

A review on the effects of different microbial strains fermentation and synergistic interactions on polyphenols during winemaking

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Abstract Polyphenols are key components in wine that contribute to its color, mouthfeel, antioxidant properties, and health benefits. Traditionally, the extraction and bioconversion of polyphenols depend on alcoholic fermentation mediated by *Saccharomyces cerevisiae*. This review summarizes recent study on non-*Saccharomyces* yeasts, lactic acid bacteria, and their synergistic interactions that significantly modulate the composition, stability, and bioactivity of polyphenols. These microorganisms regulate the extraction, transformation, and stabilization of polyphenols through enzymatic reactions and interspecific interactions. Modern winemaking techniques, such as sequential inoculation, co-fermentation, and microbial immobilization, allow targeted control over the composition and concentration of polyphenols in wine. Potential future research should systematically elucidate polyphenol–microbe interaction mechanisms. In addition, functional microbial strains will be developed to enhance wine quality and health-promoting attributes. Progress in these areas will further promote the winemaking industry toward precision and functionalization.

Keywords: polyphenols; microbial fermentation; microbial regulation

1 Introduction

Polyphenols are core components in wine that determine its sensory characteristics, quality stability, and health benefits. These compounds mainly include anthocyanins, flavonoids, phenolic acids and tannins ^[1-2]. Polyphenols contribute to wine color, astringency, and antioxidant capacity. During aging, they present evidential alterations that directly influence terroir expression and long-term stability. Polyphenol composition of wine is determined by grape variety, vineyard environment, and physicochemical treatments during winemaking. In addition, recent

studies show that diverse microbial strains and their synergistic interactions have a profound influence on polyphenol metabolism of polyphenols ^[3].

The essence of winemaking lies not merely in alcoholic conversion of grape juice, but in a dynamic biochemical process governed by a complex microbial community ^[4-5]. This process originates from the micro-ecosystem on grape skin, progresses through dynamic transformations in the fermentation tank, and continues throughout extended bottle aging. During this process, *Saccharomyces cerevisiae* converts sugars into alcohol and carbon dioxide, yielding substances that affect the basic flavor of wine ^[6-7] (Fig. 1). Fig. 1 illustrates the complete winemaking process of *Vitis vinifera*. Grapes undergo crushing, destemming, and pressing to release juice, followed by yeast-driven alcoholic fermentation that converts sugars into

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These authors have no conflict of interest to declare.

ethanol and CO₂. The wine is then separated from residual solids and aged in oak barrels to enhance flavor. Key details of fermentation involve yeast activation, sugar metabolism, and the characteristic temperature profile. However, non-*Saccharomyces* yeasts including *Candida*, *Hanseniaspora*, *Kluyveromyces* [8-10] play an indispensable role in the early stages of fermentation. These microorganisms release bound aroma compounds and synthesize diverse metabolites via multifarious enzyme systems, contributing distinctive nuances to the flavor of wine. Following alcoholic fermentation, lactic acid bacteria (LAB) conduct malolactic fermentation, wherein malic acid is decarboxylated to lactic acid. This process enhances mouthfeel and microbial stability, while generating secondary aromas of buttery and nutty notes [11,12]. In addition, other microorganisms such as acetic acid bacteria, *Brettanomyces*, and even certain specific molds including *Botrytis cinerea*, exert

unique functions under particular conditions [13-15]. In addition, microorganisms such as acetic acid bacteria, *Brettanomyces*, and *Botrytis cinerea* exert specific functions under certain conditions [13-15]. Acetic acid bacteria impart sourness and flavor complexity; appropriate levels of *Brettanomyces* enhance flavor, whereas excess causes spoilage; *Botrytis cinerea* dehydrates and concentrates grape sugars and acids, producing aromatic compounds for noble rot sweet wines. There is a delicate balance between synergy and competitive interactions exists among these microorganisms. They may compete for limited nutrients of sugars and nitrogen sources. They can also inhibit or promote each other through metabolic byproducts, collectively shaping the chemical and sensory profile of the final product. Fig. 2 shows key microbes in winemaking and their impacts on wine quality. Yeasts shape fragrance, bacteria affect taste, and molds can create unique flavors or spoil the wine.

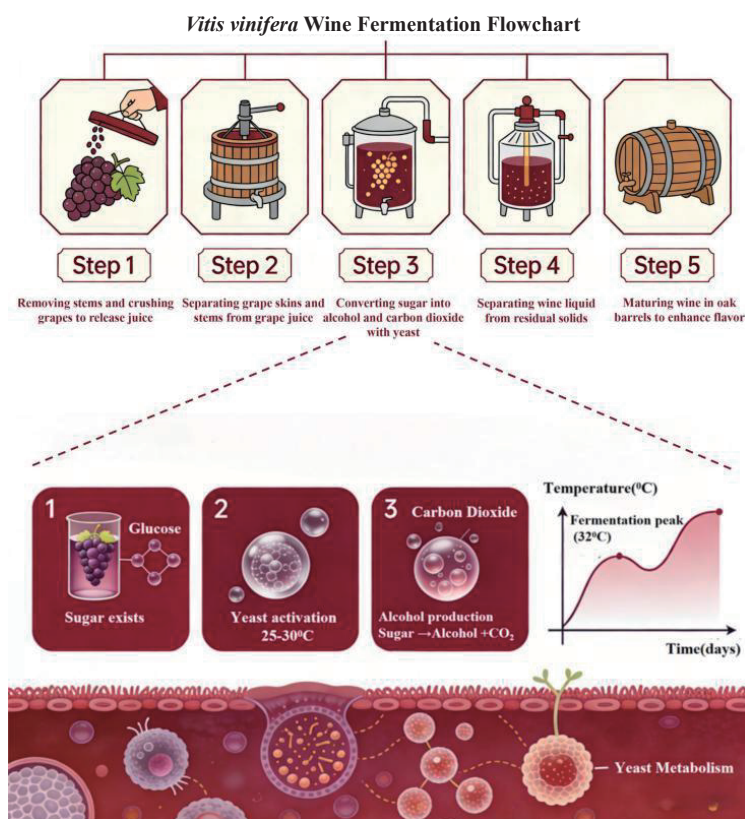


Fig. 1 Winemaking fermentation process and mechanisms

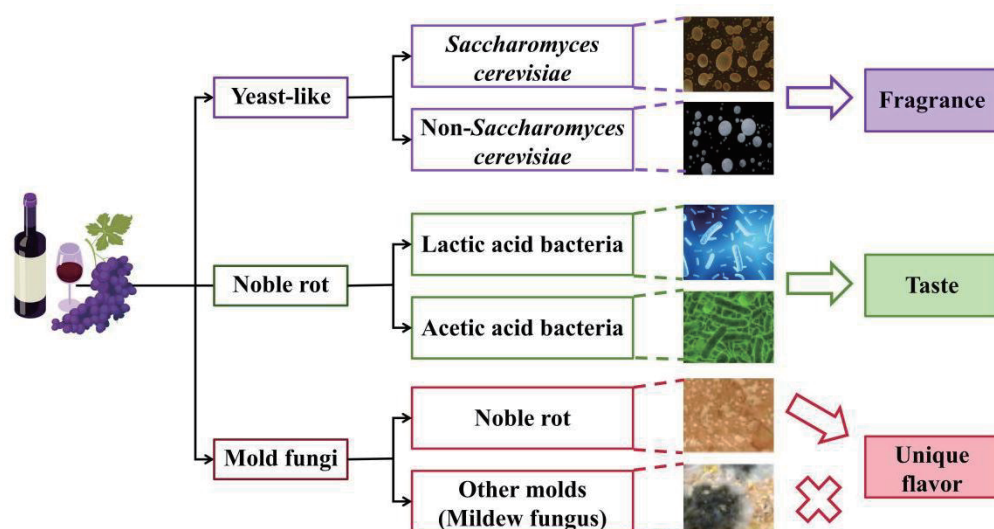


Fig. 2 Impact of different microbial strains fermentation on the quality of polyphenols in wine

Nutrient competition, metabolic inhibition, quorum sensing, and physical interactions among microorganisms establish dynamic microbial-polyphenol networks. These networks modulate polyphenol composition during fermentation and further influence the appearance and quality of *Vitis vinifera* wine during aging. The elucidation of mechanisms underlying polyphenol formation from microbial ecology and metabolic regulation has thus emerged as a frontier area in enology.

Despite extensive study of single-species strain impacts on polyphenols, the detailed reaction mechanisms of polyphenols under multi-species co-fermentation remain to be systematically clarified. A key challenge lies in integrating microbial regulatory strategies into fermentation design. This integration is essential for achieving precise control over polyphenol composition, stability, and functionality, thereby enhancing the quality and value of *Vitis vinifera* wines. This review synthesizes current insight on microbial fermentation mechanisms and their synergistic effects on wine polyphenols. It further discusses future strategies for microbial engineering-based polyphenol regulation to advance innovative winemaking practices.

2 Mechanisms of different microbial strains affecting wine polyphenols

The transformation of polyphenolic compounds in wine during fermentation is a complex biochemical process orchestrated by microbial activities. Microorganisms, via their specific metabolic routes and enzyme systems, exert profound effects on polyphenol composition in wine. By mediating the processes of extraction, transformation, modification, and degradation, they significantly influence the final sensory and functional characteristics of the product.

2.1 Yeast fermentation

2.1.1 Mechanisms influencing wine polyphenols

Saccharomyces. cerevisiae is the core microorganism in alcoholic fermentation. Its impacts on wine polyphenols are illustrated in Fig. 3. During fermentation, polyphenol extraction, conversion, stability and sensory properties release, transformation, stabilization, organoleptic traits are coordinately modulated. Carbon dioxide and ethanol disrupt grape skins and seeds to release bound polyphenols and improve phenolic solubility^[16], while

increased temperature accelerates diffusion of carbon dioxide and ethanol (Fig. 3, red arrows).

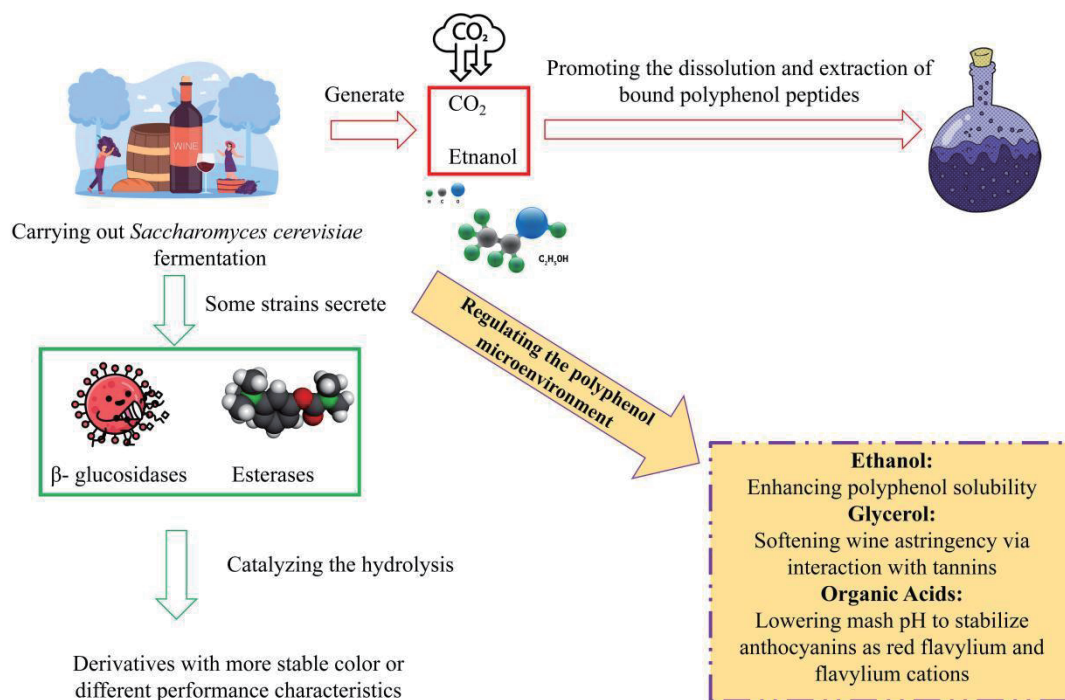


Fig. 3 Mechanisms of yeast fermentation on polyphenols during winemaking

2.1.2 Yeast enzyme-mediated polyphenol transformation

Certain strains of *Saccharomyces cerevisiae* secrete active β -glucosidases and cinnamoyl esterases that hydrolyze glycosidic or acyl bonds on anthocyanins and other phenolic compounds (green arrow, Fig. 3). Such enzymatic deglycosylation produces unstable aglycones, which can spontaneously convert into more stable color or modified astringency profiles. For instance, hydrolysis of *p*-coumaroyl or caffeoyl esters liberates free hydroxycinnamic acids, which further participate in pigmentation or oxidative browning reactions [17].

2.1.3 Yeast metabolite-mediated modulation of the polyphenol microenvironment

Primary and secondary metabolites of yeast are crucial in modulating the polyphenol microenvironment. Ethanol increases the solubility of polyphenols, whereas high ethanol concentration

trigger a salting-out effect on these compounds polyphenols [18]. The delicate balance between these two opposing actions dictates the overall extraction efficiency. As a major fermentation byproduct, glycerol forms hydrogen bonds with tannins, thereby hindering their interaction with salivary proteins and reducing astringency [19]. Organic acids like succinate, pyruvate and α -ketoglutarate contribute to pH reduction. This shifts the equilibrium of anthocyanins toward colored flavylium cation rather than colorless hemiketal form, thereby enhancing color intensity and stability [20]. Furthermore, pyruvate and acetaldehyde can directly condense with anthocyanins. This reaction yields stable vinylphenol adducts and pyranoanthocyanins resistant to sulfite fading.

2.1.4 Protective and stabilizing roles of yeast autolysis

After fermentation, yeast autolysis releases intracellular components that protect polyphenols and

enhance wine stability through two main mechanisms:

(1) Antioxidant release: Glutathione and other thiol-containing compounds act as reactive oxygen species scavengers. By neutralizing reactive oxygen species, these molecules prevent the oxidative degradation of anthocyanins and flavonols. This protective effect is critical for delaying wine browning and preserving the red hue.

(2) Mannoprotein secretion: Mannoproteins derived from the yeast cell wall form stable colloidal complexes with phenolic compounds [21]. These complexes inhibit the aggregation and precipitation of tannins and pigmented polymers, maintaining color density and reducing haze. Additionally, mannoproteins can coat the oral mucosa, physically limiting interactions between tannins and salivary proteins and further reducing astringency.

The cell wall of *Saccharomyces cerevisiae*, composed of β -glucan, mannoprotein, and chitin, exhibits differential adsorption capacities toward various phenolic fractions [22]. During fermentation, yeast cells naturally bind and remove excessive phenolic compounds. This adsorption modulates phenolic composition without harsh fining agents, reducing astringency and bitterness while preserving color and mouthfeel. In summary, these mechanisms demonstrate that *Saccharomyces cerevisiae* acts not only a fermentative catalyst but a dynamic modulator of wine phenolic composition, sensory properties, and aging potential.

2.2 Non-Saccharomyces yeasts

Non-*Saccharomyces* yeasts (e.g., *Hanseniaspora*, *Kluyveromyces*, and *Candida*) contribute significantly to aroma complexity and stylistic diversity in *Vitis vinifera* wines through their unique metabolism. Numerous non-*Saccharomyces* yeasts secrete highly active β -glucosidases capable of hydrolyzing glycosylated aroma precursors in *Vitis vinifera* grapes, releasing free terpenes and norisoprenoids to enhance varietal-specific floral and fruity notes [23–24]. Selected non-*Saccharomyces* strains help produce low-alcohol *Vitis vinifera* wines by converting more sugars into carbon dioxide instead of ethanol [25].

The symbiotic interaction between non-*Saccharomyces cerevisiae* and *Saccharomyces cerevisiae* is inherently complex and dynamically regulated (Fig. 4) [26]. In early fermentation, non-*Saccharomyces* yeasts possess strong environmental adaptability but decline as alcohol build up for their poor ethanol tolerance. Subsequent nutrient competition may induce certain non-*Saccharomyces cerevisiae* strains to produce acetic acid or antimicrobial peptides that inhibit the growth of *Saccharomyces cerevisiae*. Notably, this competition promotes nutrient release from non-*Saccharomyces* yeasts. It also supports subsequent fermentation by *Saccharomyces cerevisiae*. Together, these dual effects form the basis for the application of non-*Saccharomyces* yeasts in winemaking.

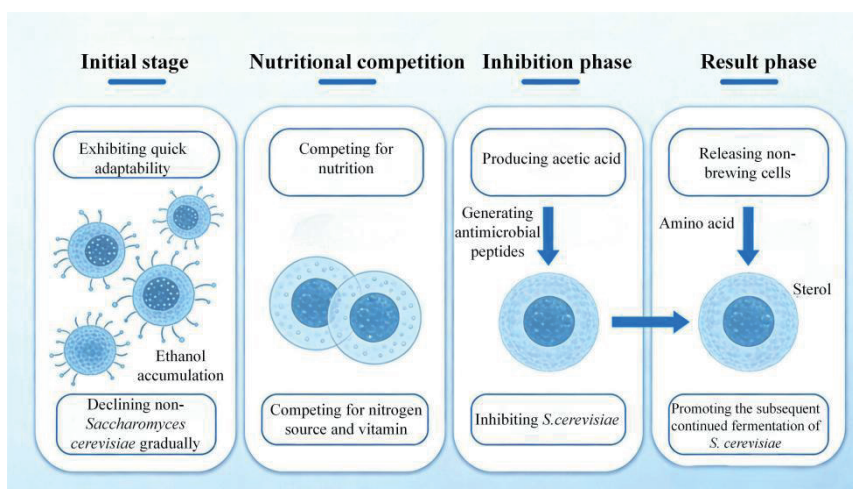


Fig. 4 Symbiotic mechanism between non-*Saccharomyces* yeasts and *Saccharomyces cerevisiae*

Non-*Saccharomyces* yeasts typically possess more robust extracellular enzyme systems, characterized by notably higher β -glucosidase and arabinosidase activity^[27]. These enzymes hydrolyze polyphenolic precursors in grapes, including aroma and pigment precursors.

These enzymes release free terpenes and anthocyanins, enhancing the varietal aroma and color expression of wine. As shown in Fig. 5, non-*Saccharomyces* yeasts regulate wine polyphenols, aroma, and color through multi-pathway metabolic activities.

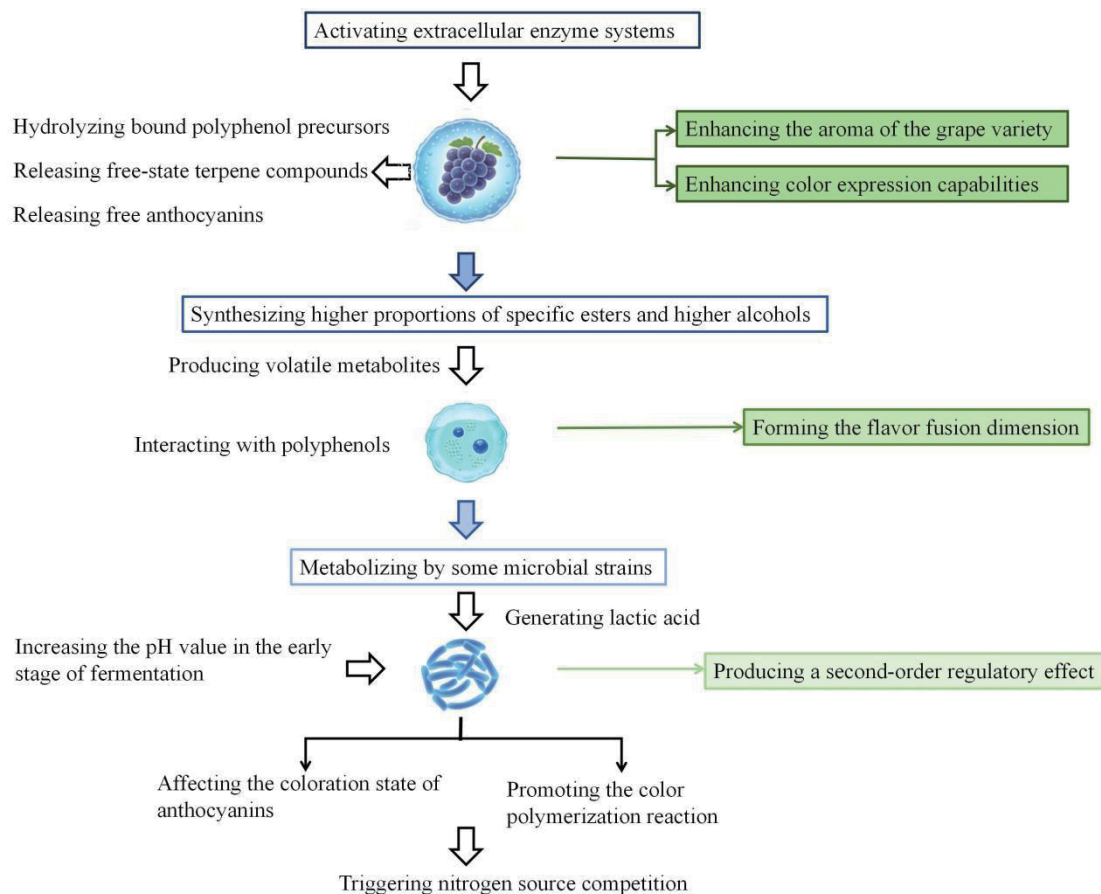


Fig. 5 Mechanism diagram of non-*Saccharomyces* yeasts regulating polyphenols and flavor in wine

2.3 Lactic acid bacteria

In addition to malolactic fermentation, LAB in *Vitis vinifera* wine play critical roles in shaping the overall flavor and ensuring wine safety. *Oenococcus oeni* exhibits remarkable tolerance to acidic conditions and high concentrations of SO₂ and ethanol, and is therefore widely used as the dominant starter culture for malolactic fermentation in *Vitis vinifera* winemaking. However, certain *Lactobacillus* and *Pediococcus* strains can also conduct malolactic fermentation (MLF) under specific conditions,

potentially generating distinctive flavor profiles^[28-29]. This allows winemakers to select appropriate bacterial species or mixed cultures according to the initial matrix of *Vitis vinifera* wine and desired wine styles.

Metabolomic studies have revealed that LAB exhibit extensive metabolic activities beyond malolactic fermentation. In addition to diacetyl production, LAB metabolize citric acid and amino acids into aldehydes and sulfur compounds^[30-33]. These metabolites contribute nutty, caramel, and roasted aromas to wine. Furthermore, some LAB strains are major producers of biogenic amines, such

as histamine and tyramine ^[34-35]. These compounds may cause adverse physiological reactions in humans. Metabolomic screening of non-amine-producing strains and optimized pre-malolactic fermentation help reduce relevant risks efficiently. In addition, LAB endure various stresses during MLF, such as low pH, high SO₂ and ethanol concentrations. Molecular stress responses involving gene and protein expression and membrane fluidity regulation support the development of stress-resistant starter strains ^[36-38]. This ensures reliable and successful MLF in diverse challenging winemaking environments.

MLF is driven by LAB and is a crucial process in the production of red wines and some white wines. By converting L-malic acid to L-lactic acid and releasing CO₂, malolactic fermentation raises wine pH by 0.2-0.3 units, influencing polyphenol composition and improving their stability ^[39]. The

elevation in pH converts anthocyanins from red to colorless or blue, leading to a short-term shift in wine color to purplish-red or brick-red. In the long-term, a more basic environment promotes copigmentation and polymerization between anthocyanins and other phenolic compounds, forming stable pigments and improving color stability. MLF also reduces perception of acidity and tannin astringency, resulting in a smoother mouthfeel. Through competition, LAB metabolites can compete with polyphenols for SO₂ binding and directly react with phenolic compounds, affecting the sensory and chemical stability of wine. Collectively, LAB enhance the color stability and mouthfeel of wine polyphenols, yet may exert adverse effects on their chemical oxidative stability. The effects of LAB on wine polyphenols and quality during malolactic fermentation are summarized in Fig. 6.

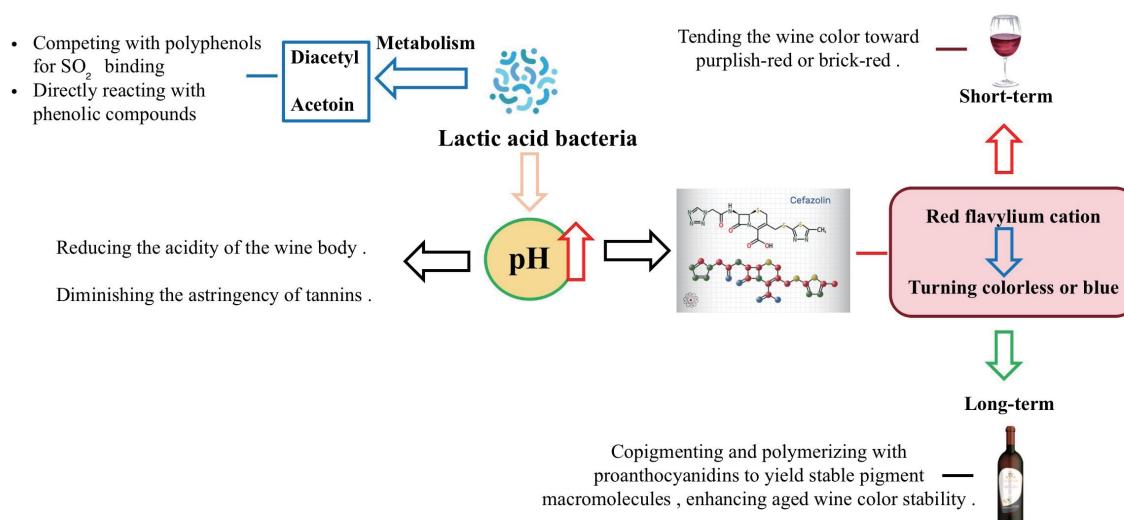


Fig. 6 Effect of lactic acid bacteria on wine polyphenols

3 Other functional microorganisms

The noble rot fungus, predominantly *Botrytis cinerea*, plays a crucial role in the production of noble sweet wines. Upon infection, it secretes polysaccharide hydrolases and pectinases, accelerating grape water loss and accumulating sugars, acids and polyphenols. Through direct catalysis of polyphenol transformations, the unique enzymatic systems and metabolites of this microbe impart complex aromas

and a round, full-bodied mouthfeel to wines ^[40]. In contrast, acetic acid bacteria are typically regarded as spoilage organisms. Under aerobic conditions, they oxidize ethanol to acetic acid and subsequently to acetaldehyde. As a potent oxidizing and polymerizing agent, acetaldehyde can cause oxidative polymerization of phenolics (e.g., anthocyanins), leading to browning and precipitation. On the other hand, it can also bind with anthocyanins and tannins to form stable pigments. However, this process often

induces uncontrolled oxidative reactions and acetic acid-related off-odors, ultimately deteriorating wine quality^[41]. *Brettanomyces* (or *Dekkera*) is also a spoilage microbe due to its production of volatile phenols. This metabolic feature directly reflects the strong biotransformation capacity of microorganisms to hydroxycinnamic acid precursors of these phenolic substrates. Though usually impairing wine sensory quality, this process can convert defects into pleasant taste, facilitating the making of premium sweet wines worldwide.

3.1 Effects of multi-strain synergistic fermentation on wine polyphenols

The selection of yeast strains shapes wine flavor structure and mouthfeel balance through strain-specific effects on fruit aroma development, ethanol production, and glycerol synthesis. The specific mechanisms and practical applications are mainly manifested in the following aspects.

3.1.1 Microbial interactions during closed-tank fermentation

In closed fermentation tanks, competition for nutrients and space drives microorganisms to develop four main types of interaction strategies. Nutrient competition is the most fundamental microbial interaction, which determines the proliferation and dominance of specific species during fermentation^[42]. Nutrient competition mainly includes three categories: carbon source competition, nitrogen source competition, and vitamin and growth factor competition.

3.1.2 Metabolic product inhibition

Microorganisms employ indirect antagonistic strategies by modifying the chemical environment to inhibit competing strains^[43].

(1) Ethanol and acid stress: High concentrations of ethanol and CO₂ produced by *Saccharomyces cerevisiae* inhibit most non-*Saccharomyces* yeasts and spoilage bacteria. The decrease in pH of during

fermenting caused by yeast-derived organic acids (succinic acid, acetic acid) further suppresses bacterial growth^[44].

(2) Antimicrobial peptides: Certain yeast strains, including some *Saccharomyces cerevisiae* and non-*Saccharomyces* species, secrete proteins or glycoproteins referred to as killer toxins. These compounds actively shape the yeast population structure by selectively eliminating sensitive, less competitive strains and clearing their microenvironment.

(3) Effects of exogenous SO₂: The undissociated sulfur dioxide molecule serves as a potent antimicrobial agent that inhibits most microorganisms. This constitutes the main chemical tool for regulating the microbial community during winemaking.

3.1.3 Quorum sensing and signal molecule communication

Microorganisms can secrete and sense specific small signaling molecules to coordinate group behavior. Intraspecific communication is mediated by quorum-sensing molecules, including aromatic alcohols such as tryptophol and phenylethanol, which are secreted by *Saccharomyces cerevisiae* during the late stages of fermentation^[45]. These quorum-sensing molecules induce entry into stationary phase and modulate stress responses, synchronizing population adaptation to environmental stress. Interspecific communication also occurs. LAB produce signal compounds that influence yeast metabolism^[46]; conversely, yeast-derived ethanol and metabolites regulate the participation of LAB in malolactic fermentation^[47–48].

3.1.4 Physical interactions

Microorganisms interact by modifying their physical environment. The most prominent example is biofilm formation. Some non-*Saccharomyces* yeasts and lactic acid bacteria can form biofilms on fermenter walls or grape skin. This growth mode provides protection and increases tolerance to stress conditions such as SO₂ and ethanol. These microorganisms subsequently exert continuous effects on the chemical

composition of fermenting must, resulting in heterogeneous fermentation kinetics or difficulties in completing fermentation.

4 Application strategies of multi-strain fermentation in winemaking

Modern winemaking applies microbe-polyphenol interaction strategies to regulate polyphenols via microbial and fermentation regulation, so as to optimize wine quality.

4.1 Strain selection and formulation

The core of strain-based strategies for polyphenol regulation is the target screening of functional strains with specific polyphenol-beneficial properties from microbial resources. By rational formulation, composite starter cultures with clear objectives and synergistic functions can be developed. Selection criteria have moved beyond traditional measures such as fermentation strength and alcohol tolerance, instead focusing on key polyphenol types directly linked to polyphenol regulation [49]. First, the enzyme activity profile can be used to predict a strain's potential to release bound aromas and pigments and to modify polyphenol structures. This potential is determined by the strain's ability to secrete β -glucosidases, pectinases, esterases, and polyphenol oxidases, as well as by its conditional adaptability. Second, the metabolite profile characterizes the levels of glycerol, glutathione, mannoproteins, specific esters and higher alcohols synthesized by the strain. Third, stress tolerance and safety screening identifies strains that are resistant to high sugar concentrations, low temperatures, and SO₂, enabling their application under diverse fermentation conditions. At the same time, this screening excludes strains that produce excessive acetic acid, biogenic amines, or undesirable volatile phenols.

Well-characterized strains enable rational mixed-culture design via functional synergy among different strains. This design can be adjusted based on the target wine style and the raw material properties. Sequential

inoculation of non-*Saccharomyces* yeasts with high β -glucosidase-activity together with glutathione-producing *Saccharomyces cerevisiae* [50], and co-fermentation of malolactic-active, flavor-positive LAB with nutrition-supporting yeast strains [51]. Indigenous microorganisms from specific viticultural regions can be isolated and combined to maximize the expression of terroir-related microbial fingerprint. Microbial synergy gives wine a unique, hard-to-replicate character by diversifying polyphenols and flavor. For instance, they produce unique esters, anthocyanin-derived pigments and tropical thiols, forming diverse oligomers and creating complex and distinctive flavor profiles.

4.2 Microbial immobilization technology

Immobilization of microorganisms or enzymes with targeted polyphenol regulation represents an emerging cell engineering strategy [51]. These biocatalysts can be immobilized in sodium alginate, carrageenan, and chitosan. Alternatively, they can be adsorbed onto inert carriers of activated carbon and porous ceramics. The carrier forms a physical barrier that protects cells from high ethanol content and acidic conditions. Thus, the substrates and products diffuse freely. This approach enables stable and controllable reuse of microbial functions and provides an innovative platform for the modulation of polyphenols in *Vitis vinifera* wines.

5 Current challenges and future perspectives

In winemaking with *Vitis vinifera*, multi-strain fermentation poses challenges regarding complexity control and safety assessment. The primary issue lies in insufficient prediction and regulation of microbial dynamics and metabolism. Furthermore, understanding of polyphenol-microbe interactions remain limited. Current technical limitations include weak causal inference from omics data, genetic instability of engineered strains, and poor control of mixed fermentation. Future progress will require integration of multi-omics approaches, synthetic biology, and

intelligent fermentation for predictive design of microbial ecosystems in modern winemaking.

6 Conclusion

Polyphenols are key components that determine the sensory quality, stability, and health benefits of *Vitis vinifera* wines. The final polyphenol profile of wine is largely shaped by microbial communities throughout vinification. *Saccharomyces cerevisiae* contributes to polyphenol extraction and stabilization. Non-*Saccharomyces* yeasts promote the release of aromatic and pigment compounds and LAB mediate polyphenol modification during malolactic fermentation. These microbial interactions form an intricate ecological network. Modern enology has increasingly focused on understanding the polyphenol–microbe ecosystem. Based on current progress reviewed herein, systems biology approaches are employed to uncover mechanisms, while synthetic biology enables targeted modulation of polyphenol metabolism. The wine industry is thus shifting from traditional practices toward more analyzable, predictable, and customizable winemaking. Overall, this review shows that these strategies enhance wine sensory complexity and stability while supporting the development of functional wines and the sustainable advancement of the global wine industry.

Acknowledgements

This project was supported by Department of Education of Liaoning Province (Natural Science, Strategic Industrialization Project (LJ212410163061)). We also thank Dr. Jinghan Li from the University of Minnesota for improving the quality of the manuscript.

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