Yeast metabolic adaptation to environment

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ABSTRACT

Yeast metabolism has been a subject of research since the XIX century, when Louis Pasteur had proved that yeast are live organisms and fermentation is one of the processes to produce molecular energy. Yeast ability to ferment is a consequence of alcohol dehydrogenase (ADH) activity, the group of enzymes responsible for sugar conversion to ethanol as ADH1, and alcohol metabolism as a source of carbohydrates (ADH2). The group of ADH enzymes play a crucial role for yeast adaptation especially in rich sugar environments such as after angiosperm occurrence. Evolution of yeast genes is based on chromosomal multiplication event, previously explained as a Whole Genome Duplication (WGD), presently it has been proven that the yeast common ancestor is a hybrid from different strains. Duplication cause that some multiplies genes accumulate mutation without cell growth burden and consequently favor formations exploiting new features of proteins. Yeast ability to ferment make them dominate in a sugar environment, however Saccharomyces cerevisiae evolve some quorum-sensing mechanism, which plays crucial role in population messengers as tyrosol which is signaling about cellular density in culture. Moreover there are scientific reports about yeast specific social-wraps which suggest that yeast surviving depends on more complex mechanisms, which pose challenges for researchers. The aim of this article is a short review of yeast metabolic strategy which allow yeast to dominate in high sugar environments and abilities which make yeast so important in nature.

Keywords: alcohol dehydrogenase, yeast metabolism, adaptation, quorum-sensing substance
1. INTRODUCTION

Yeast especially from *Saccharomycota* subdivision are microorganisms commonly used in science as a model organism, industry as a source of nutrients and base of some processes as fermentation. Yeast naturally exist on plants especially on leaves and flowers, they are present in water soil and even on skin surfaces. Since ancient people prepared alcohol beverages, even though they were unaware of yeast presence on equipment, on their clothes, skin and also in air. Nowadays yeast are used consciously alcohol production, where they are used for their ability to convert sugars into ethanol, and their metabolism is directed by optimal growth condition to maximize efficiency of fermentation. Yeast multiply by budding (*Saccharomyces*) and some species by directed divisions (*Schizosaccharomyces*) [1]. Yeast optimal conditions for growth depends on strain (lager, ale) and are created by metabolic strategy [2].

2. THE HISTORY OF YEAST METABOLIC RESEARCH

Yeast metabolism is discovered since XIX century, when fermentation process had been tested by Louis Pasteur. The father of microbiology proves that yeast are organisms which perform many metabolic processes and sugar resources are redirect into ethanol production and processes essential for cell growth and reproduction [3,4]. There was proven that yeast require nitrogen source for culture growth. Moreover high concentration of oxygen decrease fermentation efficiency, this phenomenon was named as a Pasteur effect [4]. Initial description of Pasteur effect was apparently as a misinterpretation, and the observation of effect was partly caused by lack of fatty acids and other sterols [38]. However Pasteur effect is observed in specific experimental conditions as limiting sugar culturing conditions, and also it is specific for particular yeast as *Saccharomyces cerevisiae* and *S. pastorianus* [5,6]. The latest research shows that fermentation and respiration provides molecular energy for cell, and those processes are flexible switches depending on environmental conditions [7]. Moreover the process of fermentation occurs even under aerobic condition what was called as a Crabtree effect [8]. The phenomenon was divided into short Crabtree effect (immediate occurrence of alcoholic fermentation after sugar addition) and long term effect (flexible fermentative-respiratory balance characteristic for batch cultures) [6,9,10]. Ability to ferment is not specific for all yeast but there are species like *Kluyveromyces lactis*, *Candida albicans*, which are Crabtree negative in result of inability to ferment sugar [8,10,11]. There are also yeast genera like *Brettanomyces* (Dekkera), where inhibition of fermentation is an effect of oxygen absence, what was called Custer Effect. These yeast convert sugar into ethanol and also acetic acid in aerobic conditions [6,12]. The group of scientist Kluyver and Custers proved that *Candida (Torulopsis) utilis* is able to convert D-glucose and also maltose into ethanol and carbon dioxide in anaerobic condition, despite of *Saccharomyces cerevisiae* (yeast with the highest yeast fermentation potential) inability to convert maltose without oxygen occurrence [5,13].

Study of microbiology shows that fermentation is an unusual form of yeast environmental adaptation. Rich environment favor growth of population and microorganism expansion on entire environment, however yeast strategy is based on ethanol production, which is toxic for many competitive organisms as bacteria and molds. Sugar concentration
determine strategy, when environment is rich in sugar then yeast ferment rather than propagate, but when sugar concentration is lower or decreased during the time yeast start to propagate and the last stage is ethanol used as a source of carbon [8,14].

3. YEAST GENETIC ABILITY TO FERMENT SUGARS

Yeast metabolism is based on two catabolic reactions which provides energy for cell growth and reproduction. Respiration is one of the most important metabolic process in living organisms which is based on glycolysis, oxidative decarboxylation of puruvate and Krebs cycle [15]. Respiration require oxygen from environment, active enzyme system and also productive mitochondria. There are some mitochondrial defects particularly in mtDNA as rho- (partial deficiency of mtDNA caused disability of non-fermentative sugar metabolism) rho0, (mutants without mtDNA) syn (single base mutations) mit (points mutations with protein synthesis), which cause impossibility of proper cellular respiration [16].

Even though respiration provides more ATP, the fermentation is metabolic process are more specific and often used by yeast. Fermentation process start with glycolysis and pyruvate is converted to ethanol and CO₂ in two steps, fist dependent on pyruvate decarboxylase where acetaldehyde is produced. The last step require alcohol dehydrogenase (ADH1) which converts acetaldehyde in to ethanol and CO₂. Balance between production and exploitation of ethanol is ensure by range of alcohol dehydroganase enzymes as ADH1, ADH2, ADH3, ADH4, ADH5.

The group of alcohol dehydrogenase enzymes included proteins which are responsible for ethanol machinery system, production and also alcohol exploitation as a source of carbon. ADH1 (gene YOL083C) and ADH5 (YBR145W) are responsible for reduction acetaldehyde to ethanol and they are related (ancestry) in order to whole genome duplication [14,17,18]. Alcohol dehydrogenase isoenzyme III (ADH3, YMR083W) is involved in NADH transport from mitochondria to cytosol in anaerobic conditions and also has an impact on fermentation in some cases not only ethanol but also fusel alcohols. ADH4 (YMR083W) is zinc dependent enzyme, whose gene is express as an effect of zinc deficiency [SGD-database]. Particularly important for yeast environmental adaptation is alcohol dehydrogenase ADH2 (YMR303C) these enzyme allow yeast to use previous produced ethanol as a source of carbon. Yeast ability to produce ethanol allow expansively increased the population in environment well off sugar. Toxic activity of ethanol eliminate natural competitors like bacteria and molds, furthermore alcohol is potential source of carbon to avoids starvation [14,17,19]. The strategy was called make accumulate consume, and allow yeast to survive and dominate in environments well off sugar [14,20].

There are two explanation of yeast genes origin, the hypothesis are based on genome duplication and hybridization. Yeasts whole-genome duplication could creates a range of genes originated from the same ancestor, called paralogs. Copy of the same genes were under different "selective" pressure to preserve sequence and consequently at least one of genes could accumulate mutations without serious damage or burden for cell growth and environmental adaptation [18,21]. Primitively researchers thought that yeast genome duplication appeared as a result of error in cell division after genome replication (meiosis, mitosis errors) [22,23]. Resent research had approved that yeast diploidy origin might occurs as an effect of yeast hybridization which appeared between haploid cells [24]. The hypothesis
of hybridization provides the explanation of yeast diploidy and also gives answer for question, how initially sterile hybrid after mating regain fertility [24]. Multiplication of genes from two different ancestral species, cause that interspecific yeast hybrid has at least two copy of the same genes, which might accumulate mutations without serious consequences for growth and reproduction. Either WGD or haploid hybridization show that yeast has two or even a few sequence of genes which might evolve in different ways. Multiplication of chromosomes increases probability of favorable accumulations and consequently improve feasibility of protein and enzymes functionalization [22]. There was many mechanisms which have a huge impact on yeast genome creativity after WGD as chromosomal rearrangements like translocations, gene conversion, insertion deletions, duplications etc. [25-28]. There are many examples of genes that have lost function, some genes have missense mutations and are not expressed at all. There are also genes like alcohol dehydrogenases (ADH-genes) which have evolutionary traits, an effect of mutations and the feature allow effective production and exploitation of ethanol [14].

4. ENVIRONMENTAL, SOCIAL AND CHEMICAL ADAPTATION OF YEAST

Environment has huge impact on creativity of microorganism genomes, exemplified perfectly on yeast genome. There are studies which show that yeast hybridization event may be accelerated by the stressful conditions like in high ethanol concentration [28]. There are also some other extracellular factors as temperature, pH, nutrients and osmolarity which stimulates various cellular responses [29]. The environmental factors determine survival and constitute part of natural selection which eliminate unsuited organisms. Evolution of some genes as production toxic metabolic compound cause environmental dominance and help in elimination of competitors. Ability to ferment was one of such dominant capacity which allow yeast to expand population in a high sugar environment. There was a coincidence appeared between seed plants and angiosperms occurrence which provides full of carbohydrates resources and creates unique niche for yeast growth, production of ethanol and propagation [14,30,31]. Moreover yeast were able to use ethanol as a source of energetic metabolite, which makes them dominate environments with high concentrations of sugar. Yeast are able to shift metabolism dependly of sugar concentration, however there are chemical substances which are extracellular secreted and suggest that yeast have developed system of communication. Quorum-sensing substances affecting the fermentation process, partly stimulate yeast metabolism, moreover some of them like tyrosol signaling about cellular density in population. 2-phenyloethanol and tryptohol are produced during fermentation, there function is unknown jet, however there is proven that they are not density signals [32]. Other important yeast messengers are a small peptyde as yeast pheromones a-factor, α-factor, which are intracellular mating signals informs about ploidiness (haploids) mating types a,α [33,34].

The "Make-Accumulate-Consume" strategy is not the only one direction which yeast develop over Millions of years, there are scientific reports about the social wraps between yeast and insects. Nowadays the hypothesis about yeast-insects consensus suspect that bees, wasps etc. are vectors for spreading of species and also constitute proper place for hybridization (even from different species) and mating [35,36].

The other discovery appeared that yeast especially industrial type are phenotypically and genetically separated from wild strains, moreover yeast used especially in beer production
came from five ancestral strains. These research studies show that taking advantage of yeast provoke characteristic selective pressure which provides preferable yeast strains with features which in another environment would otherwise be unsuited [37].

5. SUMMARY

Researchers which are explain many of ecological, genetic, behavioral and system biology problems based on yeast. These microorganisms are well known and helps understand many of phenomenons, which are common for rest tree of life. Yeast are represented by many species which has different metabolic strategy but they appeared how evolution and genes creativity happened. Forasmuch yeast genome in completely sequences from years, what makes ideal model for researchers. Analysis of yeast genome appeared that there are many of similar sequences between chromosomes, what constituted of theory about whole genom duplication. Nowadays is known that duplication was an effect of yeast haploid hybridzation. The duplication provoke accumulation of mutation in genes which was not under strong selective pressure to keep protein unchanged, and does not cause the cellular burden. The direct consequence of genes multiplication was improved functions of alcohol hehydrogenases which are responsible for yeast dominance in environment. Evolution of angiosperm coincidenced with yeast evolution, creates perfect niche for Saccharomyctota growth. Understanding of yeast metabolism is not only based on sugar and ethanol concentration, but it is also determined by some signaling substances which functions are not completely known. Moreover some social and ecological factors might have some impact on creativity of yeast metabolism, what appear how much we do not know jet. Complex impact on yeast metabolism created it from the begin.

Reassume yeast metabolism is depend on many factor and there is many evolution mechanisms which creates important for yeast strains genes to make them well adapted and useful for human. The solve of researchers questions about yeast metabolism is in system biology what one try proved in this article.

References


