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Review

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Relationship between lactic acid bacteria, malolactic fermentation, and wine color

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ABSTRACT

Malolactic fermentation (MLF) is a complex process that involves many reactions in addition to the decarboxylation of L-malic acid into L-lactic acid. But the complexity of MLF is far from being completely elucidated. One of the most confusing aspects is connected to the relationship among MLF, lactic acid bacteria (LAB), wine color, and phenolic composition. For instance, evidence suggests that LAB activity is inhibited by some phenolic acids but activated by others. Also, it is not clear if the phenolic composition and wine color are affected by MLF. This review summarizes current knowledge about these topics hoping to establish a guide for further research.

KEYWORDS

Malolactic fermentation; Wine color; *Oenococcus oeni*; *Lactobacillus plantarum*; Phenols; Tannins; Polyphenols.

INTRODUCTION

Malolactic fermentation (MLF) is a microbiological process carried out by lactic acid bacteria (LAB) in most red wines and some white and base sparkling wines[1,2]. The main changes produced by MLF are i) the deacidification of wine due to the decarboxylation of L-malic acid into the softer L-lactic acid; ii) the improvement of wine aroma by the production of secondary metabolites, and iii) the improvement of microbiological stability due to the consumption of the remaining carbon and energy sources.

During the last few decades, MLF has been widely studied not only to improve the development of LAB during winemaking for a better performance of MLF but also because it seems that LAB metabolism is much more complex than previously thought. MLF affects the aroma profile[3,4] and color parameters as reported by several authors[5-10].

Wine color is the first attribute that reaches our senses when it is served into a glass. This attribute can influence both wine experts and novice wine judges perception[11]. Wine color and clarity are common indicators of wine style, origin, grape variety and maturity, and winemaking technique. With the color in mind, winetasters can correlate the aroma and taste of wine or at least the

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expected attributes.

Phenolic compounds are the molecules responsible for color, bitterness, and astringency as well as aroma and flavor[12]. They are extracted from grapes during the winemaking process and the quantity present in wine depends on the grape variety, the environmental and cultural conditions, grape maturity, and winemaking techniques such as maceration[13].

Phenolic compounds comprehend a complex group that can be divided into several groups and subgroups (TABLE 1). The non-flavonoids include the phenolic acids that can be divided into benzoic acids, cinnamic acids, and other phenolic derivatives such as stilbenes[14]. The flavonoids include anthocyanins and flavan-3-ols. Flavonoids are responsible for red wine color and are located in grape skins. Flavan-3-ols are present as monomers, oligomers and polymers, called condensed tannins or proanthocyanins which are responsible for wine astringency (tactile sensation), bitterness (taste), and long-term color stability[12,15].

The relationship between MLF and phenolic compounds is somewhat confusing. As commented above, some authors have shown that MLF can affect some wine color parameters[5-10]. Other studies show that LAB activity is inhibited by some phenolic compounds[1,16] but activated by others[1,17]. Also, some winemakers seem to agree that MLF affects wine color and astringency but most of these affirmations are based on the winemakers experience than on scientific evidence[18]. In order to group all these results and aiming to establish a guide for further research in this field, this review summarizes the different results that correlate phenolic compounds with LAB metabolism and MLF.

INHIBITION OR STIMULATION OF LAB AND MLF BY PHENOLIC ACIDS AND FLAVONOIDS

It is known that the low pH in wine as well as the high ethanol content and the presence of SO_2, medium-chain fatty acids, nutrient limitation, and another potential yet still unknown factors, may inhibit LAB development and MLF[20-23]. It was also suggested that the rate of MLF does not always correspond to the rate of LAB growth or survival of the species conducting MLF[10,20]. The malic enzyme might be inhibited by some repressors and become active once those substances are removed from wine[20].

Some authors investigated the inhibitory effect of phenolic acid with the aim to avoid the development of LAB that sometimes can lead to the alteration of wine such as the "lactic disease" and the production of off-flavors[16,21,24,25]. In this sense, some phenolic acids such as caffeic, coumaric, and ferulic acids can inhibit the growth of some strains of *Lactobacillus collinoides* at concentrations higher than 500 mg/L whereas a concentration of 100 mg/L has been reported to stimulate the growth of *Lb. collinoides* strains and *Lb. brevis*[16].

Other LAB species that have been investigated in relation to phenolic inhibition (or activation) are *Pediococcus pentosaceus*, *Lactobacillus hilgardii*, *Lactobacillus plantarum*, and *Oenococcus oeni*. The last two being the most desired to carry out MLF when needed[26-28]. But the information about the relationship between phenolic compounds and *Lb. plantarum* is still confusing and more research is needed[10,29].

In the beginning, the most studied phenolic compounds were the hydroxycinnamic and hydroxybenzoic acids (TABLE 1). For instance, among the hydroxybenzoic acids, gallic acid was found to activate *O. oeni* (*Leuconostoc oenos* IB8413) cell growth and to stimulate MLF at 100 mg/L[1] and no inhibition was detected at concentrations bellow 1000 mg/L on *O. oeni* strain CECT 4100[17] or *O. oeni* IFI-CA 91 and IFI-CA 96[25]. No inhibition by gallic acid was detected on *Lb. hilgardii* strain 5 growth at 500 mg/L[30] or *Lb. hilgardii* IFI-CA 49 and *P. pentosaceus* IFI-CA 85[25]. But, gallic acid did exhibit a slight inhibition on *O. oeni* VF at the concentrations 100, 200, and 500 mg/L[30]. Apparently, the effect of gallic acid depends on the LAB species and strains or maybe on the growing conditions.

Other hydroxybenzoic acids have been investigated and 100 mg/L vanillic acid had a slight inhibiting effect on *O. oeni* cell growth[1]. The inhibition by vanillic acid was also observed in *O. oeni* VF at 100, 200, and 500 mg/L as well as the inhibition by syringic acid at the same concentrations[30]. The commercial strain *O. oeni* VF was also inhibited by the hydroxybenzoic protocatechuic and p-hydroxybenzoic acids at 100, 200, and 500 mg/L[30]. Vanillic, syringic, and *p*-hydroxybenzoic acids also caused a decrease in the growth rate of *Lb. hilgardii* strain 5 only at 500 mg/L but not at 100 and 200 mg/L[30]. When investigating four strains of *Lb. platarum*, there was found that gallic acid and its ester methyl gallate had the minimum inhibitory concentrations at 1900 mg/L

TABLE 1: Classification of non-volatile phenolic composition of grapes and wines[12,15,18].

Group	Subgroup	Compounds	Notes
Phenolic acids	Hydroxybenzoic acids (7C)	*p*-hydroxybenzoic acid protocatechuic acid vanillic acid gallic acid syringic acid	Gallic acid is the precursor of all hydrolysable tannins and is part of condensed tannins.
	Hydroxycinnamic acids (9C).	*p*-coumaric acid caffeic acid ferulic acid sinapic acid	Associated with wine browning and as precursors of volatile phenolic compounds.
Flavonoids (15C)	Flavones		These compounds are not present in significant amount in grapes.
	Flavanones		
	Flavonols	kaempferol quercetol myricetol isorhamneto	In grapes they are often glycosylated forming quercetin, myricetin, etc.
	Flavononols	Taxifolin	Also known as dihydroquercetin.
	Flavanes	The flavane nucleus forms the common basic structure for many molecules, namely flavanols	
	Flavanols	(+)-catechin (-)epicatechin (+)-gallocatechin (-)-epigallocatechin (-)-epicatechin-3-O-gallate	Monomers such as (+)-catechin and (-)-epicatechin, also known as flavan-3-ols, can polymerize into oligomers and polymers forming proanthocyanins.
	Chalcones and dihydochalcones	Chalcone derivatives are intermediates and precursors for flavonoid derivatives found in grapes orwine. They are formed during wine aging by under anaerobic conditions moving the anthocyaninequilibria toward the chalcone forms and thus, changing the colorand astringency degree of thefinal product	
	Anthocyanic pigments	cyanidin (orange red) peonidin (red) delphinidin (bluishred) pelargonidin (orange) petunidin and malvidin (bluish red)	Anthocyanic pigments are responsible for the color of grapes andwine, in part determined by their chemical structure such as their degree of hydroxylation, methylation and/or glycosylation.
Tannins	Hydrolysable tannins	Polymers of sugars and phenolic acids. The basic units are gallic and hexahydroxydiphenic acids, and their derivatives, such as ellagic acid. These acids are usually esterified with D-glucose. Aging in oak barrels promotes the extraction of low molecular weight phenolic compounds into wine. Ellagic acid is a characteristic compound formed upon barrel wine aging.	
	Condensed tannins (proanthocyanidins)	These are predominantly in grapes and wines. These polymeric compoundsthat give rise to anthocyanidins. The procyanidins and prodelphinidins, which hydrolyze to cyanidin and delphinidin, are themost abundant condensed tannins in grapes and wine.	
Stilbenes		Resveratrol Piceid piceatannol glucoside (astringin) pterostilbene pallidol	Phenolic compounds comprising two aromatic rings. Resveratrol is the stilbene most referenced as present in grapes and wine.
Coumarins		Lactones obtained by cyclisation of the *cis*-2-hydroxycinnamic acid and its derivatives.	

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for gallate and 9000 to 18000 mg/L for methyl gallate[31]. In the case of hydroxybenzoic acids, all studies point at the inhibition of LAB growth or survival.

When investigating the hydroxycinnamic acids, 1000 mg/L of caffeic, ferulic, and *p*-coumaric acids had an inhibitory effect on the growth and MLF performance of *O. oeni* strain CECT 4100, whereas 25 or 100 mg/L did not affect the increase in the population with the exception of 100 mg/L of *p*-coumaric acid. Malic acid consumption was inhibited in cases where growth was affected[17]. These same acids inhibited the growth of the *O. oeni* VF strain at the concentrations of 100, 200, and 500 mg/L[30], but had a little or no effect on *O. oeni* IFI-CA 17, *O. oeni* IFI-CA 88, *O. oeni* IFI-CA 91, *O. oeni* IFI-CA 96, *P. pentosaceus* IFI-CA 85, and *Lb. hilgardii* IFI-CA 49 considering the high inhibitory concentrations found in the study[20]. A different result was obtained using *Lb. hilgardii* strain 5 where concentrations up to 200 mg/L of hydroxycinnamic acids increased cell concentrations despite the decrease in growth rate[30]. Analyzing the influence of hydroxycinnamic acids, another study found that the concentrations able to inhibit the *Lb. plantarum* growth were 2000 to 4000 mg/L for *p*-coumaric, 9000 to 18000 mg/L for caffeic acid, and 5000 to 10000 mg/L for ferulic acid. A much higher concentration compared to other studies[31]. In this case, it seems that all these acids, their chemical structure, their concentration, and LAB species and strains are differentially affected.

Regarding flavonols, quercetin showed a stimulating effect up to 1000 mg/L for both population growth and MLF performance of *O. oeni* CECT 4100[17]. A different result was obtained with quercetin and kaempferol which presented a dose-dependent inhibitory effect on the growth of *O. oeni* VF at the concentrations of 10, 20, 40 mg/L whereas myricetin had no noticeable effect on the growth of this strain. *Lb. hilgardii 5* growth was diminished by 40 mg/L of quercetin and kaempferol[29]. Again, different results were found by different authors pointing out the differences in the concentration of the compounds and on the strains used in each work.

Little information was found on the effect of flavanols on LAB. Catechin showed a stimulating effect at 25 mg/L on *O. oeni* CECT 4100, for population growth and MLF performance[17]. But catechin (12.5, 25, and 50 mg/L) and epicatechin (3.12, 6.25, and 12.5 mg/L) exhibited no significant difference in the growth of *O. oeni* VF nor in *Lb. hilgardii 5*[29]. The inhibitory activity on *Lb. plantarum* was found to be 2900 mg/L for catechin and ranging from 1400 to 2900 mg/L for epicatechin[31].

Free anthocyanins were shown to activate *O. oeni* cell growth and stimulated MLF at concentrations of 200 mg/L[1].

Phenolic aldehydes, sinapaldehyde, coniferaldehyde, *p*-hydroxybenzaldehyde, 3,4-dihydroxybenzaldehyde, and 3,4,5-trihydroxybenzaldehyde were shown to inhibit the growth of *O. oeni* VF at the concentrations of 250-500 mg/L, which are believed to be much higher than the ones found in wines (1-2 mg/L)[29]. The phenolic aldehydes sinapaldehyde and coniferaldehyde also affected the growth of *Lb. hilgardii* 5 especially at the concentration of 500 mg/L.

Bigger phenolic compounds such as grape and oak tannins can affect LAB and MLF. Procyanidins mixed with the seed extract or used pure as a dimer procyanidin acted as inhibitors adversely affecting the viability of *O. oeni*. Total wood extract proved to be toxic whereas pure ellagitannins improved the overall viability of the bacterial population[35]. Condensed tannins were further investigated and proved a marked decrease in the number of viable cells of *O. oeni* VF and *Lb. hilgardii* 5 but with a milder effect[29]. A recent experiment found different results using commercial tannins for winemaking[32]. Two commercial strains of *O. oeni* increased their biomass and MLF performance after the addition of 500 mg/L of tannins in the culture media and in white wine. These authors correlated the variability in growth and MLF performance caused by the addition of different tannin molecules with the redox potential of the medium[32].

As mentioned above, phenolic compounds seem to have a different effect on LAB development and MLF performance depending on the type of molecule (chemical structure) and its concentration but also on the LAB species and strain[17,24,30,32].

Regarding the mechanism involved in LAB inhibition or activation, several hypotheses are being investigated. Viability inhibition may be due to the alteration of the membrane structure producing leakage of cell constituents[25,33], the change in the fatty acid composition of the cell membrane[34], or the hydrogen bonding of Gram-positive bacteria polysaccharides with oligomeric tannins causing the inhibition of vital proteins[34,35].

It is worth mentioning that most studies involving the interaction of phenolic compounds and LAB viability have been carried out using buffers and culture media with

different formulations, specific phenolic compounds, ethanol concentration, and temperature of incubation. In fact, most studies have used higher concentrations of phenolic acids than those found in wines[24,31,36]. To study these interactions in real conditions is a challenge[32]. Also, only a few studies included the consumption of malic acid which may be influenced in different ways independently of growth inhibition or stimulation as also proposed by Figueiredo and co-workers[29]. Is not the same to inoculate laboratory strains accustomed to culture media that the study of wine populations in their natural environment. In this sense, a recent study proved that some strains of *O. oeni* have different phenotypes in grape must and in wines that could indicate their level of adaptability to either red or white wine[38]. As mentioned in previous work, the simultaneous presence of activating and toxic molecules may establish an equilibrium that becomes more propitious to the growth of LAB at a given moment[35].

INFLUENCE OF LAB ON WINE FLAVOR

Another concern is the development of off-flavors due to the metabolism of some phenolic compounds by LAB. It is now known that during MLF, LAB can produce or release different compounds that have either a positive or a negative effect on the wine sensory profile[22].

Some of the studies where phenolic acids inhibition or activation was reported, also found that some of these compounds were being metabolized by some of the LAB species or strains they used. For instance, it was reported that when glucose was present, *O. oeni* could degrade gallate[1]. Also, there is some evidence that *O. oeni* and *Lb. sp*. could convert ferulic acid into vanillin (a hydroxycinnamic acid)[37]. Recent work has demonstrated the decarboxylation of gallic acid by *Lb. plantarum* strain Lp2565 and *O. oeni* strain Oo2219 with the production of *p*-hydroxybenzoic acid, *p*-hydroxybenzyl alcohol leading to a slightly fruity-sweet coconut odor[38], *p*-hydroxybenzaldehyde with vanillic/nutty odor[38], catechol and protocatechuic acid[33].

Some of the volatile phenolic compounds such ethylphenols have been described as responsible for the 'phenolic', animal', and 'stable' off-odors found in certain red wines[39]. This is a controversial subject since MLF keep occurring around the world and these off-flavors seem not to appear as often as it would be expected. In fact, at low concentrations, some of the volatile phenolic compounds may bring some complexity to the wine flavor.

Regarding hydroxycinnamic acids and their derivatives, these are believed to be the main compounds modified by MLF[40], though some authors did not find the consumption of these molecules[17] others found that *O. oeni* IŒB 8413 reduced vanillin to the corresponding vanillyl alcohol (with a mild, sweet, balsamic, vanilla-like odor)[37,38]. The production of vanillin (sweet, creamy, vanilla odor)[38], was also exhibited by *O. oeni* strain Oo2219[33]. Reguant et al.[17] also found out that a strain of *Lb. plantarum* was able to metabolize *p*-coumaric acid, as well as it was previously reported using different strains of *Lb. brevis*, *Lb. plantarum*, and *Pediococcus sp.*[41]. These authors argued that when decarboxylation was observed, volatile phenols 4-ethylguaiacol (sweet, spicy, medicinal odor) and 4-ethylphenol (woody phenolic, medicinal, yet rather sweet odor)[38], where detected. Apparently, all these enzymatic activities seem to be subjected to several factors, the most obvious being the LAB species and strains but also to the growing conditions, the genetic background and the composition of wine as well as yeast/LAB interactions[42-44]. A different study comparing the interaction of *O. oeni* with oak wood compounds showed that this LAB was able to interact with wood and form volatile compounds (woody, spicy, smoky, and vanillin) that play an important role in wine flavor[45]. Undoubtedly, this subject requires further investigation.

Anthocyanins were too metabolized by *O. oeni*, especially at the beginning of the growing phase, the same phase that was stimulated by these compounds[1]. These authors suggested that the glucose moiety of the anthocyanins was used as an energy source thanks to the β-glycosidase activity of *O. oeni*. Different strains of *O. oeni* exhibit β-glycosidase activity depending on the culture condition such as pH, ethanol, sugar concentration, and the growth phase[46,47].

Capello and co-workers[48] discuss this subject in detail allowing a better understanding of the metabolic mechanisms of LAB involved in the formation of potent flavor-active compounds in wine.

INFLUENCE OF LAB ON WINE COLOR

As mentioned above, MLF is usually desired, particularly in red wines but it is suspected that this process reduces wine color. As the concentration of

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phenolic compounds is conditioned by several factors such as grape variety, insolation, temperature, vine treatment, time of harvest, and enological practices[49], the winemakers could somehow compensate for the loss of color, with specific techniques.

When it comes to wine color, especially red wine, much work has been done but not as much when it comes to the relationship with MLF. It is of general acceptance that MLF reduces wine color[8,50], but why?

The main responsibles of young red wine color are the anthocyanins, flavanols, and their association, also affected by the wine pH[15,18].

As the wine ages its color also changes due to the degradation of anthocyanins, their combination forming polymers, or their transformation into new pigments such as vitisins (anthocyanin-pyruvic acid products and anthocyanin-acetaldehyde derivatives)[12].

It has been reported that MLF slightly reduces wine color in Shiraz wine[7]. Differences in anthocyanin and pigmented polymer composition were found depending on the inoculation regime (co-inoculation of yeast and *O. oeni*). As pointed out in a study using Chancellor wines, most differences in wine constitution result from the interactions between MLF culture, yeast strain, and fermentation temperature[51]. Surprisingly, these authors found that one culture of *O. oeni* enhanced color intensity and redness.

When studying MLF occurring in Cabernet Sauvignon wine, each bacterial strain was associated with different polymeric pigment content and concentration of total anthocyanins suggesting that the metabolic activities of each strain may affect red wine color composition depending on the wine matrix[52]. Using Pinor noir wine, it was suggested that by delaying MLF for up to three months the loss of polymeric pigment due to MLF was minimized[53]. Also, these authors demonstrated that adsorption of anthocyanins by MLF bacteria cell walls was minimal and had no impact on wine color as it was suggested by previous work[54] and that the decrease in color and polymeric pigments were not related to the pH changes caused by MLF[8], as commented above.

Some studies performed the MLF in different containers such as stainless steel and barrels in order to determine if MLF in different conditions could modify the final sensory profile of red wines. Apparently, the chemical and sensory attributes of red wines may be modified using oak wood during the MLF and by the toasting applied to the wood[55]. MLF-container seemed to modify (among others), anthocyanin polymerization reactions.

These studies considering the color of wine after MLF show some differences in anthocyanin concentration. But there is one study where the anthocyanin profile of the Sangiovese wines was maintained after malolactic fermentation[56]. Perhaps this phenomenon has a relationship with the recent report showing that some strains are better adapted to white wines while other strains seem to prefer red wines[57]

Recent work has proposed that *Lb. plantarum* facilitates the formation of acetaldehyde during MLF which favors the accumulation of pyranoanthocyanins in wine in comparison to the MLF carried out by *O. oeni*[58]. It has been proposed that *Lb. plantarum* strains display a more diverse enzyme profile than *O. oeni* strains[59]. But others believe that the competitive advantage of morphological as well as cellular fatty acid changes in *O. oeni* over *Lb. plantarum* provided additional support for the dominance of *O. oeni* during MLF[33]. This aspect is still being studied and there is yet no absolute answer[4].

Pinot noir and Merlot wines were analyzed in terms of color and LAB responsible for MLF. These authors showed that different strains of *O. oeni* and *Lb. plantarum* behave differently depending on wine variety, and that successful MLF modifies wine color but no other clear correlation could be found[10].

When looking closer at the different results in all the mentioned research, some differences can be found among them regarding the metabolism of each LAB. Some experiments lead to an increase of free anthocyanins, polymerization and copigmentation, a variable amount of flavanols, hydroxycinnamic acids, and so on. The increase in the concentration of free anthocyanins found after MLF could explain the reduction in the concentration of polymeric pigments. This could be related to the degradation of acetaldehyde by LAB which is suspected to allow the formation of polymeric pigments[53]. But it must be considered as well that when MLF occurs in barrels the micro-oxigenation favors the polymerization reactions among anthocyanins. In these conditions, it is thought that acetaldehyde is generated, and it is available to act as a link for the formation of polymeric compounds, achieving the stabilization of color and the diminution of astringency[55].

Finally, we are aware that there were recent changes in the taxonomy of the genus Lactobacillus[59], but we

decided to use the previous names as they appear in the literature for a better understanding.

CONCLUSIONS

Now more than ever is clear that MLF is a complex process that involves uncountable transformations in wine. We are discovering new molecules as the result of LAB metabolism that changes wine flavor, mainly in a positive way. However, due to the challenge that brings to study its metabolism in real conditions, most results should be taken accordingly. We have summarized most of the results that link MLF and wine color change. But there is still much to consider. Not only about LAB species and strains but also, i) interaction with yeast metabolic residues, ii) vine variety and its unique phenolic composition, iii) enological practices including the fermentation temperature, the time of the year when MLF is carried out, the container used for the MLF process, and the following up after the MLF. Continued research about these subjects can help at developing strategies to minimize the possible problems that may arise when carrying out the MLF and even improve the techniques currently used by winemakers.

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