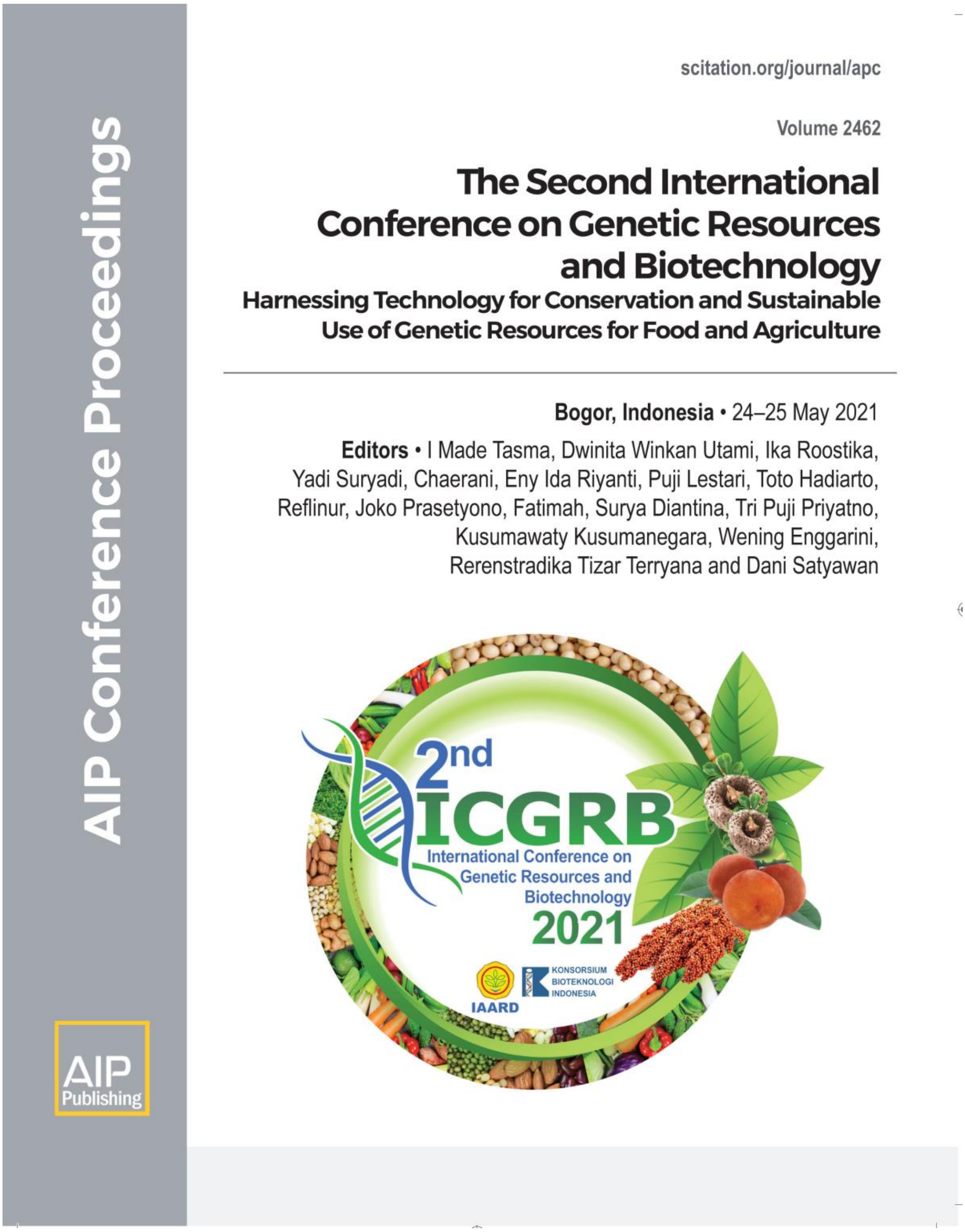

January 2022

THE SECOND INTERNATIONAL CONFERENCE ON GENETIC RESOURCES AND BIOTECHNOLOGY: Harnessing Technology for Conservation and Sustainable Use of Genetic Resources for Food and Agriculture

Committees: The Second International Conference on Genetic Resources and Biotechnology

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Preface: The Second International Conference on Genetic Resources and Biotechnology

The Second International Conference on Genetic Resources and Biotechnology, which is the continuation of the first event held in 2018, focuses on topics related to advances in biotechnology to create more opportunities for effective conservation and sustainable utilization of genetic resources for food and agriculture. This year conference's theme is Harnessing Technology for Conservation and Sustainable Use of Genetic Resources for Food and Agriculture. The conference was organized by Indonesian Agency for Agricultural Research and Development (IAARD), Ministry of Agriculture, Indonesia, in collaboration with Indonesian Biotechnology Consortium and held on 24^{th}-25^{th} of May 2021virtually due to the pandemic of COVID-19.

The conference aims to share and exchange current scientific information and technological developments on biotechnology and their applications for conservation and sustainable use of genetic, to encourage and promote quality, efficiency, and modernization of management and utilization of genetic resources, and to facilitate national and international collaboration among participants. There are five scopes discussed in this conference. They are effective management of conservation and sustainable use of genetic resources for food and agriculture, application of genomics and molecular markers for genetic resource conservation and crop adaptation to climate change, application of innovative crop improvement techniques for conservation and sustainable use of plant genetic resources for food and agriculture, plant cell and tissue culture for conservation and effective utilization of genetic resources, and the use of microbial genetic resources as biological control agents of agricultural pests and diseases, and for soil bioremediation.

Five speakers from the United States of America, Japan, India and Indonesia were invited to discuss about their expertise and knowledge on relevant subjects in the plenary sessions. This conference was attended by more than 100 participants including 75 presenters and 44 listeners worldwide. They came from diverse governmental, private, or academic institutions and also scientific communities. The presented materials have undergone peer review processes and only qualified papers were selected. Furthermore, all papers were subjected to double blind peer-review and expected to meet the scientific criteria of significance and academic excellence to be published in a conference proceedings indexed in a well-known, reputable service.

We would like to express our sincere gratitude to our speakers, presenters and all participants for their contributions in this conference. We would also like to express our appreciation for the generosity of our sponsors that support this conference: PT CropLife, PT ITS Science Indonesia, PT Fajar Mas Murni and PT Prima Instrument Analitika. Lastly, special thanks to all committee members for their exceptional work and contributions in the conference and publication.

Chair of Organizing Committee

Dr. Toto Hadiarto

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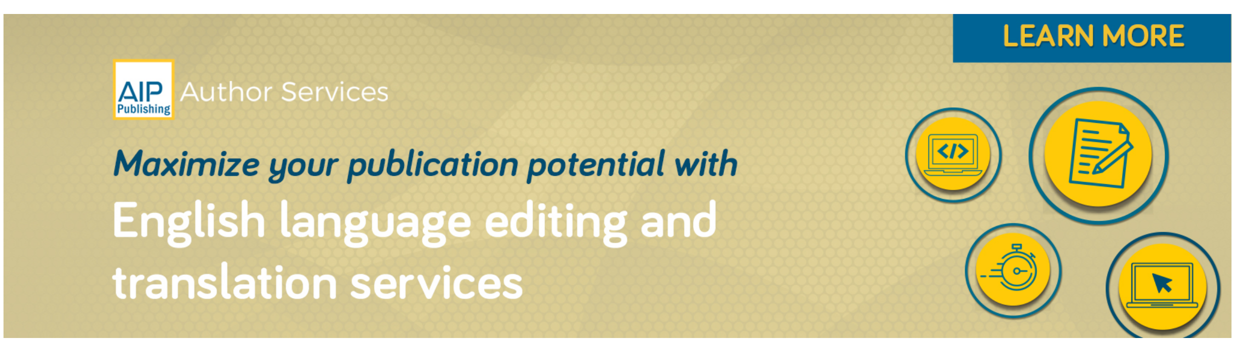

Understanding Yeast Tolerance as Cell Factory for Bioethanol Production from Lignocellulosic Biomass

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Abstract. Cell factory is the most important machinery for bioproduct. Yeast cell is known as the most productive machinery for ethanol production regarding its robustness toward high concentration of ethanol in the environment. However, it is become challenging when using lignocellulosic hydrolysate as raw material. For ethanol production, fermentation process depends on its cell's vitality under stress condition by ethanol accumulation in the environment. Furthermore, ethanol production using lignocellulosic hydrolysate undergo various challenges against inhibitory chemical complex such as 2-furaldehyde (furfural), 5-hydroxymethylfurfural (HMF), syringaldehyde, and vanillin coupled with some cell membrane-permeative acids, such as acetic acid, formic acid, and a small fraction of levulinic acid. Yeast cell maintains its survival on the stress condition by modification of its the genes regulation. Several considerations should be sought to engineered yeast as cell factory for ethanol production using lignocellulosic hydrolysate. This paper will discuss yeast survival mechanism toward its product and lignocellulosic hydrolysate environment, inhibitors effect to yeast cell, and gene regulation toward lignocellulosic hydrolysate for bioethanol production.

INTRODUCTION

In modern times, yeast applications cover a diverse range of operations not only for ethanol production or bread making, but also including the food, chemical, health care and biological, biomedical, and environmental industries. Microbial fermentation of sugars from sugarcane and corn starch to ethanol is the source of around 100 billion litters of fuel ethanol annually produced in the world using *Saccharomyces cerevisiae.*

Yeasts have advantages over bacteria for commercial fermentation due to the thickness of their cell walls, less stringent nutritional requirements, large sizes, resistance to contamination, rapid substrate consumption, and conversion to product and better growth at acidic pH of bioreactor fermenters, also ideal for cost-competitive production [1]. Cost-effective ethanol production depends several factors, such as rapid and high yielding conversion of sugars to ethanol, which depends on its survival and performance of yeast cells under industrial conditions [2].

Simple sugars and carbohydrate as raw material were used for ethanol production using *S. cerevisiae* for industrial production for many decades. However, the price fluctuation become concern as its competition for food and feed. Research using cheap raw material such as lignocellulosic biomass for bioproducts become relevant in recent decade. Using lignocellulosic biomass, the chemical differences between feedstocks have a major impact on the formation of inhibitors during pre-treatment. The major bottlenecks for lignocellulose conversion to ethanol using *S. cerevisiae* is decreasing of yeast performance, caused by high concentrations of toxic chemicals and harmful process conditions and also very low level of the pentose conversion into its products. Other drawback, using lignocellulosic as raw material for bioproducts, i.e. ethanol production requires microbes capable of resisting conditions of lignocellulose hydrolysates in the production processes while maintaining high metabolic activity.

Therefore, approach is being developed for those conditions using isolation, adaptive evolution, and genetic manipulation techniques [3–6]. Yeast cells can be exposed to inhibitory concentrations of toxic chemicals and low

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pH resulted from thermochemical pre-treatment of lignocellulose. Microbial strains with these characteristics can be isolated from natural habitats where they have been evolving these traits for a long time [7].

The ethanol stress response of *S. cerevisiae* is compromised by constraints on energy production, leading to increased expression of genes associated with glycolysis and mitochondrial function, and decreased gene expression in energy-demanding growth-related processes. Studies using genome-wide screens suggest that the maintenance of vacuole function is important for ethanol tolerance, possibly because of the roles of this organelle in protein turnover and maintaining ion homoeostasis. Accumulation of *Asr1* and *Rat8* in the nucleus specifically during ethanol stress suggests *S. cerevisiae* has a specific response to ethanol stress although this supposition remains controversial.

A major drawback to directly design *S. cerevisiae* tolerance to inhibitory conditions of lignocellulosic ethanol production processes is the lack of knowledge about basic aspects of its cellular signalling network in response to stress. Studies using genome-wide screens suggest that the maintenance of vacuole function is important for ethanol tolerance, possibly because of the roles of this organelle in protein turnover and maintaining ion homoeostasis.

This review contains basic understanding using lignocellulosic feedstock, the bottleneck using it for ethanol production using *S. cerevisiae* and research attempt for overcoming inhibitor stress resulting from lignocellulosic hydrolysate.

LIGNOCELLULOSIC BIOMASS HYDROLYSATE

Lignocellulosic biomass is known as cheap potential sustainable materials as raw material for bioproducts through fermentation process such as bioethanol compared to raw material contain sugars (sugarcane and beet) and starch (maize, casava, etc.) [8]. In general, lignocellulosic feedstocks in dry weight basis contain about 40–50% of the carbon bound as cellulose, 20–40 % as lignin and 10–26% as hemicelluloses and other polysaccharides. However, these ratios between cellulose, hemicellulose and lignin within a single plant vary with different factors like species, age, season, and culture conditions [9]. Fermentable sugars derived from lignocellulosic biomass such as agricultural crops, and wastes have considerable potential to produce bioproducts such as biofuels. Lignocellulose biomass contain high amounts of carbohydrates in cellulose and hemicelluloses compounds, but the complex and heterogeneous cell wall makes them recalcitrant to hydrolysis and subsequent ethanolic fermentation. Compared to starch, the polysaccharides of lignocellulose are more resistant to hydrolysis. Woody biomass is generally more resistant to degradation than other types of lignocellulose and also reported that softwood is typically more difficult to hydrolyse than hardwood or agricultural residues [10, 11].

For fermentation purpose this material need undergo several processes to release their glucose, such as physical, chemical and enzymatic processes [12]. Producing sugar from lignocellulosic feed stock involves a pre-treatment step for enhancing the susceptibility of the cellulose to enzymatic hydrolysis [13]. Pre-treatment is a key step in biochemical processing of lignocellulose biomass to remove the physical and chemical barriers that make native biomass recalcitrant amenable to enzymatic hydrolysis to produce sugars. While uncover the cellulose for enzymatic saccharification and fractionating the main components of the feedstock this process often involves side reactions resulting in derived by-products that are inhibitory to downstream biochemical processes.

Dilute sulfuric acid results in high recovery of the hemicellulose sugars in the pre-treatment liquid. Aliphatic carboxylic acids, phenylic compounds, and furans are released from hemicellulose, such as acetic acid and uronic acids and formic and levulinic acids resulting from sugar degradation contribute to acidification and can inhibit downstream processes. Alkaline treatment can be used for removing lignin and increasing the digestibility of cellulose. Mild alkaline pre-treatments produce to less solubilization of hemicelluloses and less formation of inhibitory compounds, and they can be operated at lower temperatures compared to acid hydrolysis. Several by-product formations such as acetic acid, hydroxy acids, dicarboxylic acids, phenolic compounds. A side effect of pre-treatment is formation of lignocellulose-derived by-products that inhibit microbial and enzymatic biocatalysts [8, 14, 15].

Based on the reports above, the choice of lignocellulosic material, pre-treatment and hydrolysis process will affect the fermentable sugars produced, fermentation process and the choice of microbes/yeast for ethanol production. So far, research on the lignocellulosic hydrolysis to serve raw material for bioethanol production is being conducted in order to achieve optimum conditions, such as maximizing sugars production, minimizing inhibitor released, and minimizing process cost and negative impact on the environment from the resulted waste.

INHIBITORS EFFECT TO YEAST CELL

During fermentation process for ethanol production using lignocellulosic hydrolysate, yeast cells need to maintain its fitness toward inhibitor challenges resulted to its product (ethanol) and lignocellulosic inhibitors (furfural, HMF, and acids). Ethanol accumulation in the culture broth can become a significant stress factor during fermentation. Although *S. cerevisiae* is highly ethanol tolerant, high ethanol concentrations in the culture inhibit cell growth and viability and limiting fermentation productivity and ethanol yield [17]. The ethanol stress inhibited ethanol formation by *S. cerevisiae* cells and the yeast responded to the stress by changing the fatty acid composition of cellular membrane, and a cell-cycle delay associated with a transient dispersion of F-actin cytoskeleton, resulting in an increase in cell size [18, 19].

The pre-treatment degrades the cellulose, hemicellulose lignin and wood extractives into sugars and other products, such as pentose and hexose sugars, sugar acids, aliphatic acids (primarily acetic acid, formic acid, and levulinic acid), and furan aldehydes 5-hydroxymethylfurfural (HMF) and furfural [16, 19] (Table 1).

TABLE 1. Degradation products from lignocellulose [16].

Lignocellulose component	Substance in lignocellulosic hydrolysate
Cellulose	Oligosacharides, disaccharides, hexoses (glucose, galactose, manoose, and ramnose), 5-hydroxymethylfurfural (HMF), leuvinic acid, formic acid
Hemicellulose	Pentose (xylose and arabinose), Oligosacharides, disaccharides, hexoses (glucose, galactose, manoose, and ramnose), aliphatic acids (primarily acetic acid, formic acid and levulinic acid), and furan aldehydes (5-HMF and furfural), leuvinic acid, formic acid
Lignins	Solid residue, minor part of phenolics and other aromatic compounds
Wood extractives	Phenols

Harmful predominant inhibitor in cellulosic hydrolysate is acetic acid with the high concentration typically ranging from 1 to 15 g/l in the hydrolysates [20, 21]. Acetic acid not only hinders bioethanol production, but also induces cell death in *S. cerevisiae*. The effect resulted in severe acidification in both cytosol and mitochondria, which was different from the effect of extracellular pH. The imbalance of intracellular acetylation was shown to aggravate cell death under this stress [22]. The toxic effects of acetic acid reported mainly derive from three aspects: high concentration, low pH, and nitrogen limitation. Analysis revealed the intracellular structures were greatly changed in many yeast cells treated with acetic acid. The untreated cells exhibited intact structures of organelles and cell nucleus, excessive accumulation of lipid droplets, with a thick and transparent cell wall. After acetic acid treatment, vacuolation of the cytoplasm was increasingly observed in yeast cells, intracellular organelles and cell nucleus were rapidly disintegrated or collapsed, and the cell wall became thinner with a darker color.

Other detrimental inhibitors resulted from lignocellulosic hydrolysate are furfural and 5-HMF which are known to cause specific biological effects. Furfural induces the accumulation of reactive oxygen species (ROS) in *S. cerevisiae* cell. They cause cellular, mitochondrial, vacuole membranes, actin cytoskeleton and nuclear chromatin damage [23] also causes DNA damage and induce DNA mutations. The inhibitory effect such as reducing fermentation rate and/or stop growing and enter an extended lag phase [31]. However, tolerance *S. cerevisiae* yeasts occurs, they could convert furfural and 5-HMF to their less reactive alcohol derivatives using NAD(P)H-dependent reduction reactions mostly during the lag phase [24, 25]. Compared to furfural, 5-HMF is less toxic, probably due to it is hard to penetrate the cell membrane. *S. cerevisiae* was also reported capable for converting 5-HMF into less toxic furan dimethanol through NADH- and NADPH-dependent reactions in both aerobic and anaerobic conditions, but more preferable under aerobic condition. By understanding this condition, we could manipulate fermentation process for serving optimum condition for certain yeast cell.

Based on the study above, research to obtain more robust yeast cell were conducted through isolation, mutation through evolution and genetic engineering to overcome the condition. Research on the bioprocess technologies also important to be sought for optimum condition reducing inhibitor effects.

GENE REGULATION TOWARD LIGNOCELLULOSIC HYDROLYSATE AND ATTEMP FOR MODIFYING TOLERANCE

During ethanol production yeast cell regulates its genes machinery which involves in several pathways such as glycolysis, pentose pathway for utilizing various sugars such as glucose and xylose. Glucose and xylose were transported into the cell regulates by different genes and enter the pentose phosphate pathway (Fig. 1). Study on the gene expression and the metabolomic analysis of non-flocculated haploid strain of *S. cerevisiae* NBRC849 during the fermentation in the medium containing inhibitory chemical complexes (ICC) at different concentrations reveals that the tolerance mechanisms involved through the upregulation of genes involved in NAD(H)/NADP(H) cofactors generations (*ALD6*, *ZWF1*, and *GND1*), membrane robustness for efflux pump (*YOR1*, *PDR5*, and *TPO3*), and cation/polyamine transport (*TPO3*) [25]. The alteration of metabolic flux to the shikimic pathway resulted in the enhanced formation of aromatic amino acid required for cell survival. Increase in expression of these genes as well as of metabolic flux to shikimic pathway were suggested to result in the robustness the strain.

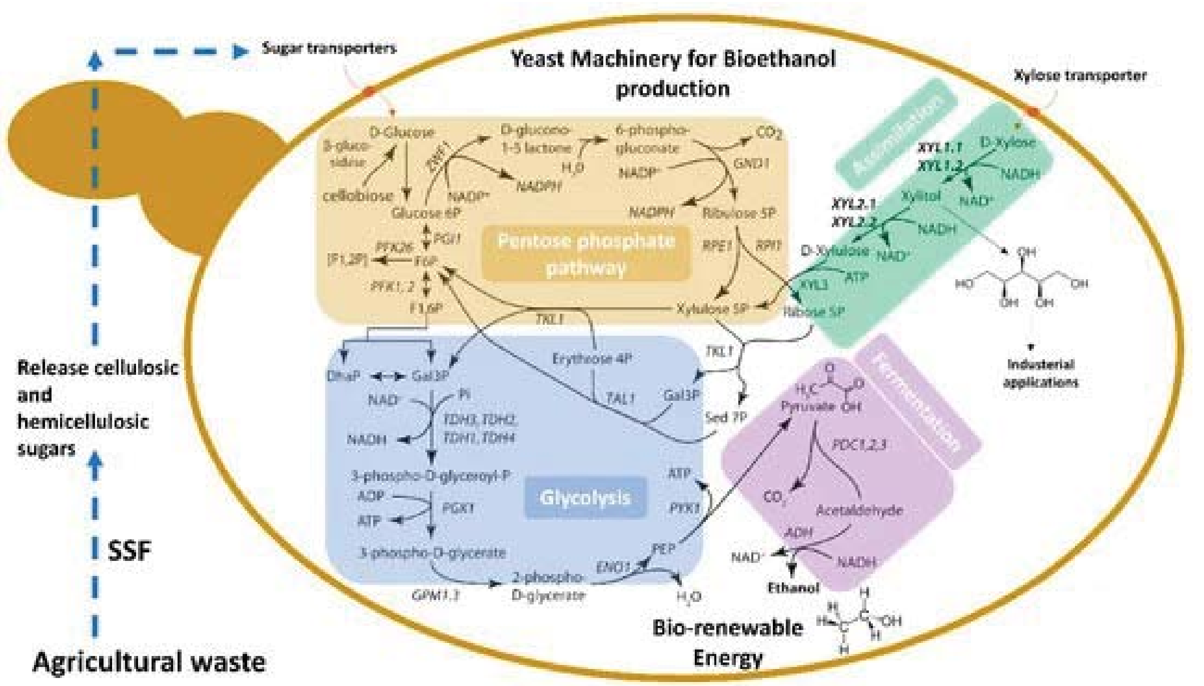

FIGURE 1. Gene regulation for ethanol production in yeast [1].

Harmful inhibitor in cellulosic hydrolyzates, not only repress bioethanol production, but also induces cell death in *S. cerevisiae* cells. Study on the RNA-Seq-based transcriptomic and metabolomic analysis reveal stress responses and programmed cell death induced by acetic acid. These affected genes were mainly involved in intracellular homeostasis, central metabolic pathway, transcription regulation, protein folding and stabilization, ubiquitin-dependent protein catabolic process, vesicle-mediated transport, protein synthesis, mitogen-activated protein kinase (MAPK) signalling pathways, cell cycle, programmed cell death, etc. [22].

Furfural tolerance affected by the performance of pentose phosphate pathway (PPP) toward the substance [26]. It is reported that when single PPP genes (*ZWF1*, *GND1*, *TKL1* or *RPE1*) are absent, yeast unable to grow when concentration of furfural (25 mM) is present, that would normally allow growth after a 24-h lag [27]. The greatest growth defect is seen when the *ZWF1* gene (encodes glucose-6-phosphate dehydrogenase) is disrupted. Glucose-6-phosphate dehydrogenase catalyses the rate-limiting step of the PPP and produces NADPH. This growth defect is probably NADPH produced in PPP is also an important cofactor used to protect cells against cellular stress caused by ROS. This finding also supports our previous research [25] which under complex inhibitors resulted from lignocellulosic hydrolysate affect genes in the PPP as results in cofactor generation.

In order for survival to environmental stresses, yeasts however have evolved to become more resilient, through a series of stress response, yeast survival and growth under stress conditions is achieved. The survival depends on a complex network of sensing and signal transduction pathways leading to adaptations in cell cycle, and adjustments in gene expression profiles and cell metabolic activities. Tolerant yeast could be acquired naturally by isolation and screening of collections from new habitats or through evolution modification or genetically engineered [28, 29]. *S. cerevisiae* SCPW 17 isolated from aging palm-wine was able to tolerate ethanol production stress conditions with minimal growth at 45°C and 20% (v/v) ethanol and intensive growth in a medium containing 200 g/l glucose [30]. In order to increase the robustness of an industrial *S. cerevisiae* strain by improving the tolerance towards both high temperature and hydrolysate-inhibitors through an evolutionary engineering strategy have been reported. A robust a long-term adaptation *S. cerevisiae* strain ISO12 was evolved from the industrial strain Ethanol Red (ER), are interesting candidates for second generation ethanol production [5]. Adaptive evolution engineering toward toxic condition was also reported [31, 44].

By understanding metabolism pathway and genes involving bioethanol under various stress condition resulted from lignocellulosic hydrolysate inhibitors using modern technologies such as proteomic and metabolomic, research focused on choosing robust host by isolation or adaptive evolution, targeted genetic engineering including genome editing in yeast become increasing. Various genetic improvements have been conducted in *S. cerevisiae* to overcome stress environment from inhibitors, increasing xylose utilisation to make efficient cell factory *S. cerevisiae*. Strong relationship between PPP genes, especially *ZWF1*, and furfural tolerance and provide additional putative target genes involved in furfural tolerance, overexpression of *ZWF1* in *S. cerevisiae* allowed growth at furfural concentrations that are normally toxic [27].

Flocculated yeast phenotype was reported has provides better inhibitor resistance. This character also enables higher cell loadings and easier separation of the product in bioethanol production and also beneficial for 2nd generation of bioethanol production. Flocculation of yeast cells has been reported dependent on flocculins, lectin-like proteins in the cell wall encoded by FLO gene family which bind to carbohydrates present in the cell wall. The higher expression level of *FLO1*, *FLO5*, *FLO9*, and *FLO10* gives rise to the flocculating phenotype of CCUG53310 strain, however *FLO8* expression in CBS8066 did not lead to flocculation phenotype [32].

Approaches for genetic engineering using simplified improved version of CRISPR-Cas genome editing for *S. cerevisiae* had been developed by using one single plasmid expressing Cas9 and one or two guide-RNAs. A high gene deletion efficiency was reported achieved with simultaneous recombination cloning of the plasmid and deletion in industrial strains [33]. The CRISPR-Cas9 system makes genome editing easier in diploid cell, enables researchers to knock-out and/or mutate multiple genes at once in a yeast genome. The CRISPR/Cas9 technology was reported to disrupt the *alcohol dehydrogenase 2* (*ADH2*) gene and introduction of a frameshift mutation in the *ADH2* locus showed that the ethanol yield improved by up to 74.7% compared with the yield obtained using the native strain [34].

Cell walls surround yeast cells acting as an exoskeleton that confers cell shape, while protecting them from harsh environments. The signalling pathways in yeasts, contain a dedicated signal transduction pathway that is activated at alkaline pH: the so-called RIM101 pathway.

Traditional and modern genetic manipulation to improve bioethanol production and xylose metabolism were also become hot topic as most wild *S. cerevisiae* only ferment glucose, but it has major barrier on fermenting xylose so far. UV-mutation was reported improve the efficiency of xylose fermentation of *Scheffersomyces shehatae* strain TTC79 [35]. A stable and manipulatable genetic system that enables overexpression or deletion of one or more of key enzymes and sugar transporters in xylose-fermenting yeast was reported [36]. Genome shuffling by combining two or more yeast genome for high efficient ethanol producer, increase resistance to stress and xylose fermenting *S. cerevisiae* were also reported [37–41]. To achieve commercialize fuel ethanol production from lignocellulosic biomass, research focused on engineering the glucose-fermenting industrial yeast *S. cerevisiae* to use pentose sugars have been extensively conducted [42]. Introduction of the heterologous xylose isomerase (XI) gene and for overexpression of endogenous xylulokinase (XKS) in a synthetic cassette in a yeast artificial chromosome (YAC) has improved xylose utilization by the INVSc1 yeast strain [43]. However, no strain either natural or engineered has yet been reported to ferment xylose as efficiently as glucose.

Obtaining more robust yeast cells through traditional way such as targeted evolution method, thorough isolation process ang genetic manipulation has been reported, however up to now an efficient yeast using lignocellulosic hydrolysate for high ethanol production have not been achieved. More research on yeast cells, efficient lignocellulosic hydrolysis processes and ethanol production process are challenge to be conducted.

CONCLUSION

Research on lignocellulosic biomass as a cheap feedstock for bioethanol production have been studied for few decades. The bottleneck of this conversion step remains challenge for commercialization since the robust efficient fermenting organisms have not been fulfilled. *S. cerevisiae* remains the primadona fermenting agent as no other microbes reportedly as robust as this microbe. Three groups of research aspect will be extensively study in these areas: (1) optimizing lignocellulosic biomass degradation into sugars, (2) minimizing inhibitors, and (3) efficient fermenting hydrolysate into bioethanol.

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