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ORIGINAL RESEARCH PAPER

Interaction between *Oenococcus oeni* and *Lactobacillus hilgardii* isolated from wine. Modification of available nitrogen and biogenic amine production

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Abstract During the mixed culture of *Lactobacillus hilgardii* 5w, a common spoilage wine bacteria and *Oenococcus oeni* X_2L, an amensalistic growth response of the malolactic bacteria was produced due to a competition for nitrogenous nutrients, mainly peptides. Arginine was fully consumed and peptide concentration diminished 60% with respect to both pure cultures at the end of exponential growth. Histamine release increased 34% with respect to *L. hilgardii* single culture. Under the poor nutritional conditions present during winemaking, *L. hilgardii* could increase histamine production and adversely affect malolactic fermentation conducted by *O. oeni* and hence the quality of the final product.

Keywords Amino acids · Histamine · Lactic acid bacteria · Mixed culture · Peptides · Wine

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Introduction

In the winemaking process, alcoholic fermentation is occasionally followed by malolactic fermentation (MLF), carried out by lactic acid bacteria (LAB) which mainly belong to *Oenococcus oeni* species. However, other LAB genera, such as *Pediococcus*, *Lactobacillus* and *Leuconostoc,* are also present in the process and can have positive or deleterious effects on the final product (Osborne and Edwards 2005). *Lactobacillus hilgardii* strains have been identified as wine spoilage bacteria (Rodríguez and Manca de Nadra 1995; García-Ruiz et al. 2009).

In natural environments, the interaction with the indigenous microflora could stimulate or restrict growth of malolactic wine bacteria (Manca de Nadra et al. 2006; Manca de Nadra and Aredes Fernández 2008). Proteins are an important carbon and nitrogen source for bacterial growth. The presence of proteolytic enzymes in the extracellular medium is important because small peptides and free amino acids are necessary to fulfil the numerous auxotrophies of wine bacteria and enable their growth in a poor nutritional ecological niche (Aredes Fernández et al. 2004; Remize et al. 2006; Ritt et al. 2008). Extracellular proteolytic activity of *O. oeni* X_2L (Rollan et al. 1993; Manca de Nadra et al. 1997, 1999, 2005; Farias and Manca de Nadra 2000) enables the organism to hydrolyze peptides and proteins from grape juice and autolysed yeast cells, which contributes to bacterial growth. However, the

amino acids released could also act as precursors of the amino acid decarboxylase activity of the starter cultures and/or wild microflora, and thus favor production of biogenic amines (Suzzi and Gardini 2003; Herbert et al. 2006; Soufleros et al. 2007; Izquierdo Cañas et al. 2008).

Lactobacillus hilgardii 5w has an absolute requirement for histidine, cysteine, tyrosine, threonine, tryptophan, valine, glycine, aspartic acid and arginine (Aredes Fernández and Manca de Nadra 2004) and possesses histidine decarboxylase activity (Farías et al. 1993, 1995).

Taking into account that a better understanding of interactions between malolactic bacteria and the wild microflora regarding available nitrogen could be helpful to optimize a commercial malolactic starter culture, the aim of this work was to evaluate the interaction between *O. oeni* X_2L and *L. hilgardii* 5w, a common wine spoilage bacterium. Growth parameters, proteins, peptides, amino acids and biogenic amines in pure and mixed cultures were analyzed in order to get a better understanding of the microbial relationship between both strains with respect to modification of the nitrogen content in the medium.

Materials and methods

Microorganisms

Oenococcus oeni X_2L and *Lactobacillus hilgardii* 5w were isolated from Argentine red wines (Manca de Nadra and Strasser de Saad 1987; Strasser de Saad and Manca de Nadra 1987).

Culture medium and growth conditions

The basal growth medium contained per l of distilled water: yeast extract, 10 g, Tween 80, 1 ml and natural white grape juice, 170 ml. The solution of yeast extract and Tween 80 was sterilized at 121°C for 20 min. Natural grape juice was heated in the autoclave to 121°C which was immediately turned off. Both fractions were pooled and pH was adjusted to 5.5 with sterile 1 M NaOH. The sterility of culture media was guaranteed controlling the microbial development after 7 days of incubation of fresh media at 30°C. Microorganisms were grown at 30°C. For mixed cultures, the inoculation rate was 1:1.

Growth measurement

Growth was measured from the OD_{560} value. Colony-forming units (c.f.u. ml^{-1}) were determined by plating 0.1 ml inoculated medium on basal medium supplemented with 20 g agar l^{-1}. From these data it was possible to calculate the average of growth rates. Growth yield were determined as the difference in cell concentration (log c.f.u. ml^{-1}) between stationary phase and inocula. Enumeration in mixed cultures was performed based on colony morphology and growth rate in agar plates, as previously described by Rodríguez and Manca de Nadra (1995). After 48 h, *L. hilgardii* 5w produced round, white colonies with irregular margins. After 120 h, *O. oeni* X_2L produced small (less than 1 mm diam.), round, smooth, white colonies. The means and reproducibility of the different growth parameters of each strain were calculated based on three independent determinations.

Analytic determinations

Protein nitrogen

The nitrogen concentration corresponding to protein, was determined following the Bradford method with BSA as standard. For expressing the results, molecular weight of BSA (66432 g mol^{-1}) and the number of nitrogen atoms in the molecule (10276 g mol^{-1}) were taken into account.

Total free amino acids and peptides

Free amino acids were quantified by the method described by Doi et al. (1981) (method 5), based on the reaction of ninhydrin/Cd with the free amino group. The results were expressed as mg of free amino nitrogen per liter. Free amino acids plus peptides, were determined following the conventional method with ninhydrin descripted by Doi et al. (1981) (method 1), based on reaction of the amino group with a mix of ninhydrin/Sn. The peptides were quantified by the difference between the results obtained by Doi's method 1 and method 5. The results were expressed in mg of peptide nitrogen per liter. The standard used in both determinations was leucine.

A discriminative analysis of the amino acids and biogenic amines modification was by HPLC (Alberto

et al. 2002). Samples were injected after filtration through a 0.45 μm filter. Results were expressed in mg/N per liter for each amino acid or amine detected. Triplicate analyses were performed.

Production of inhibitory substances

Production of inhibitory substances by *L. hilgardii* 5w against *O. oeni* X_2L was determined as described previously by Rodríguez and Manca de Nadra (1995). *O. oeni* X_2L culture of 24 h (10^8 c.f.u. ml^{-1}) was overlaid on basal medium agar (20 g l^{-1}). The supernatant fluids of *L. hilgardii* 5w obtained at different incubation times in basal medium were tested on these plates into which 10 mm hole had been punched and filled with 0.1 ml supernatant solution. H_2O_2 in culture supernatants of pure and mixed culture after different incubation periods was determined spectrophotometrically by the o-dianisidine/horseradish peroxidase method as described by Nuñez de Kairuz et al. (1988).

Statistical analysis

The data reported are the mean values of three independent experiments performed in duplicate. Experimental data were analyzed by ANOVA with repeated measurements. Variable means were compared using the Scheffe test. Statistica program for windows (ver. 7.0, StatSoft, Inc., 2006) were used for data processing. For growth experiments, the growth parameters means were compared using Student's *t*-test.

Results

Growth of pure and mixed cultures

Figure 1 shows that μ_{max} and the growth yield of *L. hilgardii* 5w in pure culture were higher than those observed for *O. oeni* X_2L ($P < 0.05$). In mixed culture, both growth kinetics parameters of *L. hilgardii* were similar to those obtained in pure culture while *O. oeni* showed a decrease of 37% in μ_{max} and 35% in the growth yield.

Lactobacillus hilgardii supernatant from pure or mixed culture did not produce inhibition of *O. oeni* growth on agar plates. *L. hilgardii* did not produce H_2O_2 during growth in pure or mixed cultures.

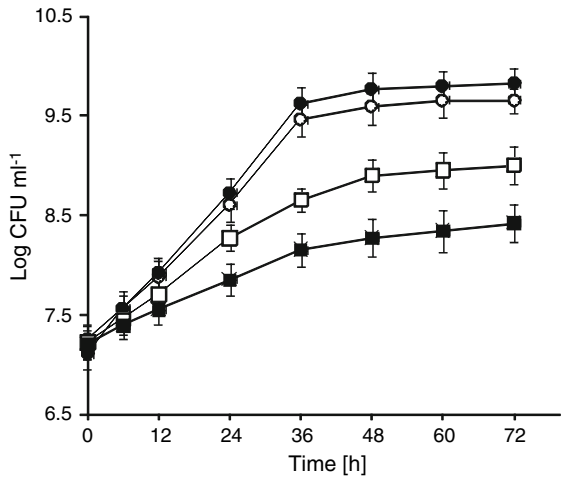

Fig. 1 Population dynamics of *Lactobacillus hilgardii* 5w in pure (*open circle*) and mixed culture (*filled circle*); and *Oenococcus oeni* X_2L in pure (*open square*), and mixed (*filled square*) culture. Values are the means of three independent determinations performed in duplicate

Modifications of proteins, peptides and amino nitrogen

Figure 2 shows a decrease of 1.49 mg N l^{-1} of protein nitrogen and 0.73 mg N l^{-1} of free amino nitrogen in the culture medium supernatant at the beginning of the exponential growth phase of *L. hilgardii* (12 h of incubation). At the same time, a release of 2.01 mg N l^{-1} of peptides was detected. From 12 h onward, protein nitrogen did not modify significantly. After 48 h of incubation, the microorganism consumed 1.43 mg N l^{-1} of amino nitrogen and at the end of the incubation period the microorganism accumulated a total consumption of 2.53 mg N l^{-1} of complex nitrogen.

After 12 h of incubation of pure cultures of *O. oeni* X_2L, a decrease of 2.11 mg N l^{-1} in protein nitrogen could be observed. At the same time, amino and peptide nitrogen increased with 0.6 and 0.9 mg N l^{-1}, respectively. Between 12 and 24 h, no significant modification was detected. After 48 h of incubation, consumption of 0.56 mg N l^{-1} of protein nitrogen was detected, whereas nitrogen from amino acids and peptides was not significantly modified; total accumulative consumption of complex nitrogen by the microorganism was 1.50 mg N l^{-1}. During the stationary growth phase the microorganism consumed 0.84 mg N l^{-1} of peptides and total consumption of complex nitrogen was 2.61 mg N l^{-1} at the end of the incubation period.

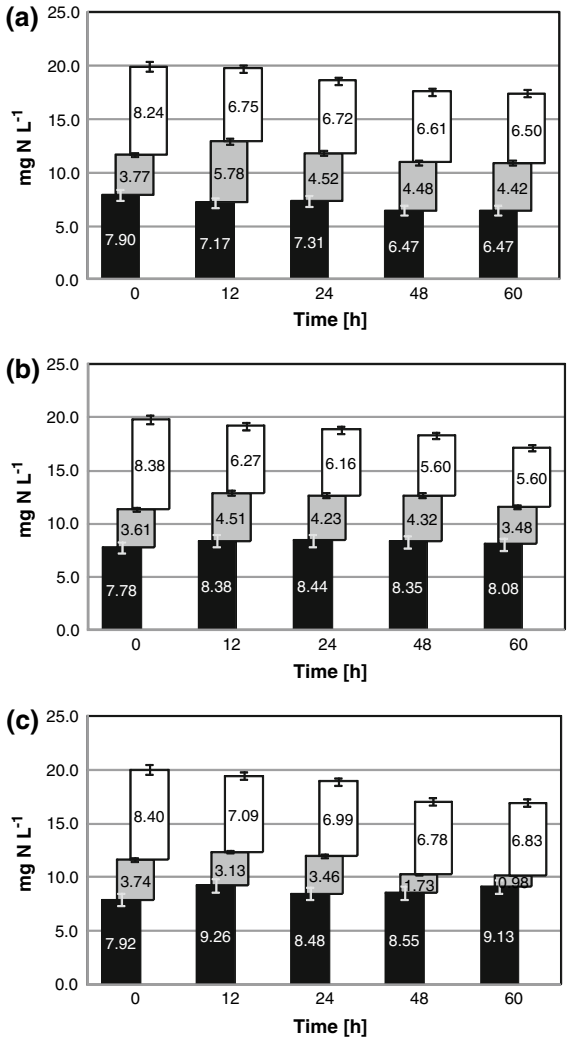

Fig. 2 Changes in protein nitrogen (*open square*), peptide nitrogen (*gray color filled square*) and free amino nitrogen (*filled square*) in **a** *Lactobacillus hilgardii* 5w **b** *Oenococcus oeni* X_2L and **c** mixed culture. Values are the means of three independent determinations performed in duplicate

After 12 h of incubation in mixed culture, a consumption of 1.31 mg N l^{-1} of protein nitrogen was observed, as well as a diminution in peptide nitrogen (0.62 mg N l^{-1}) and a release of amino nitrogen (1.34 mg N l^{-1}). From this time onward, protein nitrogen remained invariable and peptide consumption was progressive, with a final consumption of 2.76 mg N l^{-1}. Total complex nitrogen consumption after 48 h was high: 3 mg N l^{-1}. At the end of the incubation time 3.12 mg N l^{-1} of complex nitrogen was consumed.

Modification of amino acids in pure and mixed cultures

Modification of the amino acid concentration of *L. hilgardii* and *O. oeni* in pure and mixed cultures are shown in Fig. 3. After 12 h of incubation of pure culture of *L. hilgardii*, a significant decrease was observed in the arginine concentration, despite a slight increase in most of the other amino acid concentrations. A consumption of 0.23 mg N l^{-1} of arginine and a release of 0.19 mg N l^{-1} of ornithine were detected. After 48 h, arginine was completely consumed from the culture medium. In a pure culture of *O. oeni,* concentrations of most amino acids increased until 24 h of incubation, whereas arginine increased until the end of the exponential phase of growth. In mixed culture, most amino acids were not significantly modified after 12 h of incubation. However, after 12 h significant arginine consumption (0.16 mg N l^{-1}) was observed and after 48 h of growth the medium was depleted of this amino acid. Moreover, even though ornithine increased during the first stage of incubation (12 h), from this time onwards, this amino acid was consumed (0.043 mg N l^{-1}).

Histamine production

Table 1 shows the modification of histidine and histamine concentrations in pure and mixed cultures of *L. hilgardii* and *O. oeni*. In a pure culture of *L. hilgardii* 5w, histidine consumption reached 0.036 mg N l^{-1} after 48 h of incubation and at the same time histamine release was 0.029 mg N l^{-1}.

Despite the histidine modification during microbial growth, production of histamine was not detected in pure *O. oeni* X_2L culture.

In mixed culture, a significant increase ($P < 0.05$) in histamine release was observed after 48 and 60 h with respect to pure culture of *L. hilgardii*. A consumption of 0.019 mg N l^{-1} of histidine with a release of 0.017 mg N l^{-1} of histamine was detected after 12 h of incubation. Histamine release after 48 and 60 h of incubation was 0.037 and 0.044 mg N l^{-1}, respectively.

Despite modifications of other biogenic amine precursors (Orn, Lys, Tyr, Arg and Trp), histamine was the only biogenic amine detected in all samples assayed.

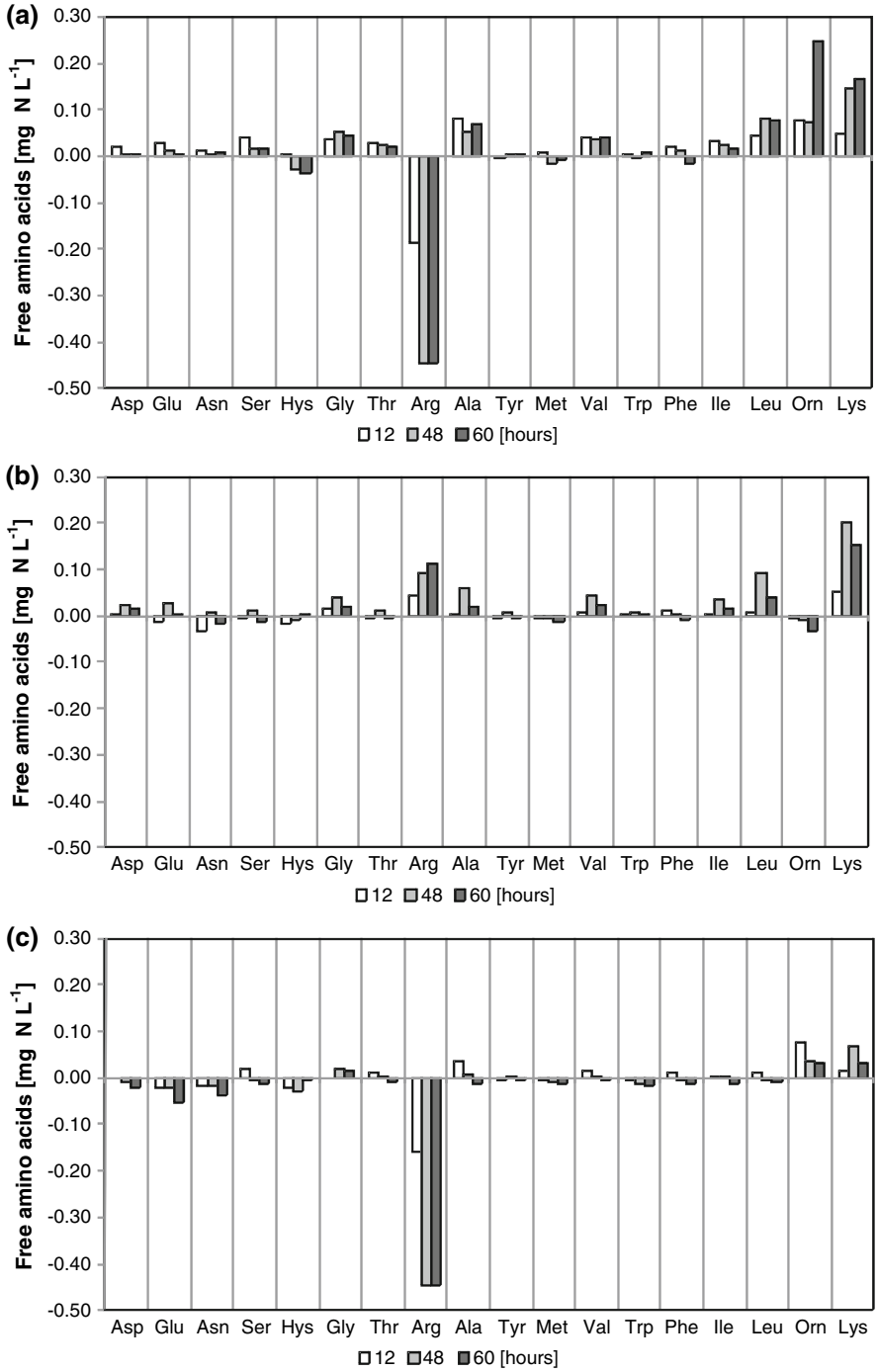

Fig. 3 Modification of amino acid profile by pure cultures of *Lactobacillus hilgardii* 5w (**a**), *Oenococcus oeni* X_2L (**b**) and mixed culture (**c**). The values of the amino acids are the differences between the concentration observed a each time and the values estimated in the basal medium (t0). Initial concentration of each amino acid was in mg N l^{-1}: Asp, 0.16; Glu, 0.5; Asn, 0.28; Ser, 0.21; His, 0.1; Gly, 0.16; Thr, 0.16; Arg, 0.46; Ala 0.46; Tyr, 0.04; Met, 0.07; Val, 0.2; Trp, 0.05; Phe, 0.14; Ile, 0.21; Leu, 0.31; Orn, 0.12; Lys, 0.34. Values are the means of three independent determinations performed in duplicate

Discussion

Pure cultures of *O. oeni* X_2L and *L. hilgardii* 5w showed a different behavior concerning growth kinetics and release of extracellular amino acids. Co-culturing of both strains diminished the growth yield of *O. oeni* but this decrease was not due to inhibitory substances or low pH. However, different results were reported by Rodríguez and Manca de Nadra (1995) who observed that the H_2O_2 production by *L. hilgardii* X_1B restricted growth of *O. oeni* X_2L in mixed culture.

Table 1 Histidine and histamine modification in pure and mixed culture of *L. hilgardii* 5w and *O. oeni* X_2L

	Time	Histidine (mg N l^{-1})	Histamine (mg N l^{-1})
Lactobacillus hilgardii 5w	0	0.109 ± 0.006	0.017 ± 0.003
	12	0.106 ± 0.005	0.040 ± 0.005
	48	0.074 ± 0.004	0.046 ± 0.003
	60	0.065 ± 0.004	0.050 ± 0.004
Oenococcus oeni X_2L	0	0.103 ± 0.004	0.016 ± 0.002
	12	0.087 ± 0.003	0.013 ± 0.003
	48	0.096 ± 0.004	0.015 ± 0.004
	60	0.103 ± 0.005	0.014 ± 0.003
Mixed culture	0	0.102 ± 0.005	0.019 ± 0.004
	12	0.083 ± 0.002	0.036 ± 0.002
	48	0.074 ± 0.004	0.056 ± 0.003
	60	0.102 ± 0.007	0.063 ± 0.005

[a] Values are the means of three independent determinations ± standard deviations

In the early exponential growth phase (until 12 h of growth) of pure culture of *L. hilgardii* 5w, protein consumption and peptide release evidenced the presence of proteolytic activity in this microorganism. Besides, at this growth stage a higher consumption of arginine and histidine, two amino acids essential for bacterial growth, was detected. From 12 h onward, protein consumption remained unchanged suggesting that the proteolytic activity could be negatively regulated by an increase in peptides. From 12 to 24 h, growth of the microorganism would be mainly supported by the peptides and from this time amino acid uptake satisfied the nutritional requirements to reach the maximal biomass (9.7 log c.f.u. ml^{-1}) at the end of *L. hilgardii* growth.

Previous reports evidenced the presence of two extracellular proteolytic enzymes during the exponential growth phase of *O. oeni* X_2L (Rollan et al. 1993; Farías et al. 1996). Our results revealed protein intake associated with an increase in peptides after 12 and 48 h of growth, consistent with the appearance of two peaks of proteolytic activity previously reported (Rollan et al. 1993). Release of amino acids, mainly non-essential ones (Gly, Arg, Lys, Val and Leu), could also be observed. According to Ritt et al. (2008), peptide utilization by *O. oeni* is linked to the release of hydrophobic amino acids. In our study, the release of hydrophobic amino acids (Ala, Val, Leu and Lys) observed could involve peptide utilization due to proteolytic activity of *O. oeni* X_2L.

Our results show that most of the amino acids were consumed in small quantities in pure and mixed cultures, which is in accordance with findings reported by Remize et al. (2006). These authors hypothesized that, except arginine and lysine, quantitative needs of *O. oeni* for amino acids to ensure growth are considerably low.

In mixed culture, the higher peptide consumption observed during growth compared to pure cultures could be related to their utilization as a primary nitrogen source to support growth of both microorganisms at the early stage of the growth phase. Previous reports (Aredes Fernández et al. 2004; Remize et al. 2006; Ritt et al. 2008) have evidenced that bound amino acids or, more precisely, dipeptides and oligopeptides are efficiently used by *O. oeni* to sustain growth. Their utilization allows this bacterium to fulfil its amino acid requirements. *O. oeni* is demanding in terms of quality of the nitrogen source, but its quantitative needs for nitrogen are low due to the low biomass reached by this microorganism (Remize et al. 2006). Peptides are considered a genuine source of essential amino acids and, as previously reported by Konings (2002), transport of peptides rather than amino acids saves a considerable amount of energy. Thus, the significant depletion of peptides in mixed culture by *L. hilgardii* could restrict growth of *O. oeni* and make its proteolytic system ineffective. Furthermore, under the current culture conditions, total consumption of arginine, reported to be a stimulant for growth of *O. oeni* (Aredes Fernández and Manca de Nadra 2004), would be responsible for a competitive interaction between both microorganisms. Different results were reported by Aredes Fernández and Manca de Nadra (2006), who demonstrated that *O. oeni* X_2L in a mixed culture with *Pediococcus pentosaceus* 12p exhibited a mutualistic growth response owing to stimulation of the proteolytic system of *O. oeni*.

Total arginine consumption and ornithine release at the end of the exponential growth phase of *L. hilgardii* 5w suggest presence of the arginine deiminase (ADI) pathway.

This system was previously reported in *L. hilgardii* X_1B isolated from wine (Arena et al. 2002). In addition, consumption of ornithine could be related to

the production of biogenic amines (Arena and Manca de Nadra 2001, 2005).

Our previous results revealed that pure cultures of *L. hilgardii* 5w isolated from wine were able to produce histamine from histidine due to histidine decarboxylase—HDC—(Farías et al. 1993, 1995). The authors also determined that maximum HDC activity was observed in the middle and at the end of the logarithmic growth phase; after that activity decreased. Presence of the *hdc* gene in this strain was reported by Landete et al. (2005). These authors utilized *L. hilgardii* 5w as positive control of a histamine producer strain. However, in mixed culture with *O. oeni* X_2L no quantitative correlation between histamine production and histidine consumption was observed during the first hours probably due to utilization of other histamine precursors like histidine-containing peptides. Suzzi and Gardini (2003) reported that a *Lactobacillus curvatus* strain produced tyramine from di- and tripeptides containing tyrosine. No significant difference in histamine concentration was detected in mixed culture compared with pure culture of *L. hilgardii* 5w during the early exponential growth phase. However, both culture conditions showed an increase in histamine production at the end of this growth phase, probably due to energetic requirements of *L. hilgardii*. At this stage, when the medium is depleted of arginine, *L. hilgardii* 5w cannot utilize arginine via the ADI system to produce ATP, and histidine decarboxylation could supply additional energy to maintain the cells viability. Konings (2006) demonstrated that amino acid decarboxylation reactions generate additional metabolic energy or regulate intracellular pH, which allows bacterial survival in poor or acid environments. Mazzoli et al. (Mazzoli et al. 2009) reported that *Lactobacillus hilgardii* ISE 5211, isolated from an Italian red wine, converted arginine into ornithine and histidine into histamine. These authors also reported that presence of arginine repressed biosynthesis of HDC and delayed accumulation of histamine in wines.

The current paper provides information on nitrogen metabolism during the interactions between *O. oeni*, a microorganism generally involved in malolactic fermentation in wine, and *L. hilgardii* 5w, a wine spoilage bacterium. In co-culture, competition for nitrogenous nutrients produces a negative growth response, decreasing the growth yield of *O. oeni* X_2L (amensalism). During winemaking, presence of the spoilage *L. hilgardii* 5w could favor histamine production. Moreover, under the poor nutritional conditions present during winemaking, the amensalistic interaction between *L. hilgardii* 5w and *O. oeni* could negatively affect malolactic fermentation, hence the quality of the final product.

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