DOROTA KRĘGIEL

Institute of Fermentation Technology and Microbiology
Technical University of Lodz

PHYSIOLOGY AND METABOLISM OF CRABTREE-NEGATIVE YEAST *DEBARYOMYCES OCCIDENTALIS*

Review: Professor Wojciech Ambroziak, Ph. D., D. Sc.

This paper is focused on the physiology and metabolism of non-conventional yeasts, especially these belonging to Debaryomyces (syn. Schwanniomyces) occidentalis. In these Crabtree-negative yeast strains, oxygen limitation induces alcoholic fermentation as well as activity of the key fermentative enzymes, pyruvate decarboxylase (PDC) and alcohol dehydrogenase (ADH).

1. Introduction

Yeast metabolism is widely exploited in many biotechnological processes, i.e. in the production of alcohol, wine, beer or bread [4, 8, 16]. Other fields include expression of heterologous proteins and fuel alcohol production [44]. However, yeast metabolism can also cause spoilage of food by production of different unwanted aroma compounds, gas or alcohols [14].

The yeast *Saccharomyces cerevisiae* is the most commonly used species in biotechnological applications and is by far the most dominating species in yeast research. The term "yeast" has in some contexts been used as a synonym to the species name *S. cerevisiae*. However, the properties of *S. cerevisiae* do not represent those of all yeast genera. Among the approximately 1500 recognized yeast species, only few ones are used commercially. The physiological and metabolic properties of a large group of non-*Saccharomyces* yeast have not yet been described.

The yeast *Schwanniomyces occidentalis* was isolated in 1909 from the soil of St. Thomas island in the West Indies by Klocker [24]. Then other species belonging to this genera that assimilate diverse carbon sources were isolated. All of these *Schwanniomyces* sp. strains show six or seven chromosomal DNA bands and similar profiles after electrophoresis. The current taxonomic classification of *Schwanniomyces occidentalis* has changed these strains into *Debaryomyces occidentalis* because no

significant difference in the sequences of 18S and 25S of ribosomal RNA between *Schwanniomyces* and *Debaryomyces* was found [46].

The yeast belonging to *Debaryomyces* genera occurs naturally in many food and feed environments. This yeast has attracted great attention due to its capacity to grow on unusual carbon sources. Some of the strains of *Debaryomyces occidentalis* produce a killer toxin lethal to sensitive *Saccharomyces cerevisiae* strains [5]. There are no reports in the literature on hazardous mycotoxin formation or the production of allergenic substances from this yeast [48]. These facts stimulate studies on improving *Schwanniomyces* sp. growth rate, biomass or ethanol production and monitoring starch hydrolysis with the use of different techniques including protoplast mutation, protoplast fusion and transformations systems [11, 12, 30, 31, 35, 36, 46, 48].

2. Yeast metabolism

All yeasts described so far can use glucose as a sole carbon source [1]. The metabolic pathways of the central carbon metabolism are generally the same among different yeast species. However, the number of isoenzymes and genes, the mechanisms for nutrient uptake, transport, and the regulation of fermentation and respiration diversify yeasts principally. In many strains glucose is transported across the membrane by facilitated diffusion [15, 20, 26, 29]. Facilitated diffusion is mediated by permease, a membrane protein, down a concentration gradient without the consumption of energy, whereas energy consuming H^+ symport can regulate glucose influx in non-*Saccharomyces* yeasts [13, 15, 38].

Based on the ability to perform and regulate alcoholic fermentation, all yeasts can be grouped as obligate aerobes, i.e., yeasts that are incapable of alcoholic fermentation, or facultative aerobes, i.e., yeasts that are capable of producing ethanol. The facultative aerobes can be further grouped into respiratory yeasts, i.e. the yeasts that induce alcoholic fermentation in response to oxygen limitation, or the fermentative yeasts, which produce ethanol during aerobic batch cultivation on glucose [16, 19]. In the facultative aerobes the resulting flux distribution depends on the environmental conditions, i.e. absence/presence of oxygen, concentration of sugar and on strains used.

In yeasts several regulatory phenomena – regulatory effects were described, including the Pasteur effect, the Crabtree effect, the Custers effect and the Kluyver effect. The most known are three first. The Pasteur effect is the inhibition of sugar fermentation by aerobiosis. In *Saccharomyces cerevisiae*, this phenomenon is only observed under special experimental conditions, notably at very low dilution rates in the chemostat and in resting-cell suspensions. The mechanism of this effect is probably the higher affinity for one of the intermediates pyruvate, acetaldehyde and NAD of respiratory system over the fermentative route [25].

The Custers effect is the inhibition of alcoholic fermentation when a yeast culture is transferred from oxygen-limited to anaerobic conditions. The Crabtree effect is described as the occurence of alcoholic fermentation under aerobic conditions after glucose pulse [10]. The Crabtree-effect – aerobic fermentation by *S. cerevisiae*, was seen as the opposite of the Pasteur effect – inhibition of fermentation by respiration and has been known as the Pasteur contre-effect. Therefore, the yeasts that produce ethanol at aerobic conditions are Crabtree-positive, whereas yeasts that do not are Crabtree-negative.

The fermentative, Crabtree-positive yeasts include the genera: *Saccharamomyces, Zygosaccharomyces, Dekkera,* and *Schizosaccharomyces*. The best known yeasts are respiratory and include strains belonging to the genera: *Pichia, Debaryomyces, Candida* or *Kluyveromyces* [7, 41]. Several differences were revealed between Crabtree-positive and Crabtree-negative yeast strains, including different kinetics of glucose uptake, rate of glycolysis and glycogen formation and the levels of a number of key enzymes involved in pyruvate metabolism. In Crabtree-positive ethanol production rates showed a clear positive correlation with the level of pyruvate decarboxylase. All Crabtree-positive yeasts contain higher levels of this fermentative key enzyme than the Crabtree-negative yeasts. Furthermore, high activity of acetaldehyde dehydrogenase and acetyl-CoA synthetase was observed in Crabtree-negative strains.

3. Regulation of respiration and fermentation

In *S. cerevisiae* yeasts, alcoholic fermentation is induced by the addition of excess glucose to aerobically grown cells [42]. This phenomenon called the Crabtree effect has been a subject to many studies and reviews [10, 13, 19, 22]. The fermentation rate of the yeasts upon transition from glucose limitation to glucose excess is positively correlated with the level of pyruvate decarboxylase (PDC) (EC 4.1.1.1).

In maximally aerated conditions and at high glucose concentration (about 20 g per liter), *Debaryomyces occidentalis* and other non-*Saccharomyces* strains dissimilate glucose predominantly by respiration. In the Crabtree-negative yeasts PDC activity is low and is not increased after adding glucose. However, in these strains there are relatively high activities of acetaldehyde dehydrogenases (EC 1.2.1.4 and EC 1.2.1.5) and acetyl-CoA synthetase (EC 6.2.1.1) [39]. Significant ethanol production is generally absent in Crabtree-negative yeasts in aerobic conditions, but a temporary production of ethanol has also been seen [7, 21, 42].

It is established that the difference between the Crabtree-positive and Crabtree-negative yeasts depends on the differences in the kinetics of glucose uptake, synthesis of reserve carbohydrates and pyruvate metabolism. The Crabtree-positive yeasts exhibit a higher rate of glucose consumption than the Crabtree-negative species. However, non-*Saccharomyces* yeasts generally produce and accumulate more glycogen as a reserve carbohydrate. This fact results in a low glycolytic rate [39].

3.1. Kluyver effect

Taxonomists have known for a long time that many yeasts can assimilate certain mono- and oligosaccharides aerobically, but not anaerobically [1, 2, 34]. These yeasts are yet capable of fermenting glucose as well as one or more components of these oligosaccharides. The phenomenon, known under the classical name of the Kluyver effect, has been described in many yeasts for the utilization of galactose, maltose, ramnnose, lactose, sucrose, cellobiose, etc. The Kluyver effect is associated with specific combinations of yeast species and sugars [9, 10]. For example, *Debaryomyces robertsiae* is Kluyver effect positive on galactose and Kluyver effect negative on maltose, whereas *Candida kruisli* and *Pichia heimii* are, on the contrary, Kluyver effect negative on galactose, and positive on maltose. *Saccharomyces cerevisiae*, which has a predominantly fermentative mode of life, is Kluyver effect negative on most sugars [18].

The Kluver effect appears to be a combination of the following four factors: fast transport of the glucosides into the cells which involves proton symport and ATP synthesis; in anaerobic conditions the transport carrier may have a lower substrate affinity; glycosidases generally have low substrate affinities. The consequence of these factors is a lowering of glycolytic flux and deactivation of pyruvate decarboxylase [3]. It was proposed that the Kluyver effect may be caused by feedback inhibition of sugar utilization by ethanol, the product of metabolism [24, 47]. The Kluyver effect has been observed in nearly 100 yeast species [18]. Strains belonging to *Debaryomyces* sp. display the Kluyver effect on lactose, maltose and starch. For these strains the Kluyver effect for maltose and starch is related to the absence of synthesis of the corresponding hydrolases [17, 44].

3.2. Cyanide insensitive respiration

As defined by van Dijken and co-workers [10], the Crabtree effect is the occurrence of alcoholic fermentation under strictly aerobic conditions in the presence of excess sugar. Therefore, the proposal is that while Crabtree-positive yeasts display, under aerobic conditions, the fermentation pathway as an option to the cytochrome pathway, Crabtree-negative and non-fermentative yeasts, i.e. *Debaryomyces* sp. display a cyanide-resistant alternative pathway (CRR) [23, 28, 33, 40, 43, 49].

The occurrence of CRR is very frequent among yeasts, so it is proposed that, as an alternative to cytochrome respiration, yeasts have developed two strategic catabolic pathways: either aerobic fermentation in the so-called Crabtree-positive yeasts, or CRR pathway in non-fermentative and Crabtree-negative yeasts – capable of fermentation but not under aerobic conditions. Only a relatively small number of yeasts is capable of aerobic fermentation and only in these CRR has not been found [41].

The CRR uses electrons from the ubiquinone pool to reduce oxygen to water, by passing complex III and cytochrome oxidase, two sites of energy conservation in the main respiratory chain (MRC). An alternative oxidase, sensitive to salicylhydroxamic acid (SHAM), is responsible for this alternative pathway.

It has been also proposed that the CRR pathway could serve a regulatory function as an "overflow" for excess electrons when the cytochrome pathway is saturated or limited, allowing the turnover of the TCA cycle to continue and supplying carbon skeletons for biosynthetic demands. The bypassing of the two cytochrome complexes in MRC results in a reduced proton gradient and ATP production compared to that of normal respiration [41]. The alternative respiration can be induced by addition of antimycin A or cyanide, which inhibits MRC. This implies that the alternative pathway has a role in sustaining growth when the main respiratory chain is inactive [45]. It has also been proposed that the alternate pathway respiration is induced under different stress conditions as a mechanism that allows the cell to survive by responding to such conditions [39].

3.3. Pyruvate

Pyruvate is a key intermediate in sugar metabolism, located at the end of glycolysis at the branch point between fermentation and respiration (Fig. 1).
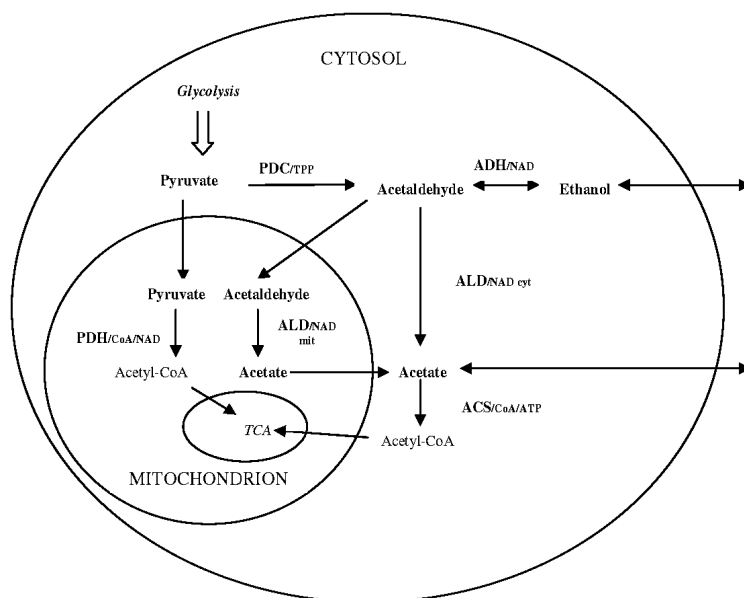

Figure 1. Pyruvate metabolism in *Saccharomyces cerevisiae*. Enzymes: **PDC** – pyruvate decarboxylase; **PDH** – pyruvate dehydrogenase; **ADH** – alcohol dehydrogenase; **ALD cyt** – cytosolic acetaldehyde dehydrogenase; **ALD mit** – mitochondrial acetaldehyde dehydrogenase; **ACS** – acetyl-CoA synthetase.

The pyruvate metabolism of *S. cerevisiae* has been reviewed by Pronk and co-workers [32]. Pyruvate can either be transported into the mitochondrion and oxidatively decarboxylated to acetyl-CoA by the multi enzyme complex of pyruvate dehydrogenase (PDH), or decarboxylated to acetaldehyde by pyruvate decarboxylase (PDC) in the cytosol. Based on the fact that the affinity for pyruvate of PDH is much higher than that of PDC, the split between respiration and fermentation should be determined by the intracellular pyruvate concentration. When the intracellular pyruvate concentration is low, pyruvate metabolism occurs predominantly via PDH, and at higher intracellular pyruvate concentrations the flux via PDC will increase.

3.4. Ethanol and acetate

The conversion of pyruvate to acetaldehyde by PDC does not necessarily result in ethanol formation, since acetaldehyde can also be converted to acetate, which in turn can be converted to acetyl-CoA (Fig. 1). The formation of acetate from acetaldehyde can take place both in the mitochondria and in the cytosol. From acetate, acetyl-CoA can be formed via acetyl-CoA synthetase (ACS) in the cytosol [32]. This indirect pathway from pyruvate to respiration of acetyl-CoA is known as the PDH bypass pathway. All Crabtree-negative yeasts have active acetaldehyde dehydrogenase and can produce acetate. Acetate accumulation inside the cell can generate a high turgor pressure as well as influence free radical production leading to oxidative stress. Most of the intracellular acetate is in the dissociated form since the intracellular pH is higher than 4.75, which is the pKa value for acetic acid and the passive diffusion of acetic acid is therefore slow. However Crabtree-negative yeasts excrete little or any acetate because this compound is immediately metabolized to acetyl coenzyme A by active acetyl-CoA synthetase [39].

Ethanol and acetate can both inhibit yeast growth if present at high concentrations. Ethanol can alter the membrane structure and permeability [6, 27, 37] and yeasts of *Debaryomyces* sp. show a low ethanol tolerance [46, 48].

CONCLUDING REMARKS

Generally, yeasts are a morphologically homogenous group of organisms, however their genetic and metabolic diversity makes it hard to transfer informations from one yeast species to another. The division of yeast species into Crabtree-positive and Crabtree-negative yeasts is useful at the level of general metabolic flux responses to glucose and oxygen limitation. A comparative analysis of several yeast species will increase the knowledge of single species, and also contribute to our general understanding of yeast metabolism [16]. *Debaryomyces occidentalis* produces different extracellular enzymes such as α-galactosidase, β-glucosidase, inulinase, invertase, phytase and amylolytic enzymes: α-amylase and glucoamylase, so this yeast can completely hydrolyze soluble starch and its derivatives.

D. occidentalis can also produce unknown enzymes to degrade the wood hydrolysate of lignocellulosics with levoglucosan It has been described as a "super yeast" because this yeast may be a useful alternative to *S. cerevisiae* in the production of heterologous proteins. Additionally, *D. occidentalis* was used to produce ethanol directly from starch and its derivatives [46]. The knowledge of yeast metabolism and regulatory effects will be helpful in application of these nonconventional, Crabtree-negative strains in large-scale fermentations for the production of heterologous proteins, ethanol or other metabolites. It will be probably a common industrial practice by the start of this century.

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FIZJOLOGIA I METABOLIZM CRABTREE-UJEMNYCH DROŻDŻY *DEBARYOMYCES OCCIDENTALIS*

Streszczenie

W oparciu o dane literatury przedstawiono fizjologię i metabolizm niekonwencjonalnych drożdży należących do *Debaryomyces occidentalis*. U tych drożdży tlen indukuje proces fermentacji i aktywność kluczowych enzymów: dekarboksylazy pirogronianowej (PDC) i dehydrogenazy alkoholowej (ADH).

Instytut Technologii Fermentacji i Mikrobiologii
Politechniki Łódzkiej