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MINI REVIEW

The use of *Torulaspora delbrueckii* to improve malolactic fermentation

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Abstract
The potential use of *Torulaspora delbrueckii* as a starter culture for wine alcoholic fermentation has become a subject of interest in oenological research. The use of this non-*Saccharomyces* yeast can modulate different wine attributes, such as aromatic substances, organic acids and phenolic compound compositions. Thus, the obtained wines are different from those fermented with *Saccharomyces cerevisiae* as the sole starter. Nevertheless, information about the possible effects of *T. delbrueckii* chemical modulation on subsequent malolactic fermentation is still not fully explained. In general, *T. delbrueckii* is related to a decrease in toxic compounds that negatively affect *Oenococcus oeni* and an increase in others that are described as stimulating compounds. In this work, we aimed to compile the changes described in studies using *T. delbrueckii* in wine that can have a potential effect on *O. oeni* and highlight those works that directly evaluated *O. oeni* performance in *T. delbrueckii* fermented wines.

INTRODUCTION

There is increasing interest in the use of some non-*Saccharomyces* as starter cultures for alcoholic fermentation (AF) in winemaking. Some of these yeast species have been associated with the aroma profile improvement and the decrease in the alcoholic content in wine (Jolly et al., 2006). The traditional procedure is to inoculate *S. cerevisiae* in the grape must to displace the non-*Saccharomyces* growth to better control AF. Currently, knowledge about non-*Saccharomyces* identification and typification techniques allows us to start studying their real impact on wine quality (du Plessis et al., 2019; Petruzzi et al., 2017). Recently, studies about their particular enzymatic activities have been performed (Belda, Ruiz, Esteban-Fernández, et al., 2017; Carrau & Henschke, 2021; Padilla et al., 2016; Russo et al., 2020). Considering *S. cerevisiae* as a model wine yeast, non-*Saccharomyces* present different metabolic characteristics and behaviours in wine. Thus, the use of these non-conventional yeasts as starter cultures is proposed in combination with *S. cerevisiae* to ensure the completion of AF. Bioprotection is another strategy where non-*Saccharomyces* can be used to inhibit the growth of spoilage microorganisms to protect the wine quality, mainly related to the aim of reducing the use of sulphur dioxide. Currently, *Metschnikowia pulcherrima*, *Lachancea thermotolerans* and *Torulaspora delbrueckii* have been used successfully in bioprotective vinifications in different winemaking processes (Escribano-Viana et al., 2022; Simonin et al., 2018; Windholtz et al., 2021).

To date, strains of *T. delbrueckii*, *M. pulcherrima*, *L. thermotolerans*, *Pichia kluyveri* and *Schizosaccharomyces pombe* are commercially available as active dry yeasts (ADY) (Jolly et al., 2006; Petruzzi et al., 2017; Roudil et al., 2020; Vejarano & Gil-Calderón, 2021).

Among them, *Torulaspora delbrueckii* is one of the most studied non-*Saccharomyces*. It was one of the first non-*Saccharomyces* available as ADY and the yeast species with more commercially available strains of this category (Table 1). *T. delbrueckii* can be found in late stages of AF due to its high resistance to ethanol and sulphur dioxide (SO_2). It also presents high metabolic activity under winemaking conditions similar to *S. cerevisiae*. Indeed, *T. delbrueckii* and *S. cerevisiae* are genetically very close (Masneuf-Pomarede et al., 2016).

After AF, the obtained wine can go through malolactic fermentation (MLF), driven by lactic acid bacteria (LAB). It consists of the decarboxylation of L-malic acid into L-lactic acid (Kunkee, 1991; Lerm et al., 2010; Pilone & Kunkee, 1970), which results in a reduction of wine titratable acidity and an increase in pH (Davis et al., 1985; Liu, 2002; Lonvaud-Funel, 1999). Because MLF reduces acidity, it is highly recommended in red winemaking and in high acidity white wines. Nevertheless, the current climate emergency situation leads to an increase in grape must pH, a scenario that may affect MLF. The higher pH may benefit the development of LAB but it may enhance the development of some spoilage species, such as *Pediococcus* spp. Moreover, in certain wines, the decrease in the acidity of grape must can turn the MLF into an undesired process (Ubeda et al., 2020). In this sense, MLF can be eventually inhibited by the use of some LAB inhibitor compounds, as fumaric acid (Morata et al., 2020, 2023), or by inoculating an AF starter not compatible with the subsequent MLF (Ruiz-de-Villa et al., 2023).

In addition, LAB consume other nutrients during MLF, impoverishing wine and therefore increasing microbial stability (Liu, 2002). Among all LAB present in wine, *Oenococcus oeni* is the best adapted. This bacterium is highly specialised to propagate in media with low pH, ethanol and limited nutrient availability due to a very developed survival strategy (Bartowsky & Henschke, 2004; Bech-Terkilsen et al., 2020; Dimopoulou et al., 2016; Grandvalet et al., 2005; Holmgren, 1985; Liu et al., 1995; Margalef-Català et al., 2016; Olguín et al., 2010, 2015; Reguant et al., 2000; Ribéreau-Gayon et al., 2006). The inoculation of *O. oeni* in wine after AF is the usual inoculation strategy used in cellar, although it can also be inoculated in the initial must together with yeasts. Nevertheless, many winemakers usually allow the autochthonous microbiota to develop spontaneous MLF.

Lactiplantibacillus plantarum can also be used as MLF starter culture. Its low resistance to ethanol—compared to *O. oeni*—and homofermentative metabolism make this bacterium candidate for inoculating in must or during AF, before ethanol concentration becomes too high (Lucio et al., 2017; Nisiotou et al., 2015). Still, MLF is usually performed by *O. oeni* both in inoculated and spontaneous fermentations.

The aim of this work was to compile the knowledge generated in recent decades about the chemical modulation of *T. delbrueckii* in wine and relate it with its effect on *O. oeni*, the main agent of MLF. Only a few studies have addressed the direct impact of those changes in MLF; thus, special attention will be given to those few works that report data of MLF assays.

TORULASPORA DELBRUECKII COMPATIBILITY WITH *O. OENI* IN WINEMAKING

Few publications considering the effect of *T. delbrueckii* on MLF are available thus far. More knowledge is needed to understand the influence of this yeast on *O. oeni*. This is due to a lack of continuity in the fermentative process after AF; most of these works do not perform MLF. In addition, because microbial interactions are multifactorial, the impact of a unique compound is difficult to assess. Nevertheless, the strain compatibility with *O. oeni* for the subsequent MLF is a relevant issue since it is one of the characteristics described for the commercial starter cultures in manufacturers' instructions (Table 1).

Ramírez et al. (2016) first described an enhancement of MLF in *T. delbrueckii* fermented wines. They observed that MLF occurred spontaneously during AF in fermentations inoculated with this non-*Saccharomyces*, which was attributed to a slowdown of *S. cerevisiae* fermentation power. After, du Plessis et al. (2017) published the first work about the direct impact of *T. delbrueckii* on MLF, evaluating the consequences of inoculating different non-*Saccharomyces* in simultaneous and sequential MLFs with *O. oeni*. Still, these interactions have been previously studied in durian wine fermentation in 2016 (Lu et al., 2016).

In general, the use of *T. delbrueckii* seems to promote MLF or at least does not have a negative impact on *O. oeni*. Nardi et al. (2019) showed that the use of *T. delbrueckii* positively modulated the organoleptic profile of wine and reported no inhibitory or stimulatory effect on MLF.

According to most recent studies, the inoculation of *T. delbrueckii* leads to shorter MLF duration regarding the performance in a *S. cerevisiae* wine (Balmaseda et al., 2021b, 2022b; Balmaseda, Rozès, Leal, et al., 2021; Ferrando et al., 2020). Nevertheless, the total fermentative process is sometimes longer due to an extended AF (Balmaseda et al., 2021b; Balmaseda, Rozès, Leal, et al., 2021; Ferrando et al., 2020; Martín-García et al., 2020). Even if the total fermentative process is extended, the use of *T. delbrueckii* is particularly interesting in difficult wines with high ethanol and polyphenolic compositions where MLF is complicated

TABLE 1 Commercially available *T. delbrueckii* starter cultures.

Commercial name	Company	Characteristics	Recommended inoculation	Compatibility with MLF
Pure cultures				
BIODIVA™	Lallemand Inc.	Low volatile acidity Increased aroma complexity: higher concentration of esters Increased mouthfeel: production of polyols	Sequential inoculation with *S. cerevisiae*	Excellent compatibility
ENARTISFERM Qτ	Enartis Sepsa S.A.U.	High production of esters Increases aromatic complexity, smoothness and mouthfeel Low volatile acidity	Sequential inoculation with *S. cerevisiae*	–
Oenovin Torulaspora BIO	Enovys srl	Low volatile acidity High nutrition requirements	Sequential inoculation with *S. cerevisiae*	Optimal compatibility
PRELUDE™	Chr. Hansen Holding A/S	Lower volatile acidity More flavour complexity: higher MCFA esters High concentrations of mannoproteins	Sequential inoculation with *S. cerevisiae*	Promotes MLF
Viniferm NS TD	Agrovin S.A.	Low volatile acidity High nutritional requirements Increased floral aromas: production of ß-phenylethanol ß-liase activity	Requires inoculation of *S. cerevisiae*	–
ZYMAFLORE® Alpha$^{TD\ n.Sacch}$	Laffort ®	Medium nutrient requirements Low volatile acidity, acetaldehyde, acetoin, diacetyl, volatile phenols.	Sequential inoculation with *S. cerevisiae*	–
Torulaspora delbrueckii 12.2	Bionova srl	Low volatile acidity Increase in glycerol, floral notes and ß-phenylethanol	–	–
Mixed cultures				
MELODY™ (with *S. cerevisiae* and *L. thermotolerans*)	Chr. Hansen Holding A/S	Tropical fruitiness and an overall aromatic intensity Round, balanced mouthfeel	–	–
Viniflora® HARMONY (with *S. cerevisiae* and *L. thermotolerans*)	Chr. Hansen Holding A/S	Enhance aroma and flavour of wine	–	Good compatibility
Oenoferm® wild & pure (with *S. cerevisiae*)	Erbslöh Geisenheim GmbH	Enhanced monoterpens and fruity esters Increased mature and exotic fruity aromas High alcohol tolerance Increased glycerol content Moderate to high nitrogen requirements	Perfect for mixing with another yeast	–
ZYMAFLORE® ÉGIDE^{TDMP} (with *M. pulcherrima*)	Laffort ®	High resistance to sulphur dioxide For bioprotection	Requires inoculation of *S. cerevisiae*	–

Note: Provided information according to manufacturer's web information.

(Balmaseda et al., 2021b). Moreover, the positive effect of *T. delbrueckii* on MLF has been also observed when added in the form of simulated yeast lees, whereas a negative effect of *S. cerevisiae* lees was observed under the same conditions (Balmaseda et al., 2021a).

The ability of *T. delbrueckii* to modulate the organoleptic profile of wine is a well-known phenomenon (Benito, 2018) and the main reason for using this unconventional yeast as a starter culture in winemaking. However, few works have evaluated these changes after MLF. Nardi et al. (2019) reported changes in red wine aroma after MLF, which were related to the MLF inoculation strategy and the previously inoculated yeast species. It has been reported that in some cases, the obtained aromatic fingerprint of *T. delbrueckii* is maintained after MLF (Balmaseda et al., 2021b; Nardi et al., 2019), and others observed a loss of the chemical modulation attributed to *T. delbrueckii* after MLF (Balmaseda, Rozès, Leal, et al., 2021). Specifically, Nardi et al. (2019) observed that in addition to the changes attributed to *T. delbrueckii*, *O. oeni* inoculation produced changes in ethyl esters of fatty acids, mainly ethyl hexanoate and ethyl octanoate, increasing fruity and floral notes. In addition, increases in ethyl decanoate, linalool and α-terpineol and a decrease in benzoic acid were achieved after MLF. Similarly, Balmaseda et al. (2021b) observed that the produced wines were clustered in terms of AF inoculation strategy in terms of aroma composition and grape maturity level before and after MLF. This work also reported an increased aroma composition in *T. delbrueckii*-fermented wines compared to a control *S. cerevisiae*-fermented wine. In contrast, the *T. delbrueckii* fingerprint was generally lost after MLF in Cabernet Sauvignon wines (Balmaseda, Rozès, Leal, et al., 2021). Wines were clustered in terms of the *O. oeni* inoculation strategy, thus losing the *T. delbrueckii* effect on the aroma profile. In addition, some wines presented different behaviours. Thus, a strain combination effect was noticed that determined the prevalence of *T. delbrueckii* impact after MLF in some wines. This wine aromatic divergency found after AF in *T. delbrueckii* fermented wines was also decreased after MLF in C. Sauvignon wines according to Zhang et al. (2021). Particularly, Zhang et al. (2018) observed that the aromatic differences found between *S. cerevisiae* and *T. delbrueckii* wines—inoculated as sole starters—disappeared after MLF, but the sequentially inoculated *T. delbrueckii* wines were still different after MLF, but sweet and floral aromas decreased. In general, it has been observed that the type of grape variety and winemaking, together with the yeast-bacteria combination and inoculation timing, will determine the final impact of *T. delbrueckii* on the aromatic profile of wines.

The *T. delbrueckii*–*O. oeni* starter combination appears to be an important aspect in aroma modulation. Nevertheless, MLF is usually spontaneously conducted under cellar conditions. Thus, understanding the impact of *T. delbrueckii* on the natural *O. oeni* microbiota is crucial to learn how to profit from these interactions. In general, the use of *T. delbrueckii* allows a higher diversity of *O. oeni* strains at the end of MLF (Balmaseda et al., 2021b; Balmaseda, Rozès, Leal, et al., 2021). In addition, it contributes to a better imposition of commercial *O. oeni* starters. This phenomenon may help to develop MLFs in difficult wines, promoting the development of different *O. oeni* strains and preserving the impact of the autochthonous microbiota on the wine organoleptic profile. Nevertheless, the population modulation of *T. delbrueckii* seems to be strain specific (Balmaseda et al., 2022a).

More recently, Ruiz-de-Villa et al. (2023) showed that the use of some *T. delbrueckii* strains can counteract the negative impact of *S. cerevisiae* Lalvin-K1, which is known as a non-compatible yeast strain for MLF. Besides, it was demonstrated that the sequential inoculation with *T. delbrueckii* reduces the acetic acid and medium-chain fatty acids (MCFA) concentration in wines after AF, negative factor for the development of the MLF.

Among different fermentative parameters or subproducts related to AF, AF duration and the production of the main compounds as ethanol, glycerol or acetic acid, together with L-malic acid that directly impact MLF are analysed in Figure 1. This figure was constructed with the data collected in Table S1. Dixon's *Q* test was used to discard outliers—which are underlined in this Table. As commented before, AF duration is usually extended in sequential inoculation, and no differences are observed in L-malic acid composition regarding to the AF inoculation strategy with *T. delbrueckii* (Figure 1A). Moreover, literature shows that *T. delbrueckii* must be used in combination with *S. cerevisiae*, since it cannot finish AF, as deduced by the high final sugar concentration found in wines (Figure 1A). Even if it is shown a tendency in the ethanol reduction, the main interested of using *T. delbrueckii* is demonstrated to be the reduction on the acetic acid production (Figure 1A). The Principal Component Analysis done for the production of ethanol, glycerol and acetic acid—per 100 g/L of sugars consumed—(Figure 1B) shows that inoculation of *T. delbrueckii* as sole starter has a different fermentative behaviour than that obtained inoculating *S. cerevisiae*—sole, coinoculated or sequentially inoculated with *T. delbrueckii*. This was confirmed by an ANOVA-Simultaneous Component Analysis (ASCA), in which *T. delbrueckii* as sole starter was determined to be a significantly different group—where the group factor explains 23% of the variance with a *p*-value of 0.0001.

The lack of literature about the effects of *T. delbrueckii* on MLF makes necessary to study the changes in compounds with known effect upon *O. oeni*. These

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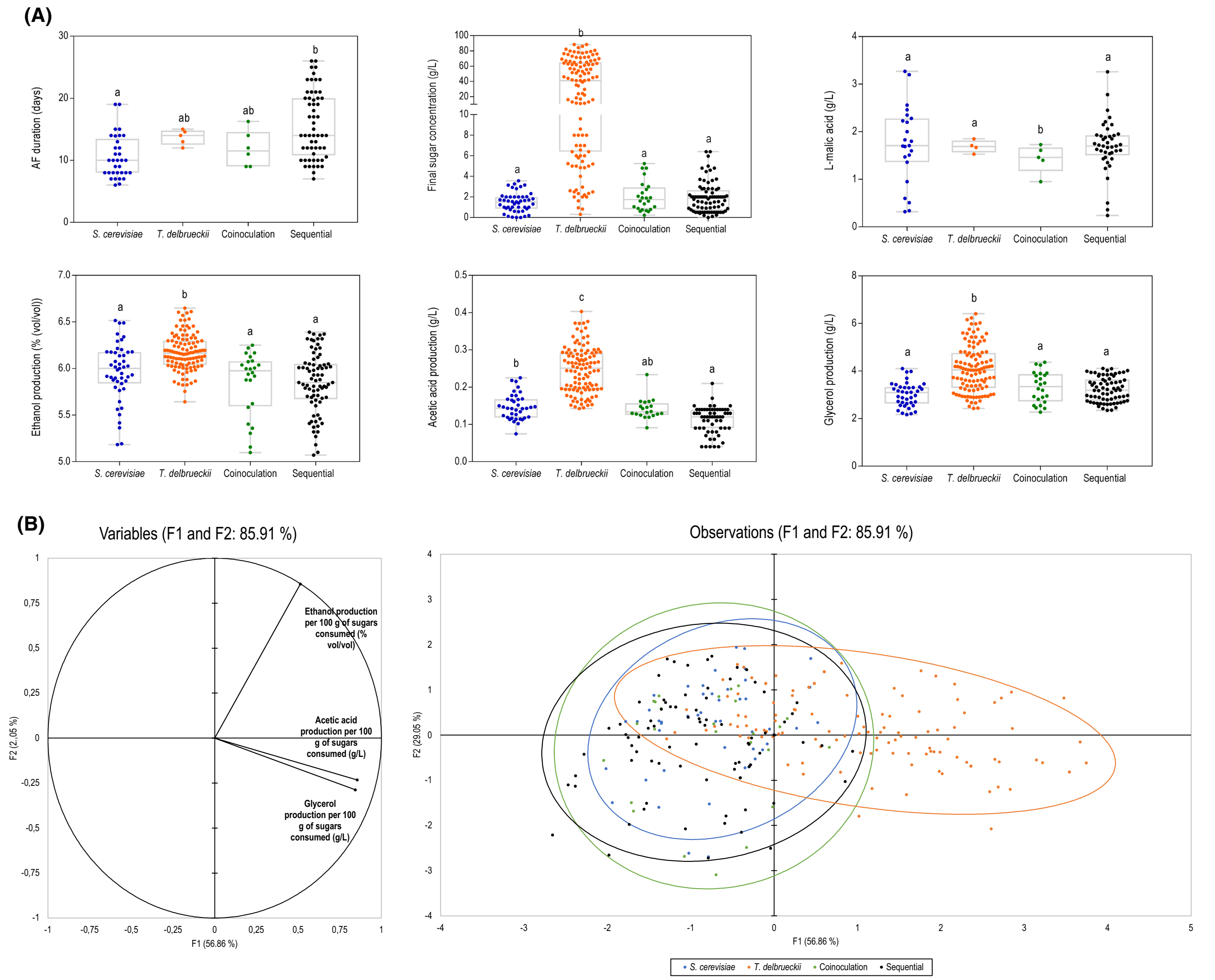

FIGURE 1 Modulation of some relevant fermentative parameters or AF subproducts using *T. delbrueckii*, as sole starter, in sequential or coinoculation with *S. cerevisiae* regarding *S. cerevisiae* wines. Values shown are those collected from literature (Table S1). (A) Values for some fermentative parameters and production of ethanol, acetic acid and glycerol (per 100 g of sugar consumed). Each value represents a value reported for a fermentation where *T. delbrueckii* and *S. cerevisiae* were used and lower case letters indicate a significant difference at $p \leq 0.05$ according to a Tukey post hoc comparison test (grey box). (B) Principal Component analysis with 95% confidence ellipses of the production of ethanol, acetic acid and glycerol (per 100 g of sugar consumed).

changes, increases or decreases, are always referred to the control AF inoculated with *S. cerevisiae* (Table 2, Figure 2). Thus, in the following lines, we will discuss the potential effects of the modulation of wine compounds composition by *T. delbrueckii* upon *O. oeni*.

YEAST METABOLISM INFLUENCES MLF

The influence of yeasts on *O. oeni* is determinant because this bacterium develops in media modified by yeasts during AF. Many of the compounds produced by yeasts, such as ethanol, SO_2, organic acids and MCFA, negatively impact *O. oeni* and generate stress (Bech-Terkilsen et al., 2020). However, yeasts can also produce or release some stimulatory metabolites towards *O. oeni*, such as mannoproteins (Balmaseda et al., 2018). Because some of the yeast metabolic traits are species-dependent, the use of different yeasts in AF, such as *T. delbrueckii*, influences wine composition and, consequently, MLF evolution. In Table 2 are shown all chemical compositions currently described in the literature related to the use of *T. delbrueckii* in finished wines after AF. The data compiled in Table 2, and graphically illustrated in Figure 2, are analysed and discussed in the following paragraphs. For constructing Figure 2, the data collected in Table 2 were analysed by a Dixon's Q test to identify the outliers—underlined in this Table—and really show the general tendencies *T. delbrueckii*'s modulation in wine compounds, clustered according to the inoculation regime. It must be pointed that there are much more works using *T. delbrueckii* in sequential inoculation than coinoculated

TABLE 2 Variation of the principal enological compounds with potential effect on *O. oeni* related to the use of *T. delbrueckii*.

***T. delbrueckii* inoculation strategy**	***T. delbrueckii* inoculation strategy**	**Variation respect to the control *S. cerevisiae* wine**	**Reference**
Ethanol (% v/v)	SE, 2% vol/vol EtOH	−0.45, −0.52, −0.59	Azzolini et al. (2012)
	SE, 3–4% vol/vol EtOH	−0.2, −0.2	Azzolini et al. (2015)
	SE, 15 g/L	−0.14	Belda et al. (2015)
	Sole	−0.15	Belda et al. (2015)
	SE 4 days	−0.47, −0.6	Belda, Ruiz, Beisert et al. (2017)
	SE, 3 days	−1.62	Canonico et al. (2015)
	SE, 15 density units	−0.7	Castrillo et al. (2019)
	SE, 4 days	−0.6, −0.6	Contreras et al. (2015)
	Sole	−0.15	Čuš and Jenko (2013)
	SE, 3 days	−0.2	Escribano-Viana et al. (2019)
	CO	−1.24, +0.93	Marcon et al. (2018)
	SE, 1 day	−0.5	Muñoz-Redondo et al. (2021)
	Sole	−1.62, −1.58, −0.51	Ngqumba et al. (2017)
	SE, 15 g/L	−0.3, −0.5	Puertas et al. (2017)
	SE, 15 density units	−0.3	Puertas et al. (2018)
	SE, 2 days	−0.47	Zhang et al. (2018)
	CO	−0.56, −0.82	Zhang et al. (2018)
	SE, 2 days	−0.36, −0.48, −0.86	Zhu et al. (2020)
pH	SE, 2 days	−0.13	Balmaseda, Rozès, Leal et al. (2021)
	SE, 2 days	−0.3, +0.2	Balmaseda et al. (2021b)
	SE, 2 days	+0.13, +0.15	Balmaseda et al. (2022a)
	Sole	+0.04	Belda et al. (2015)
	SE, 4 days	−0.05	Belda, Ruiz, Beisert, et al. (2017)
	SE, 2 days	+0.01	Dutraive et al. (2019)
	CO	+0.1, +0.1	Marcon et al. (2018)
	SE, 1 days	+0.4	Martín-García et al. (2020)
	SE, 2 days	+0.48	Martín-García et al. (2020)
	SE, 3 days	+0.36	Martín-García et al. (2020)
	SE, 2 days	−0.08	Ruiz-de-Villa et al. (2023)
	SE, 15 density units	+0.09	Puertas et al. (2018)
Total sulphur dioxide (mg/L)	SE, 2 days	−5.5	Agarbati et al. (2020)
	SE, 2 days	−4.3, −6.3	Balmaseda, Rozès, Leal et al. (2021)
	SE, 2 days	−3.5, −4.5, −5.3	Balmaseda et al. (2021b)
	CO	+73	Belda et al. (2015)
	SE, 15 g/L	+75.2	Belda et al. (2015)
	Sole	+79	Belda et al. (2015)
	Sole	+3.2	Marcon et al. (2018)
	CO	−6.4, −5.3, −3.2	Marcon et al. (2018)
	SE, 2 days	−18.8	Martín-García et al. (2020)
	SE, 3 days	−29.5	Martín-García et al. (2020)

TABLE 2 (Continued)

***T. delbrueckii* inoculation strategy**	***T. delbrueckii* inoculation strategy**	**Variation respect to the control *S. cerevisiae* wine**	**Reference**
Medium-chain fatty acids, MCFA (mg/L)	CO	−0.09 C6; −0.195 C8; −0.07 C10	Azzolini et al. (2012)
	SE, 2% vol/vol EtOH	−0.274, +0.23, +0.33 C6; −0.446, +0.132 C8; −0.125, −0.07, −0.05 C10	Azzolini et al. (2012)
	SE, 3–4% vol/vol EtOH	−1.17, −1.17, −1.14, −1.14 C6; −3.24, −3.2, −3.2, −3.1 C8; −1, −0.86, −0.59, −0.05 C10	Azzolini et al. (2015)
	SE, 2 days	−10.5 C6; −0.68, −2,4 C8; −1.43 C10	Balmaseda, Rozès, Leal et al. (2021)
	SE, 2 days	−1.9, −1.9 C6; −0.2, −0.2, −0.7, −0.7 C8; −0.4, −0.5 C10	Balmaseda et al. (2021b)
	SE, 2 days	−13.12, −13.12 C6; −2.9, −4.77 C8	Balmaseda et al. (2022a)
	SE, 4 days	+0.29, +0.77 C10	Belda, Ruiz, Beisert, et al. (2017)
	SE, 3 days	−1.5 C6; −4.2 C8; −2 C10	Canonico et al. (2019)
	SE, 10–15 units	−0.64 C6; −2.36 C8; −0.39 C10; −0.11 C12	Castrillo et al. (2019)
	CO	−1, 0.78, 0.26 C8	Comitini et al. (2011)
	SE, 3 days	−1.29 C8	Escribano-Viana et al. (2019)
	Sole	−3 C8, −2.26 C10	Marcon et al. (2018)
	SE, 2 days	−3.45, −2.43 MCFA (C6, C8, C10, C12)	Ruiz-de-Villa et al. (2023)
	SE, 1 day	−0.31 C8, +0.1 C10	Sadoudi et al. (2012)
	CO	−0.46 C6; −0.30 C8	Zhang et al. (2018)
	SE, 2 days	−0.37 C6; +0.012, +0.028 C10	Zhang et al. (2018)
	SE, 2 days	−0.1 C6; +0.21 C8; +0.04 C10	Zhang et al. (2021)
	Sole	+0.95 C6; +1.43 C8; +0.17 C10	Zhang, Liu, et al. (2022)
	SE, 4 days	+1.08 C6; +1.3 C8	Zhang, Tang, et al. (2022)
Polyphenols[a]	SE, 2 days	+63.6 anthocyanins	Balmaseda, Rozès, Leal, et al. (2021)
	SE, 2 days	+78.5, +94.9, +159.5, +234.1 anthocyanins; +0.29, +0.76 tannins; +7.1 TPI	Balmaseda et al. (2021b)
	SE, 3 days	+19 anthocyanins	Carew et al. (2013)
	SE, 4 days	+46 anthocyanins	Chen et al. (2018)
	SE, 3 days	+6.9 TPI	Escribano-Viana et al. (2019)
	Sole	+0.46 phenolic compounds	Zhang, Liu, et al. (2022)
Nitrogen-related compounds (mg N/L)	CO	+13.3, +23.3, +27 YAN	Bely et al. (2008)
	SE, 1 day	+33.2 NOPA	Martín-García et al. (2020)
	SE, 2 days	+40.5 NOPA	Martín-García et al. (2020)
	SE, 3 days	+31.3 NOPA	Martín-García et al. (2020)
Mannoproteins (equation D-mannose mg/L)	SE, 2 days	+60, +160	Balmaseda, Aniballi, et al. (2021)
	SE, 1 day	+234.2, +307.2	Ferrando et al. (2020)

(Continues)

TABLE 2 (Continued)

T. delbrueckii inoculation strategy	*T. delbrueckii* inoculation strategy	Variation respect to the control *S. cerevisiae* wine	Reference
Malic acid (g/L)	SE, 2 days	−0.16, −0.23	Balmaseda et al. (2022a)
	SE, 4 days	+0.07	Belda, Ruiz, Beisert, et al. (2017)
	SE, 3 days	−0.9	Canonico et al. (2019)
	SE, 4 days	−0.7, −1.4, −1.8, −1.8, +0.4	Contreras et al. (2015)
	SE, 2 days	−0.07	Dutraive et al. (2019)
	SE, 3 days	−0.31	Escribano-Viana et al. (2019)
	SE, 3 days	+0.34	Martín-García et al. (2020)
	SE, 15 density units	−1.56	Puertas et al. (2018)
	SE, 2 days	−0.17, +0.18	Ruiz-de-Villa et al. (2023)
	SE, 2 days	+0.6, +0.6	Zhang et al. (2018)
	SE, 2 days	+0.91	Zhang et al. (2021)
Citric acid (g/L)	SE, 2 days	+0.10, +0.14	Balmaseda, Aniballi, et al. (2021)
	SE, 2 days	+0.03	Ruiz-de-Villa et al. (2023)
	SE, 15 density units	−0.26	Puertas et al. (2018)
Succinic acid (mg/L)	SE, 2 days	−120, −50, +150, +150	Balmaseda et al. (2021b)
	SE, 2 days	−178, −192	Balmaseda et al. (2022a)
	SE, 3 days	+300	Canonico et al. (2019)
	SE, 4 days	+600, +600, +1100, +1200, +2500	Contreras et al. (2015)
	Sole	−0.14, −0.17, −0.41	Ngqumba et al. (2017)
	CO	−0.18, −0.21, −0.56, −0.44	Ngqumba et al. (2017)
	SE, 1 days	−20.41	Martín-García et al. (2020)
	SE, 2 days	−22.28	Martín-García et al. (2020)
	SE, 3 days	−17.74	Martín-García et al. (2020)
	SE, 15 density units	+0.34	Puertas et al. (2018)
	SE, 2 days	−1290, −1050	Zhang et al. (2018)
Lactic acid (g/L)	SE, 2% vol/vol EtOH	+0.41, +0.36	Azzolini et al. (2012)
	SE, 15 density units	+1.15	Puertas et al. (2018)
	CO	−0.21, +0.18	Zhang et al. (2018)
	SE, 2 days	+0.27, +0.42	Zhang et al. (2018)
	SE, 2 days	−0.28	Zhang et al. (2021)
	SE, 4 days	−0.08	Zhang, Tang, et al. (2022)
	SE, 2 days	+0.14, +0.17, +0.34	Zhu et al. (2020)
Acetic acid (g/L)	SE, 3–4% vol/vol EtOH	−0.17, −0.06, +0.07, +0.08	Azzolini et al. (2015)
	SE, 2 days	−0.12	Balmaseda, Aniballi, et al. (2021)
	SE, 2 days	−0.12	Balmaseda, Rozès, Leal, et al. (2021)
	SE, 2 days	−0.05	Balmaseda et al. (2021b)
	SE, 4 days	−0.09, −0.07	Belda, Ruiz, Beisert et al. (2017)
	CO	−0,49, −0.48, −0.47, −0.39, −0.37	Bely et al. (2008)
	SE, 3 days	−0.51	Canonico et al. (2019)
	SE, 4 days	−1.6, −0.8, −0.2	Contreras et al. (2015)
	SE, 3 days	−0.31, −0.31	Escribano-Viana et al. (2019)
	SE, 1 day	−0.11	Martín-García et al. (2020)
	SE, 2 days	−0.11	Martín-García et al. (2020)
	SE, 3 days	−0.13	Martín-García et al. (2020)

TABLE 2 (Continued)

T. delbrueckii inoculation strategy	*T. delbrueckii* inoculation strategy	Variation respect to the control *S. cerevisiae* wine	Reference
	SE, 2 days	−0.43, −0.3, −0.23	Ruiz-de-Villa et al. (2023)
	CO	+0.24	Sadoudi et al. (2012)
	SE, 1 day	−0.17	Sadoudi et al. (2012)
	CO	−0.12	Zhang et al. (2018)
	SE, 2 days	−0.33	Zhang et al. (2021)
	Sole	−0.1	Zhang, Tang, et al. (2022)
Pyruvic acid (mg/L)	SE, 4 days	+21.7, +25.7	Belda, Ruiz, Beisert, et al. (2017)

Note: Variations are calculated considering a control fermentation of *S. cerevisiae* as sole starter. Only variations considered as significant in the original paper are included. Sole: *T. delbrueckii* as sole starter; CO: *T. delbrueckii* and *S. cerevisiae* coinoculation in must; SE: *T. delbrueckii* inoculated in must and sequential inoculated with *S. cerevisiae*, followed by the inoculation timing when *S. cerevisiae* was inoculated; −, means decrease; +, means increase. Underlined values are outliers according to a Dixon's *Q* test for outlier values ($p < 0.05$), which are discarded in Figure 2.

[a]Phenolic compounds (mg/L), anthocyanins (mg/L), tannins (g/L).

with *S. cerevisiae*, or as sole starter (Figure 2), which shows the general tendency of inoculating *T. delbrueckii* with this regime. Besides, it also increases the heterogeneity of the reported changes since the conditions' variability—grape musts, operational procedures, microbial strains, etc.—is increased.

Ethanol

Ethanol interacts with lipids present in the *O. oeni* cell membrane, affecting its fluidity and, therefore, its barrier function. Thus, the main functional categories affected by ethanol in *O. oeni* are metabolite transport and cell wall and membrane biosynthesis (Margalef-Català et al., 2016; Olguín et al., 2010). In addition, *O. oeni* increases the rigidity of the cell membrane by altering its fatty acid composition to counteract the effect of ethanol (Garbay et al., 1995; Garbay & Lonvaud-Funel, 1996; Grandvalet et al., 2008; Teixeira et al., 2002). It also induces the expression of some small heat shock proteins (sHsp), which appear to be essential to the maintenance of cell membrane fluidity, particularly Lo18 (Guzzo et al., 1997). The use of *T. delbrueckii* starter cultures can reduce the concentration of ethanol from 0.14% (vol/vol) (Belda et al., 2015) up to 1.62% (vol/vol) (Canonico et al., 2015; Ngqumba et al., 2017). Still, these changes are also dependent of the initial and final sugar concentration of the wines, which is not always reported (Table S1). Regarding the inoculation regime, although the literature shows that the use of *T. delbrueckii* results in ethanol decrease (Table 2), no significant differences were found with respect to the use of *S. cerevisiae* alone (Figures 1A and 2A). The ethanol reduction induced by *T. delbrueckii* seems to be dependent mainly on the chemical composition of the must and the yeast strain. Indeed, *T. delbrueckii* as sole starter seems to increase ethanol concentration. This could be due to an early ethanol production in non-finished wines inoculated with *T. delbrueckii*.

Low pH

During AF, yeasts can also produce significant amounts of acids that can reduce the pH value from must to wine. The effect of *T. delbrueckii* on pH value reports heterogeneous results (Figure 2C) because the same strain, for instance, Viniferm (Agrovin S.A.), can increase it (Balmaseda et al., 2021b, 2022a; Belda et al., 2015) or decrease it (Balmaseda et al., 2021b; Belda, Ruiz, Beisert, et al., 2017) depending on the medium. Nevertheless, high variations have not been reported that may have a significant impact on *O. oeni* (Table 2), with the exception of Martín-García et al. (2020), who reported a pH increase of 0.48 with the use of *T. delbrueckii* in sequential inoculation with *S. cerevisiae*. These changes can represent increased bacterial survival because *O. oeni* dramatically decreases its viability in wines with pH values below 3 and some strains even below 3.3 (Breniaux et al., 2018).

Sulphur dioxide (SO_2)

SO_2 is another chemical compound with antimicrobial activity associated with winemaking. This compound is usually added to must and wine as an antioxidant and to inhibit undesired indigenous microbiota. Additionally, yeasts can produce SO_2 during AF, depending on the strain and nitrogen content, and consequently, its concentration in wine can increase (Osborne & Edwards, 2006). This compound causes a decrease in ATPase activity and affects membrane activity in *O. oeni* (Carreté et al., 2002), which is related to MLF difficulties (Lonvaud-Funel et al., 1988). *T. delbrueckii* generally reduces the total SO_2 without significant differences in the free fraction (Table 2). Indeed, it seems that the inoculation regime was a modulation effect (Figure 2B), enhancing the total SO_2 reduction *when T. delbrueckii* is more present during the fermentative

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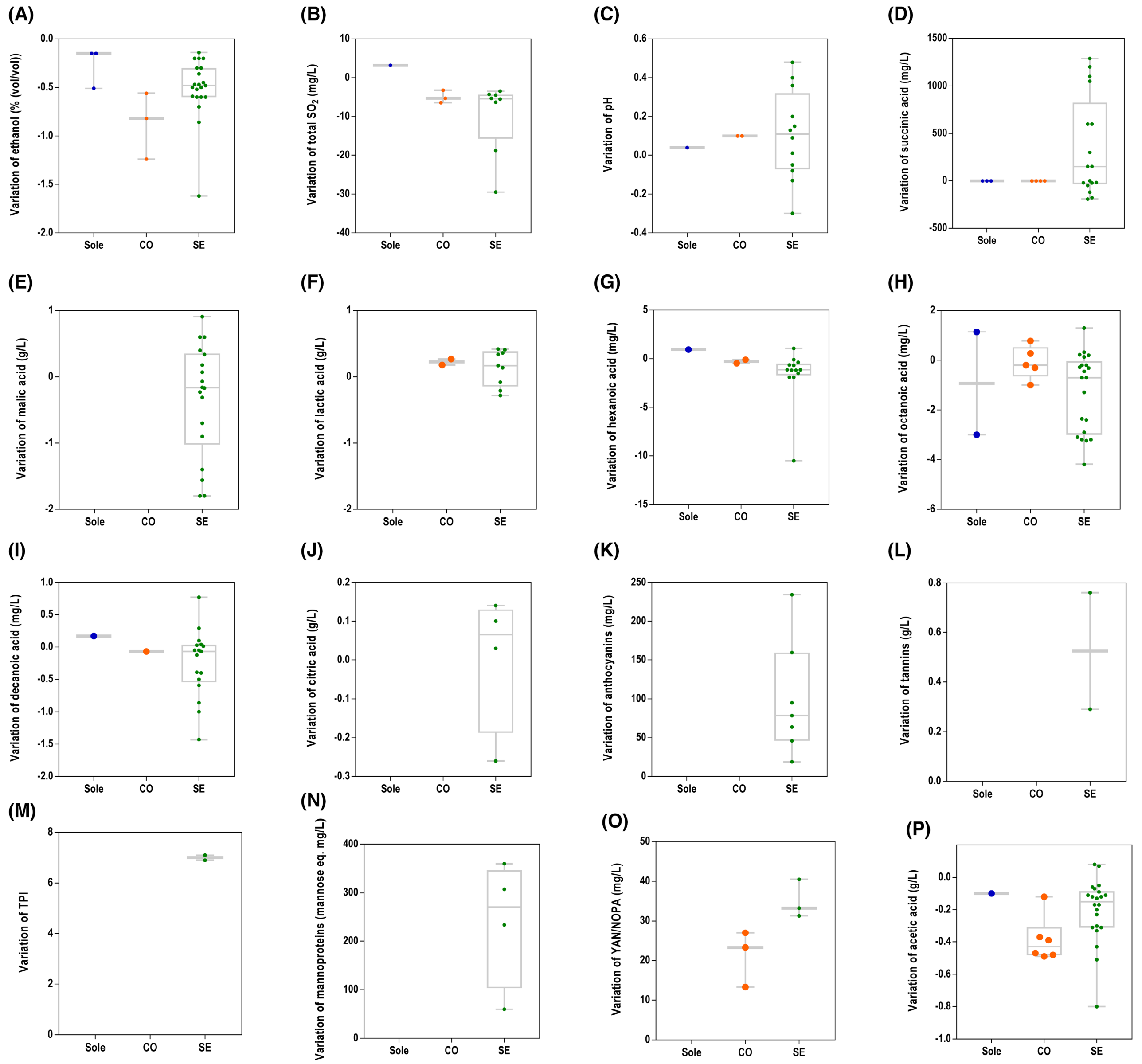

FIGURE 2 Variation of selected compounds using *T. delbrueckii*, as sole starter, in sequential or coinoculation with *S. cerevisiae* regarding *S. cerevisiae* wines. Values are reported as the difference to the control wine of *S. cerevisiae*. No value means no reported data in the collected literature. Sole: *T. delbrueckii* as sole starter; CO: *T. delbrueckii* and *S. cerevisiae* coinoculation in must; SE: *T. delbrueckii* inoculated in must and sequential inoculated with *S. cerevisiae*, followed by the inoculation timing when *S. cerevisiae* was inoculated. This figure was constructed using the data collected in Table 2.

process (Martín-García et al., 2020). Nevertheless, Belda et al. (2015) reported a dramatic increase with *T. delbrueckii* Viniferm in Tempranillo red wines in three different inoculation regimes, contrary to the general low modulation reported by other works (Table 2).

Medium-chain fatty acids

As a result of yeast metabolism, MCFAs are released to the medium in greater quantities in white winemaking. This group of fatty acids (C6-C12) can also alter the fluidity of the membrane and even reduce L-malic acid consumption, causing fermentative problems in *O. oeni* (Edwards & Beelman, 1987; Guilloux-Benatier et al., 1998; Lonvaud-Funel et al., 1988). *T. delbrueckii* is generally related to a decrease in MCFA, mainly due to the reduction of octanoic and decanoic acids in sequential inoculation (Figure 2G–I). Reductions up to 0.46 mg/L in hexanoic acid (Zhang et al., 2018), 0.30 mg/L in octanoic acid (Zhang et al., 2018), 2 mg/L in decanoic acid (Ciani et al., 2016) and 0.11 mg/L in dodecanoic acid (Castrillo et al., 2019) have been reported in the literature. Even so, other authors have reported modest significant increases in MCFA due to the use of *T. delbrueckii* (Belda, Ruiz, Beisert, et al., 2017; Zhang et al., 2018; Zhang, Liu, et al., 2022).

The high variability observed in the production of MCFA respond not only to the yeast strains, but also to the fermenting conditions. In addition, their effect upon *O. oeni* will also be strain dependent with some critical concentration levels fixed in 5–10 mg/L of decanoic acid by Capucho and San Romao (1994), concentrations rarely found in wine.

Phenolic compounds

One of the main attributes of red wines is colour and astringency, and phenolic compounds, such as anthocyanins, proanthocyanidins and phenolic acids, are responsible for them. They are not directly related to yeast metabolism; however, their concentration can vary depending on the fermenting yeast strain due to particular pectolytic activity (Belda, Conchillo, et al., 2016) and adsorption by the yeast cell wall (Morata et al., 2016). Indeed, non-*Saccharomyces* seem to enhance polyphenolic composition (Escribano-Viana et al., 2019). In addition, they can cause difficulties for *O. oeni* in MLF performance depending on the type of phenolic compound (Reguant et al., 2000). This family of compounds has been described as stress compounds (Bech-Terkilsen et al., 2020), and some of them (e.g. stilbenes at low concentrations such as 5 mg/L) are related to the inhibition of L-malic acid consumption in some *O. oeni* strains under wine conditions (Zimdars et al., 2021). Even though only few studies address this specific inhibition mechanism, it seems to depend on the structure of the polyphenol (Devi & Anu-Appaiah, 2018; García-ruiz et al., 2011) and on the *O. oeni* strain (Zimdars et al., 2021). One of the advantages of *T. delbrueckii* is the maintenance of polyphenolic compounds in wine, which can be enhanced in final wines respect to *S. cerevisiae* as sole starter (Balmaseda et al., 2021b; Benito, 2018; Escribano-Viana et al., 2019). Sequential inoculation with *T. delbrueckii*, which is the main inoculation regime reported in the literature, increases anthocyanins concentration and TPI value (Figure 2K–M). Nevertheless, this increase in polyphenolic compositions—from a TPI value of 30.2 in *S. cerevisiae* wines, up to 37.4 in *T. delbrueckii* wines—has not been related to an inhibitory effect (Balmaseda et al., 2021b). Besides, the observed effect could also vary in different conditions due to the use of different grape varieties, vinification processes, yeast and bacterial strains, etc.

Nitrogen-related compounds

Nitrogen compounds, such as peptides and amino acids, are essential for microbial development. Indeed, *O. oeni* is considered a fastidious bacterium due to its strain-dependent amino acid auxotrophy, but its nitrogen demand is very low (Remize et al., 2005). The nitrogen composition in wine is mostly composed of proteins, peptides and free amino acids. In general, the free amino acid composition is very low, approximately 20 mg N/L (Gobert et al., 2017; Roca-Mesa et al., 2020), but peptides can represent up to 100 mg N/L in wines after AF (Alcaide-Hidalgo et al., 2008; Martínez-Rodriguez et al., 2001), constituting the preferred nitrogen source for *O. oeni* in wine (Remize et al., 2006). Thus, the preferences for amino acids of each yeast strain (Roca-Mesa et al., 2020) and the production of peptides will determine the nitrogen availability for *O. oeni* in wine. In terms of free amino acids, it has been reported that *T. delbrueckii* can increase them (Figure 2O) from 13.3 mg N/L (Bely et al., 2008) to 40 mg N/L (Martín-García et al., 2020) that could be related to an earlier autolytic process, known as beneficial for MLF (Balmaseda et al., 2021a; Guilloux-Benatier & Chassagne, 2003).

Mannoproteins

Mannoproteins are the main polysaccharides from the yeast cell wall released to wine during AF (Vejarano, 2020), especially during wine ageing (Belda, Navascués, et al., 2016). Thus, some works reported significant increases in mannoprotein concentration after AF with *T. delbrueckii* (Figure 2N) (Balmaseda, Aniballi, et al., 2021; Ferrando et al., 2020; Ruiz-de-Villa et al., 2023). Studies in yeast-derived compounds have demonstrated a stimulatory effect on *O. oeni* growth in the presence of these macromolecules (Diez et al., 2010; Guilloux-Benatier et al., 1995; Liu et al., 2017). Currently, we can relate this positive effect to an uptake of mannose hydrolysed from mannoproteins, which can be a substrate of the bacterial phosphotransferase system (PTS) (Cibrario et al., 2016; Jamal et al., 2013). Throughout this system, *O. oeni* can ferment sugars, such as mannose. Thus, an increased transcriptional response of some genes related to the PTS system of *O. oeni* in wines fermented with *T. delbrueckii* has been recently reported (Balmaseda et al., 2021a, 2021b; Balmaseda, Aniballi, et al. 2021; Balmaseda, Rozès, Leal, et al., 2021).

In addition, amino acids and perhaps peptides, released from the breakdown of these molecules may also positively impact MLF.

Organic acids

L-malic acid

The L-malic acid concentration can be altered from must to wine as a result of yeast metabolism. Some yeast strains can decrease the concentration available in grape must (Su et al., 2014) and thus limit the substrate of MLF. Moreover, the reduction in wine acidity is a current problem in winemaking due to climate change (Ubeda et al., 2020). In general, the reported modulation of L-malic acid content due to *T. delbrueckii* is heterogeneous but represents little up or down variation with respect to *S. cerevisiae* wines (Figure 2E). Nevertheless, Contreras et al. (2015) showed a reduction of 1.4–1.8 g/L in synthetic medium. These reductions, which were also reported for other non-*Saccharomyces* species in the same work, represent a high modulation of this acid regarding to the general modulations described in other works (Belda, Ruiz, Beisert, et al., 2017; Dutraive et al., 2019; Ferrando et al., 2020).

Citric acid

Citric acid is one of the carbon sources that *O. oeni* can metabolise in wine. Its consumption contributes to the generation of proton motive force (Liu et al., 2016), related to an increase in bacterial survival. It can also produce end products that can directly impact the wine organoleptic profile by increasing buttery aromas (Bartowsky & Henschke, 2004). In general, the use of *T. delbrueckii* does not represent a significant variation in citric acid concentration (Figure 2J).

Other organic acids: Succinic, lactic and pyruvic acids

Organic acids represent an important biosynthetic pathway for some intermediary metabolites in yeast under oenological conditions (Waterhouse et al., 2016). Apart from citric acid, which is considered a stimulatory compound for *O. oeni* and comes from grapes, succinic acid is the next most generated organic acid formed by the reductive branch of the tricarboxylic acid pathway from pyruvate (Camarasa et al., 2003). Succinic acid is considered an MLF inhibitor because it is structurally analogous to L-malic acid. Thus, it can act as a potential competitive inhibitor of the active site of the malolactic enzyme (Davis et al., 1985; Lonvaud-Funel & Strasser de Saad, 1982; Torres-Guardado et al., 2022). The effect of *T. delbrueckii* on succinic acid concentration is quite heterogeneous (Figure 2D, Table 2). Indeed, it can increase the amount of succinic acid by more than 1 g/L (Contreras et al., 2015) or even decrease it in the same manner (Zhang et al., 2018).

Moreover, *T. delbrueckii* can increase the lactic acid concentration (Table 2) up to 0.42 g/L (Zhang et al., 2018). Thus, because the L isomer of lactic acid is the product of MLF by *O. oeni*, its concentration increase can inhibit the fermentative process (Bech-Terkilsen et al., 2020). Nevertheless, the reported increase should not be related to a potential inhibition of *O. oeni*. In addition, the acetic acid concentration can be reduced by *T. delbrueckii*. Reductions of 0.05 g/L (Balmaseda et al., 2021b), up to 0.51 g/L (Canonico et al., 2019) or even 1.6 g/L in synthetic medium (Contreras et al., 2015) have been reported (Table 2). Indeed, the reduction of acetic acid could enhance MLF, since it can affect *O. oeni*'s growth rate (Augagneur et al., 2007). Besides, it is associated with organoleptic defaults in wine (Waterhouse et al., 2016).

Another organic acid that may play a stimulating role in *O. oeni* is pyruvic acid, which is a metabolite of yeast and LAB. It can be used as an external electron acceptor, facilitating the regeneration of NAD^+ (Maicas et al., 2002) or promoting the production of buttery aromas (Mink et al., 2015). The influence of *T. delbrueckii* on this acid has been reported only by Belda, Ruiz, Beisert, et al. (2017), where an increase of 21–25 mg/L was observed (Table 2). In addition, pyruvic acid together with acetaldehyde can bind to sulphur dioxide and exhibit an inhibitory effect in wine LAB (Wells & Osborne, 2012).

CONCLUSION AND FUTURE PERSPECTIVES

The positive influence of *T. delbrueckii* on wine quality and subsequent MLF has been confirmed by different works using a wide variety of approaches. As previously stated, this reported stimulatory effect cannot be attributed to a single chemical modulation, but it is the sum of different changes that contribute to producing wines that are more MLF-friendly. The exhaustive study of compounds modulated by the use of *T. delbrueckii* and how they may affect the yield of *O. oeni* and MLF would help to better understand all parts of the *T. delbrueckii_O. oeni* puzzle. Of note, many of the positive interactions reported in the literature cannot be attributed to variation of a single compound.

The available evidence points to the positive effect of *T. delbrueckii* not only on wine quality but also on MLF performance. As a result, research in this direction should be conducted to continue revealing the bases of these interactions to apply the generated knowledge in winemaking. Extending the current knowledge to more fermentative conditions with more strain combinations should allow us to find the most compatible *T. delbrueckii–O. oeni* strain in tandem. Finally, the study of *T. delbrueckii* as a potential yeast for the development of MLF activator extracts should be exploited.

AUTHOR CONTRIBUTIONS

Aitor Balmaseda: Data curation (equal); formal analysis (equal); investigation (equal); writing – original draft

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(equal). **Nicolas Rozès:** Formal analysis (equal); funding acquisition (equal); writing – review and editing (equal). **Albert Bordons:** Supervision (equal); writing – review and editing (equal). **Cristina Reguant:** Formal analysis (equal); funding acquisition (equal); project administration (equal); supervision (equal); writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare that this work was conducted in the absence of any known potential conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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