-1-propanol, acetoin, and 2-methyl-propanoic acid, whereas a more pronounced decrease was observed in the case of isoamyl alcohol, phenylethyl alcohol, ethyl lactate, butanedioic monoethyl, and diethyl esters. Wine made by co-inoculation had more red and ripe fruits tones, while the one made by sequential inoculation more spice and herb tones. | [159] |
| Chardonnay | *S. cerevisiae* D47; *T. delbrueckii* Vinoflora PreludeTM; *O. oeni* Beta | 1. *S. cerevisiae* simultaneously with *O. oeni*<br>2. *O. oeni* inoculated after AF by *S. cerevisiae*<br>3. *T. delbrueckii* (15 or 21 °C for 48 h), then *S. cerevisiae* simultaneously with *O. oeni*<br>4. *T. delbrueckii* (15 or 21 °C for 48 h), then *S. cerevisiae* and *O. oeni* inoculation after AF | Higher ethanol content was observed in sequential fermentation at both 15 and 21 °C. Aroma and mouthfeel differed significantly between inoculation strategies. Temperature affected aroma in sequential inoculations. Acetic acid increase was associated with lower fermentation temperature. | [29] |
| Chardonnay | *S. cerevisiae* CY3079; *O. oeni* EQ54, Alpha | for each LAB strain<br>1. LAB inoculation after AF<br>2. LAB co-inoculation with the yeast | Simultaneous fermentation had no effect on ethanol and glycerol content. However, it resulted in reduced acetaldehyde, citric, and fumaric acid and increased acetic acid concentration. No statistically significant differences were observed in sensory evaluation. | [160] |
| Fiano | *S. cerevisiae* FE; *Lp. plantarum* M10 | 1. *Lp. plantarum* inoculated at ca. 5% ethanol<br>2. LAB inoculation 24 h after yeast inoculation<br>3. LAB inoculation after AF<br>4. LAB inoculation (with cells pre-adapted to sub-optimal pH) after AF<br>5. no MLF | No effect on yeast growth and ethanol production. MLF was only evident in strategy 4. Increased 2,3-butanediol, 2-nonanol, 2-phenylethanol, linalool, 4-terpineol, geraniol, and reduced 1-propanol, 1-methyl-propanol, 3-methyl-1-butanol, 2-pentanol, 1-pentanol, methyl-tyo-propanol, methanol, and hexanoic acid concentration in the wine produced with strategy 4 compared to the rest. | [161] |

**Table 1.** *Cont.*

| Cultivar | Yeasts/LAB | Inoculation Strategy | Comment | Reference |
|---|---|---|---|---|
| Incrocio Manzoni | *S. cerevisiae* CY3079; *O. oeni* Lal1, Lal2 | for each LAB strain<br>1. LAB inoculation after AF<br>2. LAB inoculation 48 h after yeast inoculation | LAB addition had no effect on yeast growth and ethanol production. Strain-specific differences in MLF were observed. Total acidity, acetic acid, and citric acid concentration were not affected by simultaneous fermentation. On the contrary, ethyl acetate and acetaldehyde concentration increased. | [162] |
| Malbec | *K. apiculata* mc1, *S. cerevisiae* mc2; *O. oeni* X2L | 1. AF by *K. apiculata* mc1<br>2. AF by *S. cerevisiae* mc2<br>3. AF by both yeasts<br>4. simultaneous inoculation of both yeasts and LAB<br>5. LAB inoculation after AF by both yeasts | Better development and alcoholic fermentation kinetics of *S. cerevisiae* compared to *K. apiculata*. No effect on *S. cerevisiae* development by simultaneous LAB inoculation. No effect of co-inoculation on ethanol content. Co-inoculation resulted in higher volatile acidity, reduction of color intensity and the concentration of acetaldehyde, ethyl caproate, ethyl caprylate, 2-phenylethyl acetate, and specific esters. On the other hand, increase in the concentration of ethyl acetate and isoamyl acetate was noticed. Sequential inoculation resulted in better fruity and floral aromas and high equilibrium-harmony rating. Simultaneous inoculation scored higher phenolic aroma and low equilibrium-harmony rating. | [163] |
| Malbec (2 vintages) | *S. cerevisiae* INTA MZA, ICV D80; *O. oeni* Uvaferm Alpha | for each yeast strain<br>1. LAB inoculation after AF<br>2. LAB co-inoculation with the yeast | Must composition and yeast strain affected volatile acidity in both sequential and simultaneous fermentations. Co-inoculation had no effect on yeast and LAB viability, histamine, and putrescine content as well as the sensorial quality of the wines. | [164] |
| Merlot | *S. cerevisiae* Laffort Actiflore®; *P. fermentans* H5Y-28; *Lv. brevis* 26 | 1. *S. cerevisiae* simultaneous and sequential with *Lv. brevis*<br>2. *S. cerevisiae* and *P. fermentans* simultaneous and sequential with *Lv. brevis* | *P. fermentans* seemed to enhance *Lv. brevis* viability and the production of higher alcohol acetates and fatty acid ethyl esters. Strong jammy and temperate fruit aromas produced by the co-fermentation of the three strains. | [165] |
| Merlot (different wineries, two vintages) | *S. cerevisiae* (5 strains); *O. oeni* (3 strains) | 1. LAB inoculation after AF<br>2. LAB inoculation 24 h after yeast inoculation | Volatile wine composition depended upon microbial strain, MLF strategy, vintage, and winery. In all cases, an increase of γ-decalactone and a decrease of ethyl isovalerate, 2-methyl-butanol, and 3-methyl-butanol concentrations were noticed in simultaneous, compared to sequential fermentation. In addition, fruity aroma intensity was increased with simultaneous fermentation. | [166] |
| Negroamaro | *S. cerevisiae* CY1, CY2; *O. oeni* CL1, CL2 | each yeast strain was combined with each LAB:<br>1. LAB inoculated after AF<br>2. LAB inoculated 24 h after yeast | Strain-specific microbial development and L-malic acid consumption in both strategies. Co-inoculation strategy had no effect on ethanol content. However, differences in the production of specific esters, alcohols, and acids between the strains and inoculation timing were observed. Co-inoculation enhanced red and ripe fruit notes as well as buttery and creamy notes. | [167] |
| Riesling | *S. cerevisiae* Uvaferm GHM®; *O. oeni* R1105, R1124; | For each LAB strain:<br>1. LAB inoculation 24 h after yeast inoculation<br>2. LAB inoculation at 40% of AF<br>3. LAB inoculation at 60% of AF<br>4. LAB inoculation after AF completion | Simultaneous AF and MLF had no negative impact on fermentation and the final wine volatile aroma composition. Modified concentration of specific alcohols, acids, ethyl, and acetate esters in simultaneous compared to sequential fermentation, for each strain, were observed. Both LAB strains resulted in higher butyric acid ethyl ester and lower acetic acid ethyl ester and propionic acid ethyl ester concentration upon co-inoculation (regime 1) compared to sequential fermentation. | [168] |

**Table 1.** *Cont.*

| Cultivar | Yeasts/LAB | Inoculation Strategy | Comment | Reference |
|---|---|---|---|---|
| Shiraz | *S. cerevisiae* AAV2, ITB, 101; *Lp. plantarum* Lp 1; *O. oeni* Oo 1 | for each yeast and LAB strain:<br>1. AF without MLF by each yeast strain<br>2. Co-inoculation of both LAB strains with each yeast strain<br>3. Inoculation of both LAB after AF conducted by each yeast strain | Volatile and polyphenolic wine composition depended upon yeast strain and MLF strategy. In all cases, co-inoculation resulted in the increase of p-hydroxybenzoic acid, vanillic acid, coutaric acid, quercetin-3-glu, quercetin-3-gal, myricetin, 2,3 butanediol, syringol, ethyl lactate, 2-phenylehtyl acetate, ethyl butanoate, ethyl decanoate, ethyl hexanoate, isoamyl acetate, citronellol, and butyrolactone, and the decrease of gallic acid, fertaric acid, epicatechic, 2-phenylethanol, propanol, and propanoic acid concentration. Co-inoculation resulted in more fruity, floral, nutty, and smoky odors, compared to sequential inoculation | [169] |
| Shiraz | *S. cerevisiae* AWRI 1490; *O. oeni* Viniflora oenos™ | 1. no MLF<br>2. LAB inoculated 24 h after yeast<br>3. LAB inoculated 4 d after yeast<br>4. LAB inoculated 7 days after yeast<br>5. LAB inoculated 10 days after yeast (post AF) | Strategy 2 resulted in better LAB development, faster degradation of L-malic acid and reduction of total vinification time. Time of inoculation had no effect on ethanol, acetic acid, citric acid, lactic acid, and glycerol content. Succinic acid production was reduced in strategy 2. Changes in specific acetate and ethyl esters and higher alcohols according to time of inoculation were noted. Color density was decreased compared to no MLF but no significant differences were observed at the time of inoculation. | [170] |
| Tannat | *S. cerevisiae* LD80, FUY4; *O. oeni* VP41 | For each yeast strain<br>1. LAB inoculation after AF<br>2. simultaneous inoculation of LAB<br>3. LAB inoculation 3 d after yeast inoculation | Inoculation timing had strain specific effect on both yeast and LAB development. Inoculation timing had no effect on ethanol content but strain-specific effect on organic acid content and volatile acidity. | [171] |
| Tempranillo | *S. cerevisiae* Viacell C-58® *O. oeni* PN4™, Omega™ | 1. each LAB inoculated 24 h after yeast<br>2. spontaneous MLF | No differences in alcoholic strength, total acidity, glycerol content, color intensity, or tone between inoculated and spontaneous fermentations. In general, wines with inoculated MLF presented with higher ethyl acetate, 1-hexanol, acetaldehyde, and guaiacol concentration and lower valeric acid, isovaleric acid, 2,3 butanodiote and eugenol, compared to spontaneous MLF. Inoculated wines reached more fruity and floral flavors; spontaneous ones had stronger astringency and milky, raisin flavors. | [172] |
| Tempranillo; Merlot | *S. cerevisiae* VRB, VN; *O. oeni* C22L9 | For each yeast strain<br>1. LAB inoculation after AF<br>2. LAB inoculation 24 h after yeast inoculation | Inoculation time had no effect on yeast growth and ethanol production. Different L-malic acid degradation kinetics between cultivars. Volatile acidity, as well as the concentration of specific alcohols, acids, aldehydes, ketones, esters, furans, terpenes, volatile phenols, vanillate derivates, and norisoprenoids were affected by yeast strain, cultivar, and MLF regime. In all cases, co-inoculation resulted in increased isobutanol, c-3-hexen-1-ol, ethyl lactate, diethyl succinate, citronellol, and zingerone, and decreased 3-methyl-thio-propanol, 3-ethyl-thio-propanol, furfuryl alcohol, 3-hydroxy-2-butanone, 3-hydroxy-2-pentanone, benzyl acetate, and linalool concentration. Slight differences in the organoleptic properties were assigned to inoculation timing. | [173] |
| Teran | *S. cerevisiae* Uvaferm 299; *O. oeni* Uvaferm Alpha, Lalvin 31 | 1. no MLF<br>2. spontaneous MLF<br>3. co-inoculation of the yeast with each LAB<br>4. sequential inoculation of each LAB after AF | Co-inoculation had no effect on alcoholic fermentation kinetics. Inoculation timing had no effect on volatile acidity. Timing and LAB strain affected volatile compounds concentration. In all cases, increased diethyl succinate, ethyl lactate, and 2,3-butanediol, and decreased ethyl acetate and isoamyl acetate concentration was observed in co-inoculation compared to sequential fermentation. | [174] |

*K.: Kloeckera; Lp.: Lactiplantibacillus; Lv.: Levilactobacillus; O.: Oenococus; P.: Pichia; S.: Saccharomyces; T.: Torulaspora*; AF: alcoholic fermentation; MLF: malolactic fermentation.

## 6. Conclusions

MLF is gaining more and more attention from the wine industry, confirming the fact that it is much more than a deacidification process. The metabolic potential of LAB is complex and continuous efforts are being made to elucidate it. As already discussed, through the activation of various metabolic pathways, LAB significantly influence the organoleptic profile of wine, contributing to the enhancement of aroma and flavor complexity and at the same time impart microbiological stability. However, the same bacteria could produce volatile phenols, which negatively affect wine aromas or biogenic amines, which represent a risk to consumer health. This uncertainty can be controlled with proper malolactic fermentation management. The right inoculation moment as well as the selection of the appropriate strain, are critical points for a successful completion of MLF, leading to wines with desired characteristics. In the future, it will be important to investigate the genomic diversity of LAB, as the basis of their promising metabolic characteristics. New strains, ideal for a region's unique climate, red versus white wines, or even grape variety, deserve to be thoroughly explored. Different genera as well as mixture of species/strains could be considered for future application as malolactic starters.

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