Targeting Demalication and Deacetification Methods: The Role of Carboxylic Acids Transporters

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Received date: November 17, 2017; **Accepted date:** November 28, 2017; **Published date:** December 05, 2017

Abstract

As weak organic acids, carboxylic acids partially dissociate in aqueous systems, like wine, establishing equilibrium between uncharged molecules (undissociated form) and their anionic form, according to the medium pH and their pKa. This property influences yeasts cell-behaviour, particularly the mechanisms by which the molecules can cross biological membranes. Occasionally wines may present an excessive amount of organic acids. In the mouth they will seem unbalanced and sometimes excessive sourness diminishes their quality. Moreover, these acids originated from grapes or from the fermentation process itself, negatively affect wine yeasts, yeast fermentation process and the final wine quality. Two of those acids are L-malic acid and acetic acid. The first one affects the wine mainly in his tastiness, making it much to sour; the second one, being a volatile compound, besides the excessive

As mentioned above, the ability of yeasts strains to degrade extracellular L-malate is dependent on the e f cient transport of the dicarboxylic acid into the cell. In *Kluyveromyces lactis* the transport of this acid is carrier-mediated [17] as it is also in *Z. bailii*, able to transport malic acid by facilitated di f usion (Figure 1, A1). In this later strain, malic acid transport is induced by glucose and repressed by fructose [18].

In *S. cerevisiae* L-malate enters the cells by simple di f usion (Figure 1, A2), while in the yeasts *Candida utilis*, *Candida sphaerica*, *Hansenula anomala* and *Kluyveromyces marxianus* the transport of malate is performed by a proton symport/induced (Figure 1, A3) and glucose repressed system [11,19-21]; *Schizosaccharomyces pombe* also possesses a proton symport system (maelp) (Figure 1, A3) [11]. Recently, in the article Vilela [22], we have made some considerations about these transport systems.

Figure 1: Schematic representation of the yeast plasma membrane and the several malic acid acids transport systems in the yeast cell: A1-Permease channel; A2-Simple di f usion system; A3-Proton symport mediated; A4-Pump associated with yeast stress responses due to acid anion (XCOO-) accumulation inside the cell cytoplasm [23].

A f er entering the yeast cell L-malate must enter the yeast mitochondria. T e Dic1p dicarboxylates carrier protein was isolated and studied by Lancar-Benba et al. [24]. T is carrier transports malate (Km=0.56 mM) [25] succinate or malonate. T e main function of the Dic1p carrier is to transport dicarboxylates from the cytoplasm into the mitochondria, being an anaplerotic transporter for the Krebs cycle [26].

Another mitochondrial aspartate/glutamate carrier named Agc1p [26], as also being studied. T is transporter plays a role in the malate/ aspartate shuttle, and this role is critical for growth on acetate and fatty acids.

Odc1p and Odc2p carriers (61% identical to each other) transport and kinetic properties show that they are isoforms of a novel mitochondrial transporter. T ey transport oxoadipate and oxoglutarate and the corresponding dicarboxylates and malate by a counter-exchange mechanism [27]. T e expression of Odc1p is strongly repressed by glucose and galactose, whereas Odc2p is expressed on all carbon sources that were tested [27]. So, under respiratory conditions Odc1p is the major carrier, and in the presence of glucose and anaerobiosis Odc2p is the one that dominates. An important physiological role of the oxodicarboxylate carrier in yeast is to export oxoglutarate, in exchange for malate, to the cytoplasm [26].

Saccharomyces transporter proteins that facilitate deaceti f cation process

S. cerevisiae is able to metabolize acetic acid during a refermentation process [6,28]. Several works have being done about this subject [1,7,8,28,29] and they all agree that excessive volatile acidity can be removed by refermentation with an appropriate *S. cerevisiae* wine yeast. T e transport of acetate into the yeast cell is an imperative step for its metabolism [1]. In glucose-repressed yeast cells, at low pH, acetic acid enters mainly by simple di f usion [30]. However, Jen1p, a transport carrier studied by Casal et al. [31], required for the uptake of lactate in *S. cerevisiae* is also able to transport acetate (Figure 2).

At pH 4.5 passive di f usional f ux of undissociated acetic acid into

Later, it was found that the protein Ady2p was vital for acetate transport in acetic acid-grown cells [33]. Jen1p mediates the transport of lactate, pyruvate, acetate and propionate whereas Ady2p mediates the transport of acetate, propionate, formate and lactate, being both induced by non-fermentable carbon sources, and repressed in the presence of glucose [34].

Exposure of *Saccharomyces cerevisiae* to sorbic acid strongly induces two plasma membrane proteins, one of which was identified as the ATP-binding cassette (ABC) transporter Pdr12 [35]. It was later found that overexpression of PDR12 increased tolerance to acids with longer chain length, such as sorbic, propionic and levulinic, whereas deletion of the gene increased tolerance to the shorter acetic and formic acid [36]. The induction of a weak acid efflux pump (Pdr12)

28. Vilela-Moura A, Schuller D, Falco V, Mendes-Faia A, Côrte-Real M (2010) Effect of refermentation conditions and micro-oxygenation on the reduction of volatile acidity by commercial *S. cerevisiae* strains and their impact on the aromatic profle of wines. Int. J Food Microbiol 141: 165-172.