Microbial conversion of waste biomass into bioethanol: current challenges and future prospects

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Abstract

Fast exhaustion of fossil fuel stocks, as well as problems allied with air pollution, has created a worldwide attention in searching for alternative, renewable lignocellulosic macromolecule–based sources of energy. Bioethanol is one of the valuable substitutes produced by fermentation process. It significantly reduces the consumption of fossil-based fuels and thereby the net carbon dioxide emission. The looming requirement for replacing the fuels based on fossils with a more eco-friendly renewable solution has created much attention in finding out abundant and cheap resources for biofuel production. The utilization of easily available, cheaper, and renewable lignocellulosics would make bioethanol more competitive than fossil fuels. Novel substrates, strain improvements, limited byproducts, product tolerance, and fermentation conditions have been drawing researchers' attention to increase bioethanol productivity. The present paper discusses the bioethanol production from lignocellulosic-based renewable resources. It also focuses on present challenges and prospects for efficient bioethanol production.

Keywords Lignocellulosic biomass · Biofuel · Bioethanol · Pretreatment · *Saccharomyces cerevisiae*

1 Introduction

The most abundant and sustainable asset in the biosphere is lignocellulosic biomass. Its photosynthetic formation reached more than 200 billion tons consistently [1]. Biomass holds stored energy, which can be utilized as a fuel energy source. In the core, sun-powered energy is caught by the biomass (plants) through the cycle called photosynthesis in which light energy is converted into chemical energy that can be later exploited as fuel. The chemical energy which is fixed or stored in the form of carbohydrate molecules gets synthesized from carbon dioxide and water molecules in the plant leaves [2]. Agricultural remnants such as fruits and vegetables are the organic content–enriched materials, not perfectly utilized and sometimes end up as polluters of the environment. These underutilized parts can be valorized into bioethanol production. It can be produced by the fermentation of any sugar-containing raw materials. A successful bioconversion of these carbohydrate resources is considered the most valuable phase for bioethanol production [3].

Renewable resource–based ethanol may improve energy accessibility, reduce air pollution, and lessen the atmospheric CO_2 accumulation [4, 5]. Many problems which arose due to the consumption of fossil fuels, viz. global warming, environmental pollution, and economic depletion, compel the researchers to find renewable, sustainable, and eco-friendly alternatives. However, confronts undergo in converting lignocellulosic biomass into cost-effective and energy-efficient sustainable biofuels [6]. Renewable energy has been categorized into various fuels, viz. solar, wind power, biomass, geothermal, and tidal energy. Biomass-based energy shares a major portion of renewable energy. Biomass feedstock used for bioenergy is grouped into agricultural, forestry, industry, garden residues, and food residues [7, 8]. First-generation bioethanol (1G) was mainly produced from food crops such as corn and sugarcane; therefore, increased production can indirectly create a worldwide food scarcity. Therefore, it is an urgent need to develop lignocellulosic bioresource–based second-generation bioethanol (2G) production. The highly explored feedstocks for potential ethanol production are agricultural (crop residues), forestry wastes (mill residues), corn, sugarcane, sugar beet, pulp and paper, municipal solid wastes,

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and microalgae, etc. [4, 7, 9–11]. Bioconversion is rather challenging due to the complex structural veracity of plant cell wall materials which is integrally designed to resist microbial degradation [12]. Non-wood lignocellulosic biomass is abundantly available, low cost, and easy to process and consists of a short growth and harvest period, all these properties make it much useful for biomass conversion technology [13]. The major components in lignocellulosic biomass are cellulose, hemicellulose, and lignin. Cellulose- and hemicellulose-based sugars are the most useful feedstocks for future bioethanol production [14]. Lignin is a complex polyphenolic polymer made up of coniferyl, sinapyl, and p-coumaryl alcohol–based phenyl propanoid units. Lignin creates structural stability and rigidity of plant cell walls and hinders the enzymatic hydrolysis of biomass [15]. The production of ethanol from lignocellulosic comprises three major steps: pretreatment, hydrolysis, and fermentation [16, 17].

Pretreatment of the material is necessary to alter the size, structure, and chemical constituents of the biomass, loosen the cellulose fibers from the matrix of lignin, and thereby enhance the accessibility of the enzymes to the substrate. Several pretreatment strategies have been studied, including chemical, physical, and biological strategies. Recent approaches in pretreatment technology may improve saccharification efficiency and thereby reduce the overall production cost [9, 14, 16]. Several phenol-based inhibitory compounds are formed due to lignin degradation under the pretreatment process. Such inhibitory compounds badly affect the enzymatic hydrolysis as well as fermentation process in terms of cell growth and sugar metabolism [15, 18]. Cellulosic bioethanol production mostly depends upon the bioconversion of rigid fibers into fermentable sugars. Therefore, necessary pretreatment processes, viz. physicochemical and biochemical, are essential to improve the accessibility or porosity of recalcitrant lignocellulosic [19, 20].

Lignocelluloses have played a vital role in the production of fermentable sugars for the manufacturing of biocommodities [21]. The yeast *Saccharomyces cerevisiae* has long been used as an efficient agent for ethanol production at the laboratory as well as industrial level with high efficiency, thus considered as the world's premier industrial microorganisms in terms of exploitation and applications. Yeast better tolerates under a wide range of pH, ethanol, and inhibitory compounds as compared to other ethanol producers [3, 22]. *Zymomonas mobilis* is also acting as a promising alternative for ethanol production because of its high glucose uptake and high ethanol tolerance. The key enzymes for ethanol fermentation are alcohol dehydrogenase and pyruvate decarboxylase [23].

The pentoses basically D-xylose and D-arabinose produced from hemicellulose hydrolysis are not directly uptake by *Saccharomyces* strains; therefore, genetic modification is required. *Candida shehatae* is capable of co-fermenting

pentoses and hexoses for ethanol production [4]. Scientists are working upon designing organisms through genetic engineering tools to integrate desired enzymes into a single organism. Studies on designer cellulosomes and microbial consortia development relating to consolidated bioprocessing are exciting to overcome the issue of appropriate lignocellulose conversions [24, 25]. Regardless of the goal of nonstarch source–based 21 billion gallons of biofuels by 2022, only 142 million gallons of lignocellulosic-based biofuel was produced in 2015 in the USA [5]. The present review paper discusses the utilization of various raw materials in bioethanol production. It also focuses on the various recent approaches and different aspects used for enhancing bioethanol production.

2 Microorganisms involved in bioethanol production

A conventional and traditional player of industrial bioethanol production is *S. cerevisiae*, due to its high productivity, high inhibitor tolerance, and ease to genetically engineer. Its toughness enables it to handle tough industrial conditions. Novel pathway introduction and cellular process optimization by metabolic engineering are making its wide range of applications [26, 27]. Several thermotolerant ethanologenic species, i.e., *Clostridium thermocellum*, *C. thermohydrosulfuricum*, *C. thermosaccharolyticum*, *Caldicellulosiruptor* sp., *Thermotoga* sp., *Thermoanaerobium brockii*, *Thermoanaerobacter ethanolicus*, *T. thermo-hydrosulfuricus*, *T. mathranii*, *Thermoanaerobacter* BG1L1, *T. pentosaceus*, *Thermoanaerobacter* sp. DBT-IOC-X2 etc., have been identified as potential ethanol producers.

Since *Saccharomyces cerevisiae* is unable to ferment pentose-based sugars, the search for pentose-fermenting microorganisms could be an option for better utilization. A yeast strain identified as *Meyerozyma guilliermondii* utilized pentoses [28–32]. Glycerol-resistant mutant strains of *Enterobacter aerogenes* ATCC 13048 are also used for ethanol production [33]. *Debaryomyces nepalensis*, an osmotolerant yeast, utilized both hexoses and pentoses [34].

Co-cultivation of *S. stipitis* and *S. cerevisiae* is used for the utilization of mixed C6/C5 sugars [35]. Functional rumen bacterial consortia (FRBC) is also used for production [36]. Consortia of cellulolytic *Bacillus* sp. THLA0409 and ethanolic *Klebsiella oxytoca* THLC0409, *Saccharomyces cerevisiae* OVB 11 and *Pichia stipitis* NCIM 3498, and *Saccharomyces cerevisiae* and *Candida tropicalis* as well as *Saccharomyces cerevisiae* MTCC 173 and *Zymomonas mobilis* MTCC 2428 were found satisfactorily [23, 37–39].

Xylose utilizable *Saccharomyces cerevisiae* strain NAPX37 was used [40]. *N. crassa* strain utilized both hexose and pentose sugars [41]. *Spathaspora passalidarum* is a non-*Saccharomyces* yeast also used in bioethanol production [42].

A new yeast strain of *Clavispora* sp. NRRL Y-50464 is used which utilizes cellobiose [43]. Other strains such as probiotic yeast *Saccharomyces boulardii* and *Clostridium ragsdalei* were also found effective [44, 45]. After exhaustive evaluation, three main bioethanol producers, i.e., *Saccharomyces cerevisiae*, *Zymomonas mobilis*, and *Escherichia coli*, have emerged. Engineered bacterial and yeast strains have been constructed with better features through metabolic and genetic engineering that are advantageous for ethanol production [46].

3 Enzymes involved in biomass hydrolysis

There are several enzymes that have been utilized in the bioconversion process. Thermophilic bacteria–based thermostable enzymes play an important role in efficient biomass hydrolysis [47]. Laccases (E.C. 1.10.3.2) (benzenediol, oxygen oxidoreductase, or p-diphenol oxidase) belonging to the oxidoreductase class are used in breaking the plant's lignocellulosic wall and responsible for degrading the complex polyphenol structure that constitutes lignin. After laccases, lignin peroxidase (LiP) and manganese peroxidase (MnP) are the most significant ligninolytic enzymes. They belong to the heme proteins because they have the protoporphyrin IX as a prosthetic group. Lignin peroxidase (LiP) (E.C. 1.11.1.14) can catalyze and degrade a wide number of aromatic structures such as veratryl alcohol (3,4-dimethoxybenzyl) and methoxybenzenes. LiP oxidizes aromatic rings moderately activated by electron-donating substitutes [48].

Glyoxal oxidases (GLOX) are a type of extracellular H_2O_2-generating peroxidases mainly oxidizing aldehydes generated during lignin and carbohydrate degradation [49]. Aryl-alcohol oxidase (AAO) is providing H_2O_2 needed by ligninolytic peroxidases for lignin degradation. Thermostable endoglucanase (EndoI) produced by the thermophilic fungus *Thermoascus aurantiacus* was also found effective [50]. Zhang et al. [51] reported that permeases are responsible for incorporating various essential nutrients and excluding harmful products. Family 1 carbohydrate-binding modules (CBHI) enhance saccharification rates by cloning and expressing CBHI CBM from *T. harzianum* (CBMCBHI) into *Escherichia coli* by small ubiquitin-like modifier (SUMO) [52].

Deesterification of the plant biomass is achieved by carbohydrate esterases to make it more approachable for the hydrolytic enzymes such as cellulases, hemicellulases, ligninolytic, and pectinases [53]. A thermostable laccase was produced from *Thermus* sp. 2.9 for the delignification of Eucalyptus biomass [54]. A new thermo and solvent-stable xylanase was extracted from *Bacillus oceanisediminis* strain SJ3 by three-phase partitioning [55].

To enhance the activity and thermal stability as well as flexibility of proteins, disulfide bonds present in *Trichoderma reesei*–based endoglucanase II have been eliminated by site-directed mutagenesis. Replacement of Cysteine99 with valine and Cysteine323 with histidine caused the elimination of two disulfide bonds [56]. To improve the degradation efficiency of cellulases, endoglucanase (Endo5), exoglucanase (Exo5), and different carbohydrate-binding modules (CBMs) were fused to yield several bifunctional cellulases, containing Endo5-2CBM-Exo5, Endo5-CBM3b-Exo5, and Endo5-CBM28-Exo5 [57].

Laccase derived from *Trametes maxima* IIPLC-32 is used for the detoxification of phenolic inhibitors [58]. *Escherichia coli*–based laccase CueO was fused with the Dockerin domain of a cellulosome system and finally assembled with the scaffoldin miniCbpA to make a laccase–miniCbpA complex with increased laccase activity [59]. Lytic polysaccharide monooxygenases (LPMOs) have recently been shown to significantly enhance the degradation of recalcitrant polysaccharides. The copper-containing LPMOs utilize electrons to oxidatively cleave polysaccharides [60]. Chimeric thermostable GH7 cellobiohydrolases in *Saccharomyces cerevisiae* were engineered along with overexpressed glucose-tolerant β-glucosidase [61]. Expressing glycosyl hydrolases in the lignocellulosic-based feedstock is an approving alternative for its utilization. Yeast having laccase with ABTS was effective for direct fermentation of cellulosic materials [5, 62].

4 Raw materials used in bioethanol production

Lignocellulose is a renewable structural component of all plants. Lignocellulose consists of three major components (cellulose, hemicellulose, and lignin) linked by non-covalent forces as well as covalent crossed connections. Lignin acts as a barrier for any treatment due to strong networking with both hemicelluloses and cellulose, therefore prevents the penetration of lignocellulolytic enzymes used for bioconversion [4, 19].

There are various raw materials, which have been used as a potential source for bioethanol production, viz. wheat straw [63–65], baggasse [66], corn cobs [67–69], pineapple waste [70], Jabon wood [71], cotton waste biomass [72, 73], banana residue [74], old newspapers waste [75], acid hydrolyzate of rice water waste [76], rice husk [77, 78], rice straw [79–82], rice bran [83], rice hull [84], seed cake [85], dairy industry effluents (cheese whey) [86, 87], domestic food waste [88], papaya peel (PP) [89], spent tea waste (STW), spent wash [90]. sorghum bagasse [91, 92], and sugarcane leaves [93].

Other waste biomasses used are kitchen wastes [94], castor plant [95], potato pulp [96], algal hydrolysates [97], solid digestate from anaerobic digestion [98], oat hulls [99], *Arundo donax* biomass [100], loblolly pine [101], distillery stillage [102], banana peels [103], *Prosopis juliflora* [104], olive tree biomass (OTB) [105], jackfruit outer rind [106],

Jerusalem artichoke [107], coffee residue waste (CRW) [108], coffee pulp [109], Jerusalem artichoke (*Helianthus tuberosus* L.) tubers [110], napier grass [111], aloe vera leaf rind [112], waste newspaper hydrolysates [113], safflower plant [114], and palm wood [115].

Other resources are, viz. citrus peel [116], globe artichoke crop residues [117], date waste [118], sorghum milling waste [119], switchgrass [120], Miscanthus grass [121], *Conocarpus erectus* leaves [122], pineapple fruit peel [123], duckweeds [124], seaweed biomass [125, 126], grape winery waste [127], horticultural waste [128], synthesis gas [129], sweet sorghum juice [130], sugi pulp [131], cow manure [132], cotton gin trash (CGT) [133], high rate algal pond (HRAP) [134], Isoberlinia doka sawdust [19], *Ulva fasciata* seaweeds [135], palm date [136], orange peel [137], pomegranate peels [138], anaerobic digested sludge (ADS) [139], okara (soybean residue) [140], spent maitake culture medium (SMCM) [9], palm kernel cake [141], kans grass biomass [142], carob solid waste [143], cardoon (*Cynara cardunculus*) and rockrose (*Cistus ladanifer*) [144], lemon peels [145], cogongrass [146], *Salicornia bigelovii* (halophyte plant) [147], cotton stalk [148], and water hyacinth biomass [149].

Scientists have also utilized rapeseed and corn stalks for bioethanol production [150]. Turkish hazelnut husk into lignocellulosic ethanol was investigated [151]. The application of ultrasonic treated sweet lime peel for bioethanol production was also investigated [152]. Stillage from distiller's dried grains with solubles (DDGS), a by-product of the bioethanol industry, has also been used for bioethanol production [153, 154]. Aloe vera rind (AVR) obtained after extraction of the gel was used for bioethanol production [155]. Hydrolyzed spirulina biomass along with molasses serves as a substrate in bioethanol production [156]. Raw oil palm leaves were used as a substrate for ethanol production [157]. Partially delignified cellulignin (PDCL) was studied for biothanol production [158]. Olive mill waste (OMW), a semisolid waste generated from olive oil production, acts as an attractive substrate for bioethanol production [159]. Hemicellulose fraction of palm fiber is used as a source of sugars for the production of bioethanol by *Scheffersomyces stipites* [160].

Acid-hydrolyzed broth of banana pseudostem is a potential candidate for ethanol production [161]. Fermented rice noodle wastewater was investigated for ethanol production under an entrapped yeast cell sequencing batch reactor (ECSBR) [162]. Supplementation fruit pulps (mango, banana, and sapota), 4% fruit pulp/puree, enhanced ethanol production (up to 83.1%) in very high-gravity (VHG) fermentation [163]. Switchgrass is a potential source of renewable biomass for conversion to bioethanol [164]. Hardwood spent sulphite liquors (HSSLs) were used in bioethanol production [165]. Soft drinks industry–based wastewater was examined as a media source for bioethanol fermentation [166, 167]. Bioethanol production from autohydrolyzed green coconut shell was also

investigated [168]. A wild-growing glucose-rich (56.7% glucose content) brown seaweed species *Laminaria digitata* was used as the feedstock for bioethanol production [169]. Corn hybrids with high stalk sugar content or "sugarcorn" were used for bioethanol production [170]. *Gelidium latifolium* was selected as a potential resource [171]. Recycled paper sludge was valorized by a bioethanol production process with cellulase recycling [172].

Bioethanol was also produced from the macroalgae *Sargassum* spp. [173]. Breadfruit starch hydrolysate (BFSH) was used as the sole carbon source for bioethanol production [174]. Water hyacinth (*Eichhornia crassipes*), a fast-growing aquatic weed, was used for bioethanol production [175]. Deoiled *Pongamia pinnata* seed cake acts as a promising feedstock for ethanol production [176]. *Kappaphycus alvarezii* biorefineries are used for bioethanol production [177]. Bioethanol was also produced from the delignified coconut fiber [178]. Eastern gamagrass C4 perennial grass was used as an alternative cellulosic feedstock for bioethanol production [179].

Waste cotton materials were used as a substrate for bioethanol production [180]. Bioethanol was also produced from *Parthenium hysterophorus* biomass [181]. The potential of *Brachiaria mutica* (Para grass) for bioethanol production from Loktak Lake was investigated by Sahoo et al. [182]. Bioethanol production from Japanese bamboo was studied by Singh et al. [183]. Kitchen waste was utilized for bioethanol production [184]. *Saccharum* biomasses (*Saccharum munja* and sugarcane bagasse) were used for bioethanol production [185].

Bioethanol production from black tea waste biomass was investigated by Priharto et al. [186]. Ethanol was also produced from rice straw hydrolysate by non-conventional yeasts [187]. Empty fruit bunch was considered a substrate for bioethanol [188]. Oil palm frond juice was used as a renewable source [189].

Salicornia sinus-persica, a succulent halophyte, was used as a raw material for bioethanol production [190]. Eucalyptus sawdust was used for ethanol production [191]. Sulla (*Hedysarum coronarium* L.) was used as a potential feedstock for biofuel and protein [192]. High solid SSCF of alkaline-pretreated corncob is also used for ethanol production by recombinant *Zymomonas mobilis* CP4 [193].

Seaweed biomass (*Kappaphycus alvarezii*, red algal biomass) was utilized by marine yeast for bioethanol production [194]. Bioethanol was also produced from seaweeds (*Laminaria digitata*, *Ulvalactuca*, and *Dilsea carnosa*) [195]. N-Acetyl-d-glucosamine (GlcNAc) was used for ethanol production by *Scheffersomyces stipitis* strains [196]. *Acacia mangium*, *Paraserianthes falcataria* wood, and *Elaeis guineensis* trunk were investigated for ethanol production by Kaida et al. [197]. Microalgae (*Microcystis aeruginosa*) were used for efficient bioethanol production. The valorization of coffee byproducts for bioethanol

production was studied by Dadi et al. [198]. Eco-friendly processes were studied for soft drink industry wastewater reuse as a growth medium for *Saccharomyces cerevisiae*–based bioethanol production [167].The utilization of various raw materials for bioethanol production is also illustrated in Table 1.

5 Fermentation strategies used

A number of fermentation strategies have been already used for the effective and economical production of bioethanol such as separate hydrolysis and fermentation (SHF), simultaneous saccharification and fermentation (SSF), and simultaneous saccharification and co-fermentation (SSCF). The new approaches such as simultaneous isomerisation and fermentation (SIF) of xylose and simultaneous isomerisation and co-fermentation (SICF) of a glucose/xylose mixture were carried out by *Saccharomyces cerevisiae* in the presence of xylose isomerase [303]. Simultaneous saccharification and fermentation of waste wheat–rye bread were investigated and achieved a final ethanol concentration of 128.01 g/L [304]. Semi-simultaneous saccharification and fermentation (SSSF) of ethanol production has also been investigated [305]. Dilute phosphoric acid and steam-based pretreatment of *Eucalyptus benthamii* for biofuel production was carried out under liquefaction plus simultaneous saccharification and co-fermentation (L+SSCF) process [306]. Biomass was subjected to simultaneous pretreatment and saccharification (SPS) using a cocktail of hydrolytic and oxidizing enzymes for bioethanol production [307]. Bioethanol production was improved by *Scheffersomyces stipitis* using retentostat extractive fermentation at high xylose concentration [308]. Bioethanol production from pretreated mango stem bark after maceration (MSBAM) was evaluated. The highest yield (84.5%) was obtained under pre-saccharification followed by simultaneous saccharification and fermentation (PSSF) process [309]. Damaged rice grains were used for bioethanol production using presacchararification step followed by simultaneous saccharification and fermentation (SSF) by using waste brewer's yeast [310]. Sequential fermentation by *Saccharomyces cerevisiae* and *Pichia stipitis* improved bioethanol production [311]. A fluidized bed fermenter under a magnetic field was also used for bioethanol production [312].

6 Strategies used for improvement in ethanol production

6.1 Engineered biomass for efficient utilization

The volatile matter and fixed carbon influenced the biological conversion process of the fuel. Woody biomass has a much higher fixed carbon content as compared to LCB. The biomass fuel efficacy does depend not only on the proximate and ultimate analysis but also on the atomic ratio of H/C (hydrogen/carbon) and O/C (oxygen/carbon). The lower the ratio, the higher the energy content. The material with a relatively low O/C ratio has more energy density and higher heating value. LCB feedstocks are primarily composed of carbohydrate polymer and a lower concentration of proteins, acids, salts, and minerals [2].

The structural configuration, arrangement, and chemical composition of wood cell walls have directly affected the hydrolysis process of biofuel production. The understanding of the construction patterns and nature of the cell wall is the key point of second-generation biofuels, which has been done by glycome profiling [313]. Control of phase transition between vegetative to reproductive may also improve biomass yield with reducing lignin content. Delayed floral initiation may be used as a convenient tool for improving biomass quantity and quality [314]. For improved saccharification efficiency, the genetic variability of cell wall degradability has been accessed [315].

Quantitative trait locus (QTL) analysis was used to determine the zones of the phenotypic variation of chemical traits in the genome of interest. Signals for QTLs were assigned to G-lignin and S-lignin, and the ratio between them determines the cellulose, hemicellulose, and water contents. QTL mapped onto chromosomes V, X, XI, and XVI signifies that the saccharification process is under the influence of genetic impact. There may be opportunities to improve the breeding programs for willows for increasing enzymatic saccharification yields and biofuel production [316, 317]. Altering the "Glycomic Code" of cell wall polysaccharides may improve bioenergy production efficiency. The identification of pointrons (hydrolysis resistant) possibly transformed into pexons (available for enzyme attack) is important so that walls would become susceptible for hydrolysis [318].

Cell wall engineering was carried out by heterologous expression of cell wall–degrading enzymes for better conversion of lignocellulosic biomass. Cell wall–hydrolyzing enzymes alter the structural arrangements of the cell wall and reduce cell wall rigidity [319]. The various interactions in the cell wall architecture based on acetyl and phenolic linkages as well as polysaccharide–polysaccharide linkage play a vital role in the development of efficient bioethanol production [320]. Cell wall modification may enhance saccharification [321].

The wall structure of sengon (*Paraserianthes falcataria*) has been modified through overexpression of poplar cellulase in the cell walls. The overexpression caused a decrement in xyloglucan bound to the walls [322]. To determine lignocellulosic biomass biodegradability, cellulose nanowhiskers gel, lignocellulosic-based xylan matrix, and synthetic lignin were constructed. Application of these materials indicates that the

Table 1 Utilization of various waste biomass in bioethanol production

Raw materials	Microorganisms	Microbial improvement or modifications/fermentation	Pretreatment	Bioethanol conc/yield (g/l)(g/g) or (v/v)	Theoretical yield (%)	References
Sweet sorghum juice	*Saccharomyces cerevisiae* TISTR 5048	Microbes immobilized on support material corncob pieces($6 \times 6 \times 6$ mm^3)	-	102.39 ± 1.11 g/L	-	[130]
Corncob	*Kluyveromyces marxianus* 6556	-	-	5.68 g/L	-	[199]
Soybean cake				2.14 g/L	-	
Hydrolysate from floriculture waste (*Chrysanthemum*)	*Pleurotus ostreatus*	-	-	0.45 g/g	88	[200]
Citrus waste (musambi peel)	-	-	Acid-catalyzed steam pretreatment	-	85.97	[201]
Palm fronds		Hydrolyzed with Cellic H-Tech2.	Combined NaOH/H_2SO_4 pretreatment	42.6 (± 0.8 g)		[202]
Delignified sugarcane bagasse	*Saccharomyces cerevisiae* SC90	Microbes immobilized on support material sugarcane baggase	-	0.42 ± 0.02 g/g	82.35	[203]
Oil palm frond hydrolysate	*Pachysolen tannophilus*			13.79 g/L.	79.4%.	[204]
Aquatic weed water hyacinth (*Eichhornia crassipes*)				0.043 g/g		[205]
Household food waste		Non-isothermal simultaneous saccharification and fermentation (NSSF)		53.90 g/L	73.26%	[206]
Cotton stalks		Non-isothermal simultaneous saccharification and fermentation	Alkali treatment	34.80 g/L	55.40%	[207]
FAW (cattle manure)				56.32 mg/g	52.59%	[208]
FAW (pig manure)				27.98 mg/g	88.66%	
FAW (poultry manure)				12.69 mg/g	31.32%	
Household food waste (HFW)		Non-isothermal simultaneous saccharification and fermentation (NSSF)		42.66 g/L		[209]
The leaves of sugarcane (*Saccharum officinarum*)	*Pichia stipitis* BCC 15191		Dilute acid	0.20 g ethanol/g sugar		[210]
	Candida shehatae TISTR 5843			0.21 g ethanol/g sugar		
Peels of Ananas cosmosus	*Mucor indicus* MTCC 4349		1% H_2SO_4	10.4293 g/L		[211]
Manihot esculenta Crantz YTP1 Stem	*Zymomonas mobilis* MTCC 92.		Thermochemical	9.39 ± 0.33 g/L		[212]
Bamboo			Combined alkaline/alkaline H_2O_2	68.2 g/L		[213]
Oil palm trunk residues	*Saccharomyces cerevisiae* TISTR5055			4.15g/L		[214]

Table 1 (continued)

Raw materials	Microorganisms	Microbial improvement or modifications/fermentation	Pretreatment	Bioethanol conc/yield (g/l)(g/g) or (v/v)	Theoretical yield (%)	References
Hydrolysate of lignocellulosic biomass	*Saccharomyces cereviasie* NCIM 3078 and *Pichia stipitis* NCIM 3497		Ionic liquid (IL)	0.092 g ethanol/g of PNB		[215]
Hemicellulose fraction of cocksfoot grass	*Pichia stipites* CBS 6054		Wet explosion (WEx)	158 mL/kg DM	92.2%	[216]
Electron beam irradiated rice straw	*Mucor indicus*	Fungal-based simultaneous saccharification and fermentation (FBSSF)			57.2%	[20]
Bagasse hydrolysates	*Scheffersomyces (Pichia) stipitis* CBS6054		Wet exploded	18.7±1.1 g/L	-	[217]
Corn stover	*Pleurotus sajor-caju*			0.124 g/g		[218]
Sweet sorghum stalk	*Fusaium oxysporum* F3			24.4 g/100 g dry stalks		[219]
	Fusaium oxysporum F3+ Saccharomyces cerevisiae 2541			33.5 g/100 g dry stalks		
Corn meal	*Saccharomyces cerevisiae var. ellipsoideus*			9.91% (w/w)	92.27%	[220]
Banana bulbs			Hydrothermally	310 kg EtOH/tonD-M_RBB	93%	[221]
Opuntia ficus-indica cladodes	*Kluyveromyces marxianus*			19.5g/L	66%	[222]
	Saccharomyces cerevisiae			20.6g/L	70%	
Bagasse pith hydrolysate	*Kluyveromyces sp. IIPE453*			17.44 g/L	88%	[223]
Corn cob	*Kluyveromyces marxianus 6556*			5.68 g/L		[199]
Soya bean cake				2.14 g/L		
Tropical maize	*Saccharomyces cerevisiae*			8.1% (v/v) to 15.6% (v/v)	90.3–92.2%	[224]
Waste cotton (pyrolytic anhydrosugars)	*Saccharomyces cerevisiae 2.399*		Acid-hydrolyzed	14.78 g/L	91%	[225]
Defatted rice bran (DRB)	*S. cerevisiae*	Ultrasound waves on *S. cerevisiae*		1.55 g/L		[226]
Olive tree pruning hydrolysates	*Pichia stipitis* CBS 6054			3.8 g/L		[227]
Wheat bran hydrolysate	*Saccharomyces cerevisiae MTCC 174*			4.12 g/L		[228]
Whey permeate	*Kluyveromyces marxianus URM 7404*			8.90 g/L		[229]
Constructed wetland plants (*P. australis, T. dealbata,* and *J. effusus* L.)	*Saccharomyces cerevisiae BY4742*			30 and 35 g/L		[230]
Rice straw				26.9 g/L		[231]

Table 1 (continued)

Raw materials	Microorganisms	Microbial improvement or modifications/fermentation	Pretreatment	Bioethanol conc/yield (g/l)(g/g) or (v/v)	Theoretical yield (%)	References
Leaf juice of Agave plant	Kluyveromyces marxianus and Candida akabanensis		Sequentially pre-treated with sulphuric acid (3% v/v) and sodium hydroxide (4% w/v)			[232]
Tomato waste from tomato processing industries	Kluyveromyces marxianus DSM 5422, Saccharomyces cerevisiae Ethanol Red®, S. cerevisiae Hercules and Lachancea thermotolerans DSM 3434			20.1–21.7 g/L	88	[233]
Italian ryegrass (Lolium multiflorum Lam)	Escherichia coli KO11, S. cerevisiae				84.6	[234]
Leaves of Quercus aegilops	Pichia stipitis / Kluyveromyces marxianus			6.01 g/L / 6.93 g/L		[235]
Hydrolysate of pine needles of Pinus roxburghii	S. cerevisiae (MTCC-36) and P. stipitis (NCIM-3498).		Thermochemical pretreatment	0.144 g/g biomass	90%,	[236]
Tobacco product waste (TPW)			Mild sodium hydroxide		~97%	[237]
Spirodela polyrhiza (starch)	Saccharomyces cerevisiae QG1 MK788210				100%	[238]
Sugarcane tops (SCT)			Alkaline hydrogen peroxide (AHP) subsequently acid hydrolysis	9.9 vol% ethanol		[239]
Coconut meal	Saccharomyces cerevisiae			8.5 g/L	82.4%	[240]
Eucalyptus grandis hemicellulose prior to kraft pulping	Scheffersomyces stipitis NBRC 10063			5.0 g/L		[241]
Conocarpus erectus leaves	Saccharomyces cerevisiae	PSSF		0.47 g/g		[122]
Rice straw	S. cerevisiae / S. stipites(ATCC 58784) / S. stipites(ATCC 58785)		Acid Pretreatment	0.37 g/L/h / 0.09 g/L/h / 0.07 g/L/h	47.20% / 42.95% / 48.81%	[242]
Banana peels	Saccharomyces cerevisiae			32.6 g/L		[243]
Rice straw	Saccharomyces cerevisiae SHY07-1		Sodium perborate	15.29 g/L		[244]
Forage sorghum biomass			Steam explosion	55 g/L		[245]
Corn pericarp	S. stipitis		Dilute acid pretreatment	between 4.62 ± 1.73 and 14.22 ± 0.98 g/L		[246]
Hemicellulosic fraction of sunflower meal biomass			Dilute acid hydrolysis with 6% (w/v) H_2SO_4	8.8 g/L		[247]
Liquefied cassava	Flocculent hybrid, Saccharomyces cerevisiae CHFY0321	Repeated-batch fermentation with cell recycling		84.5 g/L		[248]

Table 1 (continued)

Raw materials	Microorganisms	Microbial improvement or modifications/fermentation	Pretreatment	Bioethanol conc/yield (g/l)(g/g) or (v/v)	Theoretical yield (%)	References
Scenedesmus obliquus	*Kluyveromyces marxianus*			11.7 g/L		[249]
Jerusalem artichoke	*Kluyveromyces marxianus* PT-1			73.6 g/L	90.0	[250]
	Saccharomyces cerevisiae JZ1C			65.2 g/L	79.7%	
Brown macroalgae	Recombinant strain of *S. cerevisiae*	alginate-assimilating *S. cerevisiae* recombinant strain		8.8 g/L	32%	[251]
Corncob	*K. marxianus* CICC 1727-5			42.6g/L		[252]
	S. passalidarum ATCC MYA-4345			31.9 g/L		
Sweet sorghum cultivar SIL-05	*Saccharomyces cerevisiae* BY4741		Produced sucrose-rich fraction by Nanofiltration	102.5–109.5 g/L	84.4–89.6%	[253]
Potato peel wastes				22.54 g/L		[254]
Date palm sap	*Wickerhamomyces anomalus* X19			73.11 g/L	90%	[255]
Broken rice	Amylolytic yeast strains(ER T12)				93%	[256]
Hydrolysed wheat bran's	Recombinant yeast *S. cerevisiae* MEL2[TLG1-SFA1] and M2n[TLG1-SFA1]			5.3 ± 0.14 g/L; 5.0 ± 0.09 g/L		[257]
Manihot glaziovii		FB-SSF		190 g/L	94%	[258]
Rapeseed straw	*Saccharomyces cerevisiae*		1% (w/w) H₂SO₄	53.1 g/L		[259]
Sesame (*Sesamum indicum* L.) plant residue	*Saccharomyces cerevisiae*			1.90 g/L		[260]
Vetiver grass (VG)				5.85 g/L		[261]
Rice straw	*P. stipitis* NCIM 3499		Alkali pretreatment (2% v/w NaOH)	25.3 g/L		[262]
Spent seaweed biomass (SSB)	*Saccharomyces cerevisiae*			4.98% w/w		[263]
Deoiled algal biomass (DAB)	*Saccharomyces cerevisiae*			(0.145± 0.008 g/g DAB)		[264]
Rice straw	*Saccharomyces tanninophilus*		NaOH-pretreated	9.45 g/L		[265]
Rice husk	*Saccharomyces cerevisiae*		20% ammonium carbonate pretreated	10.61 g/L		[266]
Root biomass of *Coleus forskohlii*	*Saccharomyces cerevisiae*			33.57 g/L		[111]
Macroalgal biomass (*Sargassum* sp.)	*Saccharomyces cerevisiae* Hanseniaspora opuntiae GK01		Acid and enzyme treatment	19.9±0.3 g/L; 28.7±0.4 g/L		[267]
Macroalgal biomass (*Gracilaria* sp.)	*Saccharomyces cerevisiae* Hanseniaspora opuntiae GK01			18.37±0.3 g/L; 27.0±0.6 g/L		
Sugarcane tops	*Saccharomyces cerevisiae*			11.365 g/L	50%	[268]
Momentary pine slurry			Sulfite pretreated	82.1 g/L		[269]

Table 1 (continued)

Raw materials	Microorganisms	Microbial improvement or modifications/fermentation	Pretreatment	Bioethanol conc/yield (g/l)(g/g) or (v/v)	Theoretical yield (%)	References
Carnauba straw	Kluyveromyces marxianus ATCC-36907		AL pretreatment	7.53 g/L		[270]
Wheat straw	Saccharomyces cerevisiae SR8u strain		Combined alkaline/alkaline-peroxide pre-treatment.	31.1 g/L		[271]
Peels of wild cassava Manihot glaziovii (Posidonia oceanica)			Dilute sulfuric acid	0.46 kg/L/h		[272]
Water hyacinth	Thermotolerant Kluyveromyces marxianu strain K213		NaOH/H$_2$O$_2$-pretreated	7.34 g/L		[273]
Cassava stem			Acid hydrolysis	37.5 g/L		[274]
Leaves of Stevia rebaudiana				20 g/L,		[275]
Waste streams of rice milling	Amylolytic strains			52 g/L	~88%	[276]
Waste money bills			Dilute H$_2$SO$_4$ pretreatment., adding 0.4 mM benzoic acid under anoxic condition	22.01 mg/mL		[277]
Gracilaria biomass	Immobilized S. cerevisiae		Sequential acid and enzymatic hydrolysis	4.72 g/L		[278]
Sugarcane trash	Saccharomyces cerevisiae			31.928 g/ g of dry biomass		[279]
Sugarcane bagasse (SCB)	Candida shehatae NCIM 3501.			15.54 ± 0.3 g/L		[280]
Cotton stalk			1% alkaline hydrogen peroxide (AHP)	3.956 g/L		[281]
Waste house wood (WHW)	Ethanologenic recombinant Escherichia coli KO11.		Dilute acid	35.4 g/L		[282]
Sugar beet pulp Juice	Saccharomyces cerivisiae			52.26 ± 2.0 g/L		[283]
Fruit waste; citrus peel waste (CPW)		Limonene removal column LRC was coupled with an immobilized cell reactor (ICR)		14.4–29.5 g/L	90.2–93.1%	[284]
Potato starch residue	Saccharomyces cerevisiae y-1646		1% H$_2$SO$_4$	5.52 g/L		[285]
Hemicellulose rich Populus nigra	Candida shehatae		AFEX pretreatment	5.43 g/L		[286]
Lantana camara	Pichia stipitis Saccharomyces cerevisiae		Acid hydrolysis (3.0%, v/v) + sodium sulphite (5.0% w/v) + sodium chlorite (3.0% w/v)	5.16 g/L 17.7 g/L		[287]
Perennial C4 grass Miscanthus floridulus	Dried yeasts		Alkaline pretreatment	0.124 g/g-dried raw material		[288]
Scenedesmus raciborskii WZKMT				30.43 g/L	89.60%	[289]

Table 1 (continued)

Raw materials	Microorganisms	Microbial improvement or modifications/fermentation	Pretreatment	Bioethanol conc/yield (g/l)(g/g) or (v/v)	Theoretical yield (%)	References
Rice bran hydrolysate	Zymomonas mobilis ZM4	Biofilms formed on plastic surfaces		13.40 ± 2.43 g/L	72.47 ± 6.13%	[290]
Wheat straw			4% (v/v) dilute sulfuric acid		87.9%	[291]
Saccharina japonica			Extremely low acid (ELA) pretreatment using 0.06% (w/w) sulfuric acid	6.65 g/L		[292]
Agave tequilana leaves	Saccharomyces cerevisiae		Dilute acid pretreatment 2.0% H_2SO_4	to 38.6 g/L	68%	[293]
Pomegranate peel (PP)	S. cerevisiae / P. stipitis		H_2SO_4 pretreatment	5.58 g/L / 2.95 g/L		[294]
Nacetylglucosamine and chitin substrates	M. circinelloides NBRC 6746 / M. circinelloides NBRC 4572			18.6 ± 0.6 g/L / 6.00 ± 0.22 g/L		[295]
Starch / Wheat bran / Rice straw	White rot fungus Trametes hirsuta			9.1g/L / 4.3 g/L / 3.0 g/L	89.2% / 78.8% / 57.4%	[296]
Bamboo			Alkaline treatment / Neutral treatment / Acidic treatment	50.1 g/L / 46.3 g/L / 49.0 g/L	70.5% / 68.9% / 65.1%	[297]
Saccharum spontaneum hemicellulosic hydrolysate	Pichia stipitis NCIM3498 / Saccharomyces cerevisiae-VS3 / Pichia stipitis NCIM3498 + Saccharomyces cerevisiae-VS3		Acidic treatment	12.08 ± 0.72 g/L / 1.40 ± 0.07 g/L / 15.0 ± −0.92 g/L		[141]
Mixture of waste paper and kitchen waste		(L+PSSF)		46.6 g/L		[298]
Wheat bran	Neurospora intermedia		Dilute phosphoric acid pretreatment		66%	[299]
Sweet sorghum fresh stalks (Keller cultivar)	Saccharomyces cerevisiae			35.00 g/L		[300]
Sweet sorghum fresh stalks (Cowley cultivar)				20.46 g/L		
Sugarcane bagasse	Saccharomyces cerevisiae		Formalin pretreatment	80 g/L	82.7%	[301]
Water Hyacinth (Eichhornia crassipes) with (FME) +(FBE) +(HD)	Saccharomyces cerevisiae			5.1±1.2 g/L	82%	[302]

lignocellulosic utilization depended strongly on the xylan Ara/Xyl ratio and the cellulose crystallinity [323].

6.2 Pretreatment approaches used

Pretreatment of raw materials has often been found useful to improve its digestibility and accessibility for microbial attack (by removing core and noncore lignin fractions). It results in enlargement of the inner surface area of substrate particles, accomplished by partial solubilization and/or degradation of hemicellulose and lignin [324, 325]. The goal of any pretreatment process is to alter or remove structural and compositional impediments by breaking the lignin seal, thereby separating the carbohydrates from the lignin matrix as well as disrupting the crystalline structure of cellulose. An efficient pretreatment must free the highly crystalline structure of cellulose and extend the amorphous areas [326–328]. Various pretreatment methods such as physical, chemical, physicochemical, and biological methods are described in Table 2.

Pulsed-electric field (PEF) pretreatment exposes the cellulose present in the biomass by creating the pores in the cell membrane, thereby allowing the entry of agents that will break the cellulose into constituent sugars. Under this treatment, biomass is subjected to a sudden burst of high voltage between 5.0 and 20.0 kV/cm for short durations (nano to milliseconds) [330]. Another method is by using a deep eutectic solvent (a fluid generally composed of two or three cheap and safe components) that are capable of self-association, often through hydrogen bond interactions, to form a eutectic mixture with a melting point lower than that of each component. Choline chloride (ChCl)–based deep eutectic solvents (DES) are used for the pretreatment process [331].

H_2O_2 (0.5% v/v)–based pretreatment at 121°C for 30 min was used as an effective method for the conversion of waste office paper and newspaper into fermentable sugars and after bioethanol [332]. *Retama raetam* biomass was pretreated by thermo-mechanical process for effective utilization [333]. Soaking-assisted and thermal-pretreated cassava peel waste was investigated for bioethanol production [334]. Bioethanol was also produced from *Calliandra calothyrsus* shrub pretreated under hot water–based hydrothermal explosion [335]. Acid impregnation-steam explosion was used as a pretreatment method for ethanol production from oil palm empty fruit bunch (EFB) [336]. A series of ionic liquids including conventional, protic, and brønsted acidic type ionic liquids were evaluated as a source for the pretreatment of Taiwan grass [337]. Sonication after acid hydrolysis enhanced the total reducing sugar (TRS) extraction from sugarcane bagasse [338]. Cactus (CAC) and green and mature coconut shells were pretreated by $NaClO_2$–$C_2H_4O_2$ and sequential $NaClO_2$–$C_2H_4O_2$/autohydrolysis for their better utilization [339].

The combined effect of ionic liquid (1-butyl-3-methylimidazolium chloride, [BMIM]Cl) and radiation (Tungsten–Halogen) on hydrolysis of waste papaya epidermis was explored by Chatterjee et al. [340]. Chitosan-coated magnetic nanoparticle (C-MNP)–based immobilized laccase was applied for agave biomass pretreatment [341]. Ionic liquid 1-ethyl-3-methylimidazolium acetate pretreated with the *Agave tequilana* bagasse has shown promising results [342]. The modified thermochemical disk refining pretreatment (TCDRP) has a greater effect on agricultural biomass and hardwood (white birch) utilization [343].

Microwave-assisted lignin solubilized in protic ionic compounds containing 2,3,4,5-tetraphenyl-1H-imidazolium and inorganic anions was used as pretreatment [344]. For effective biomass utilization, mild photocatalyzed and catalyzed green oxidation of lignin was investigated. Lignins showed some mineralization when irradiated in the presence of $H_5[PMo_{10}V_2O_{40}] \times H_2O$ (POM-1), $K_5[Ru(H_2O)PW_{11}O_{39}]$ (POM-2), $K_4[SiW_{12}O_{40}]8H_2O$ (POM-3), and TiO_2 [345]. Dielectric barrier discharge (DBD) plasma can be used for the pretreatment of lignocellulosic materials. Such plasmas are sources of highly reactive species (radicals, ozone, atoms, ions, and excited molecules) [346]. Low-moisture anhydrous ammonia (LMAA) was used for the pretreatment of napier grass (*Pennisetum purpureum Schumach*) [347].

Electron beam irradiation–based biodegradation (EBIBB) was used for rice straw depolymerizations [348]. Microwave-assisted chemical pretreatment of miscanthus was studied [349]. Alkaline wet oxidation (WO) was used for the pretreatment of wheat straw, resulting in a formation of hemicellulose-rich hydrolysate and a cellulose-rich solid fraction [350].

Hydrothermal carbonization (HTC) is used as a method of pretreatment for efficient biomass utilization [351]. Phosphoric acid (1% w/w)–based steam explosion is used for olive tree pruning utilization [352]. Lower S/G ratio, as well as reduced number of phenolic OH group in acid-pretreated lignin, may affect simultaneous saccharification and fermentation [353]. S/G/H ratios of lignin fractions are important to rationalize the differences among the feedstock behavior [354]. Holocellulase immobilized on iron oxide (Fe_2O_3) nanoparticles improved hydrolysis of paddy straw. It has also been suggested that magnetic enzyme nanoparticle complexes (MENC) showed better immobilization efficiency (60–80%) for different enzymes [355]. Membrane-based separation increased the ethanol yields during fermentation which suggests the importance of separation after pretreatment [356]. The effect of ultrasound on enzymatic hydrolysis of a newspaper was investigated. The combined effect of ultrasound and enzymes lowers the diffusion-limiting barrier to enzyme/substrate binding to increase the reaction rate [357].

High solid loading hydrolysis (HSLEH) of sugarcane bagasse (SCB) pretreated by low-temperature aqueous ammonia

Table 2 Various pretreatment methods applied in utilization of lignocellulosic biomass

Pretreatment methods	Agents	Procedure	Temperature/ pressure	Reaction time (min)	Pretreated materials	Remarks
Physical methods						
Mechanical comminution	-	Chipping, grinding, milling	-	-	Wood, forestry waste, cane baggase, alfalfa	Vibratory ball mill (size 0.2–2 mm) or hammer mill (3–6 mm)
Pyrolysis	-	Intense heating, cooling, condensing	>300°C	-	Wood, corn stover	Formation of volatile products and char
Physicochemical methods						
Steam explosion	Saturated steam	Saturated steam treatment then decompression	160–300°C, 0.69–4.85-MPa	Sec or min	Poplar, eucalyptus, soft wood, bagasse straw	It can handle high solid loads, inhibitor formation, lignin is not solubilized, 80–100% hemicelluloses hydrolysis
Liquid hot water	Hot water	Pressurized hot water	170–230°C, p>5MPa	1–45 min	Bagasse, alfalfa, corn stover	Cellulose depolymerization, 80–98% xylose recovery, no formation of inhibitors, partial solubilization of lignin
Ammonia fiber explosion	Ammonia	1–2 kg ammonia/kg dry biomass	90°C, 1.12–1.36-MPa	30 min	Switch , bermuda grass, news print, MSW, bagasse straw	Ammonia recovery is required, no inhibitors formation,10–20% lignin solubilization
CO_2 explosion	CO_2	4 kg CO_2/kg fiber	5.62 MPa	-	Bagasse, recycled paper	Cellulose conversion can be >75%, no inhibitors formation
Chemical methods						
Dilute acid hydrolysis	0.75–5%H_2SO_4, HCl, or HNO_3	Continuous process for low solids loads , batch process for high solids load	120–200°C, 1MPa	2–10 min	Poplar wood, bagasse, grass, wheat straw	Lignin is not solubilized but it is redistributed,pH neutralization is required
Conc acid hydrolysis	10-30%H_2SO_4	Same as dilute hydrolysis, 1:1.6 solid :liquid ratio	170–190°C	-	Bagasse, saw dust	Residence time greater, acid recovery is required
Alkaline hydrolysis	Dilute NaOH, $Ca(OH)_2$	Dilute NaOH, $Ca(OH)_2$ addition, H_2O_2 added at 35°C	60°C for NaOH, 120° for $Ca(OH)_2$	-	Hardwood, bagasse	Reactror cost lower compared to acid, cellulose swelling, 24–55% lignin removal for hard wood, lesser for soft wood
Biological methods						
Fungal treatment	Brown, white, and soft rot fungi	Fungi produces cellulase, hemicellulases, ligninase	-	-	Corn stover , wheat straw	Brown rot fungi degrades cellulose, white and soft rot degrades cellulose and lignin.

Source: [328, 329]

soaking (AAS) was performed to obtain high concentrations of glucose [358]. Surfactant-assisted ionic liquid 1-ethyl-3-methylimidazolium acetate ([EMIM]OAc)–based pretreatment of beech wood waste was used for enhanced ethanol production [359]. WO (wet oxidation) and BM (ball milling)–based pretreatment of the macroalgae *Chaetomorpha linum* showed the highest ethanol yield [360].

Acid-catalyzed choline acetate ionic liquid pretreatment of paperboard mill sludge was used for effective production [361]. Zirconium metal–based organic framework (MOF)–assisted hydrothermally pretreated *Platanus × acerifolia* exfoliating bark was used for bioethanol production with promising results such as altered the morphology and higher the porosity and surface area [362].

Eucalyptus globulus and *Nothofagus pumilio* residues were pretreated with ionic liquids (IL) such as 1-N-ethyl-3-methylimidazolium chloride (C_2mimCl) and 1-N-ethyl-3-methylimidazolium acetate (C_2minOAc) for efficient conversion [363]. Steam-exploded and N-methylmorpholine-N-oxide (NMMO)–treated pinewood was investigated for biofuel production [364]. Two different acid-functionalized magnetic nanoparticles (MNPs), i.e., alkylsulfonic acid (Fe_3O_4-MNPs@[Si@AS]) and butylcarboxylic acid (Fe_3O_4-MNPs@Si@BCOOH), were synthesized and evaluated for the pretreatment of sugarcane bagasse. Both Fe_3O_4-MNPs@Si@AS and Fe_3O_4-MNPs@Si@BCOOH showed the maximum amount of sugar (xylose) liberated, i.e., 18.83 g/L and 18.67 g/L, respectively [365].

A sequentially two-stage pretreatment process of autohydrolysis and alkaline extraction was carried out for effective bamboo utilization [366]. Phosphoric acid along with hydrogen peroxide (HP) pretreatment was employed on wheat straw for ethanol conversion [367]. Acidic ionic liquids (AILs) are a type of IL that has emerged as very attractive pretreatment solvents for biomass utilization [368]. Enhancement of enzymatic digestibility of *Miscanthus* biomass was improved by chemical-based electron beam irradiation [369]. The saccharification process was improved by gamma irradiation [370]. High pressure–assisted alkali pretreatment (HPAP) of cotton stalk led to the highest reducing sugar and ethanol yields (271.70 mg g^{-1} and 45.53%, respectively) [371].

Bioethanol production from ultrasonic irradiated waste newspaper by *Saccharomyces cerevisiae* was investigated by Preeti et al. [372]. Microwave irradiation accelerated pine cones act as a potential feedstock for bioethanol production [373]. Microwave-assisted ionic liquid–based catalytic conversion of non-edible lignocellulosic sunn hemp fibers to bioethanol was reported [374]. Bermuda grass, reed, and rapeseed were pretreated with phosphoric acid–acetone for ethanol production [375]. Two-stage pretreatment of *Eucalyptus* woody biomass with alkaline sulphonation and steam was carried out to enhance its enzymatic digestibility for bioethanol production [376]. Cellulase-bound magnetic nanoparticles were used as nanobiocatalyst for the hydrolysis of *Sesbania aculeate* biomass [377]. Microwave-assisted acid hydrolysis (H$_2$SO$_4$ and HCl with >0.5 mol/L) to produce bioethanol from sago pith waste (SPW) was studied [378]. The application of nano-biocatalyst (NiO) in simultaneous saccharification and fermentation of potato peel waste meaningfully enhanced bioethanol production (>65%) [379].

The nanofiltration (NF) and reverse osmosis (RO) membranes were chosen to evaluate their sugar rejection and inhibitor removal performance [380]. NaIO$_4$ + H$_2$SO$_4$ and electron beam irradiation (EBI) pretreatment was used in the process to enhance the efficiency of straw conversion [381]. Alkali metal salt along with orthophosphoric acid was used for the pretreatment of microwave-assisted biomass to enhance sugar and bioethanol generation [382]. Organosolv pretreatment removes lignin from the biomass and makes the sugars available for conversion [383].

Pretreatment of sugarcane bagasse with liquid hot water (LHW) and aqueous ammonia (AA) showed better performance in terms of hemicellulose solubilization and lignin removal [384]. Ozonation of lignocellulosic waste (municipal trimmings) acts as an energetically suitable pretreatment method [385]. Two-stage dilute acid pretreatment was performed for effective utilization of Loblolly Pine [386]. *Pycnoporus cinnabarinus*–based laccase-mediator 1-hydroxybenzotriazole (HBT) was found effective for pretreatment of wheat straw [387]. The utilization of blue agave

bagasse was enhanced under a combined extrusion–saccharification process [388]. Oxidative depolymerization along with acidic hydrolysis has consistently been used for the pretreatment of lignocellulosic biomass (wheat straw, sawdust, and lignin), which makes it possible to obtain a high content of soluble organic compounds in the hydrolysate (44–94 g COD/L) and to enhance the concentration of reducing sugars from 1 to 36% [389]. Peracetic acid–ionic liquid pretreatment was used for utilization of seaweed waste biomass from the carrageenan industry for bioethanol production [390]. During the pretreatment process, various toxic compounds may be generated that cause strong inhibition on cell growth and the metabolic capacity of fermenting strains. These are furan aldehydes, 2-furylaldehyde (furfural), and 5-hydroxymethyl-2-furaldehyde (HMF) produced by the degradation of pentose and hexose sugars respectively [391]. Inhibitory effects of phenolic components of spruce hydrolysates, viz. homovanilyl alcohol, vanillin, syringic acid, vanillic acid, gallic acid, dihydroferulic acid, p-coumaric acid, hydroquinone, ferulic acid, homovanillic acid, 4-hydroxybenzoic acid, 4-hydroxy-3-methoxycinnamaldehyde, and vanillylidenacetone, were investigated on the cell growth of *Saccharomyces cerevisiae* and it was observed that 4-hydroxy-3-methoxycinnamaldehyde was found to be the most toxic that inhibits the growth even at a very low concentration at 1.8 mM [392].

6.3 Genetic engineering aspects

For the holistic development of interesting microbes used in bioethanol production, genetic engineering could be playing a vital role. The host organism generally used for bioethanol production may not be tolerant of certain conditions such as temperature, pH, and ethanol stresses. Therefore, the host organisms used for bioethanol production need to be genetically engineered to make an effective and efficient condition for ethanol production. Recently, several genome engineering techniques have been developed. These techniques include (a) CRISPR/Cas system, (b) nuclease-based TALEN system, (c) zinc finger domain–based ZFN system, (d) meganuclease system, and (e) oligonucleotide-based YOGE system. Protein engineering studies as well as whole genome sequencing of bioethanol producers suggest that alteration of one or more nucleotides can bring out large changes in the direction of improved bioethanol production [393].

A lot of attention has also been focused on genetically engineered strains that can efficiently utilize both glucose and pentoses, and convert them to ethanol. Metabolic strategies seek to generate efficient biocatalysts (bacteria and yeast) for the bioconversion of most hemicellulosic sugars to products such as ethanol [394]. The biochemical production capacity of *E. coli* has been enhanced by the combinatorial application of recent approaches, viz. metabolic engineering,

systems biology, synthetic biology, and evolutionary engineering [395].

CRISPR/Cas9 is used to disrupt the alcohol dehydrogenase-2 gene in *Saccharomyces cerevisiae* via complete deletion of the gene and introduction of a frameshift mutation in the ADH2 locus for improved ethanol yield [396]. For better utilization of xylose, metabolically engineered *Saccharomyces cerevisiae* was produced by integrating xylitol dehydrogenase gene (XYL2) into the chromosome [397]. A putative thermostable endoglucanase gene was inserted into a pET21 vector and transformed in *E. coli* BL21 for expression [398]. Bioethanol from lignocellulosic biomass requires robust *Saccharomyces cerevisiae* strains with improved tolerance capacity for toxic compounds. Genes (ADH6, HAA1, or PMA1) involved in detoxification and tolerance to inhibitors have been recognized. Overexpressing genes encode the transcription factor (YAP1) and the mitochondrial NADH-cytochrome b5 reductase (MCR1) for faster hexose catabolism [399].

Redox imbalance is the major challenge in the recombinant strains expressing *S. stipitis* XR-XDH pathway–based xylose-metabolizing cells, because xylose reductase prefers NADPH, whereas xylitol dehydrogenase strictly utilizes NAD+, leading to the accumulation of NADP+ and NADH. The ratio of NADP+/NADPH directly influences the activity of glucose-6-phosphate dehydrogenase and thereby affects sugar utilization [400]. *Acremonium cellulolyticus* was transformed (YKX1) by the β-xylosidase gene driven by the cellobiohydrolase I (cbh1) promoter by the protoplast-polyethyleneglycol (PEG) method. Now YKX1 can produce a higher amount of β-xylosidase [401].

Cloning of novel bacterial xylanases from lignocellulose-enriched compost metagenomic libraries was performed for the complete hydrolysis of lignocellulosic biomass into fermentable sugars [402]. To develop multiple stress tolerance (high-temperature and osmotic stress) in *Saccharomyces cerevisiae*, intracellular osmolyte glycerol production was quickly induced by osmotic shock due to overexpression of GPD1 and GPD2 genes encoding isoenzymes of NAD-dependent glycerol 3-phosphate dehydrogenase under the regulation of high osmolarity glycerol (HOG) pathway [403].

Tolerance for ethanol and heat stresses in *Saccharomyces cerevisiae* strains are important for industrial ethanol production. Genes accountable for ethano-thermotolerance were identified by transposon mutagenesis in *Saccharomyces cerevisiae*. Seven responsible genes (CMP2, IMD4, SSK2, PPG1, DLD3, PAM1, and MSN2) were identified. Knockout mutants of seven individual genes were ethanol tolerant whereas three of them (SSK2, PPG1, and PAM1) were tolerant to heat. The genes identified under this investigation may be helpful in the development of industrial yeast strains [404].

In another investigation, stress tolerance and the performance of ethanol fermentation of the four euploid strains were compared. Triploid showed a higher fermentation rate even in the presence of lignocellulosic hydrolysate–based inhibitors [405]. The thermotolerant *Kluyveromyces marxianus* is a potential candidate for high-temperature ethanol fermentation. At high temperatures, mitochondrial respiration is stimulated, leading to more reactive oxygen species (ROS) formation and lowered ratio of reduced NADH/oxidized NAD+ [406]. Overexpressed SNARE genes increased heterologous cellulase secretion in *Saccharomyces cerevisiae*. Soluble N-ethylmaleimide-sensitive factor attachment receptor proteins (SNAREs) play an important role in yeast protein-trafficking [407]. Adaptive evolution of xylose-fermenting *Saccharomyces cerevisiae* strains was performed with δ-integration of different xylA genes of the fungus *Orpinomyces* sp. and bacterium *Prevotella ruminicola*, thereby constructing two industrial *S. cerevisiae* strains, O7 and P5 [408].

A rumen metagenomic DNA fragment (Csd4) expressed in *Escherichia coli* MS04 improves ethanol fermentation. Csd4 acts as a saccharification enhancer to reduce the enzymatic load and operating time required for cellulose deconstruction [409]. A recombinant *Saccharomyces cerevisiae* strain was transformed with xylose reductase (XR) and xylitol dehydrogenase (XDH) genes from *Pichia stipites*; increment in ethanol production may be due to cofactor imbalance between NADPH-preferring XR and NAD+-dependent XDH [410]. Sometimes high hydrostatic pressure activates gene expression that leads to enhancement in ethanol production [411].

Proline acts as an osmotic stress protectant in yeast. Proline-accumulated *S. cerevisiae* cells were constructed by disrupting the PUT1 gene. Engineered strains revealed higher tolerance to many stresses, viz. freezing, desiccation, oxidation, and ethanol as well [412]. The efficient fermentation of glucose and xylose can improve by a two-stage transcriptional reprogramming (TSTR) strategy. The TSTR strategy improves ethanol production efficiency [376]. The thermotolerant methylotrophic yeast *Hansenula polymorpha* can ferment xylose, glucose, and cellobiose at elevated temperatures. Recombinant alcohol dehydrogenase 1 of *H. polymorpha* (HpADH1) overexpressed in *Escherichia coli* exhibited much higher catalytic efficiency for ethanol production [413]. The ethanol fermentation ability of the thermotolerant yeast *Kluyveromyces marxianus* (able to utilize glucose, mannose, galactose, xylose, and arabinose) was examined. It was found that KmGAL1 and KmXYL1 genes are responsible for sugar utilization [414].

Clustered regularly interspaced short palindromic repeats (CRISPR)–associated protein (CRISPR-Cas) technology with targeted genome editing exhibits a more precise and accurate gene knockout and knock-in system as compared to zinc finger nucleases (ZFN) and transcription activator-like effector

nucleases (TALEN) [415]. Improvement in multiple stress tolerance capacity of yeast strain RPR39 by sequential mutagenesis (ethyl methane sulfonate, N-methyl-N′-nitro-N-nitrosoguanidine, near and far ultraviolet radiations) for enhanced bioethanol production [416]. Activation of β-glucosidase expression system in the multiple stress-tolerant (acid, ethanol and thermo) yeast *Issatchenkia orientalis* MF-121 strain for efficient ethanol production [417]. Formic acid–tolerant recombinant yeast strains were constructed by upregulation of formate dehydrogenase genes (FDH1 and FDH2) [418].

Furfural is one of the major inhibitors generated during bioethanol fermentation. Enhanced furfural tolerance of Tn 2 may be deliberated by the combined effect of lesser ROS (reactive oxygen sp) accumulation (early event) and an efficient detoxification of furfural (late event) [419]. For better biomass utilization, the endoglucanase I and II genes (egI or Cel7B and egII or Cel5A) of *Trichoderma reesei* QM6a were successfully cloned and expressed in *Saccharomyces cerevisiae* under the transcriptional control of the yeast ENO1 promoter and terminator sequences [420]. Co-expression of a cellobiose phosphorylase and lactose permease allows intracellular cellobiose utilization by *Saccharomyces cerevisiae* [421]. *Scheffersomyces stipitis* strain expressing xylose reductase–xylitol dehydrogenase (XR-XDH) pathway under adaptive evolution treatment affects sulfur amino acid biosynthesis and redox stress as well. These findings provide new insights for engineered bioethanol-producing strain through reverse metabolic engineering [422]. *Neotermes koshunensis* (termite) secretes endogenous β-glucosidase in the salivary glands and this was successfully expressed in *Aspergillus oryzae* [423].

A xylose-metabolizing yeast was constructed by the integration of XI overexpression cassettes into the genome of the *Saccharomyces cerevisiae* MT8-1 strain. Knockout of GRE3 (a gene encoding nonspecific aldose reductase) of the host yeast strain improved ethanol productivity [424]. A recombinant of xylose and cellooligosaccharide-assimilating yeast strain has been constructed by integrating genes responsible for the expressions of xylose reductase and xylitol dehydrogenase from *Pichia stipitis*, and xylulokinase from *Saccharomyces cerevisiae* as well as β-glucosidase from *Aspergillus acleatus* on the cell surface [425]. Improvement in tolerance of *Saccharomyces cerevisiae* for hot-compressed water-treated cellulose by expression of ADH1 [426]. Pyruvate decarboxylase (PDC) of *Gluconobacter oxydans* was considered to be a suitable candidate for heterologous expression in the thermophile *Geobacillus thermoglucosidasius* for ethanol production [427]. A combination of UV mutagenesis and protoplast fusion was used to construct strains with improved stress performance [428]. One major barrier to the economic conversion of biomass to ethanol is the inhibitory compound such as furfural and 5-

hydroxymethylfurfural (HMF). Ethanologenic yeasts undergo a genomic adaptation process during the adaptation phase for various inhibitors [429].

SUMOylation acts as a novel potential mechanism to reduce the multiple inhibitory effects of fermentation inhibitors by regulating the lag phase [430]. More oleic acid in the plasma membrane contributes to the acetic acid tolerance of yeast [431]. Ethanol production from xylose is improved by mating recombinant xylose-fermenting *Saccharomyces cerevisiae* strains. Xylose-fermenting, haploid, yeast cells of the opposite mating type were hybridized to produce a diploid strain hiding two sets of xylose-assimilating genes encoding xylose reductase, xylitol dehydrogenase, and xylulokinase resulting in improvements in fermentation ability [432]. *Zymobacter palmae* directly fermented cellulosic materials by co-expressing foreign endoglucanase and β-glucosidase genes [433].

Engineered microbes with vgb/VHb could be useful in enhancing bioethanol production [434]. Ethanol is directly produced at high temperature using the thermotolerant yeast *Kluyveromyces marxianus* displaying cellulolytic enzymes. The strain was genetically engineered to display *Trichoderma reesei* endoglucanase and *Aspergillus aculeatus* β-glucosidase on the cell surface [435]. Genetically engineered *Zymomonas mobilis* efficiently produced bioethanol from the hydrolysate of wood biomass containing glucose, mannose, and xylose as major sugar components [436]. Pyruvate decarboxylase (pdc) and alcohol dehydrogenase II (adhII), from *Zymomonas mobilis*, were heterologously expressed in the gram-positive bacterium *Streptomyces lividans* TK24 [437]. A novel endoglucanase encoding gene was cloned from *Alicyclobacillus vulcanalis* and expressed in *E. coli* for hydrolysis [438]. A recombinant *S. cerevisiae* strain is constructed displaying phytase on the cell surface which could improve ethanol production performance and effectively reduce the discharge of phosphorus [439].

A novel agglutinin expression system is constructed as well as immobilization β-glucosidase1 on the surface of wild-type *Saccharomyces cerevisiae* Y5 exhibiting a strong bioethanol fermentation capacity [440]. A novel aldehyde reductase encoded by YML131W from *Saccharomyces cerevisiae* gives tolerance to furfural derived from lignocellulosic biomass conversion [441]. The expression of cellulolytic genes is elicited using a recombinant endoxylanase from *Trichoderma harzianum* IOC-3844 [442]. Engineering of cellulolytic *Saccharomyces cerevisiae* strains is a promising way for lignocellulosic ethanol production [443]. Komeshu et al. used genetically engineered microbes for bioethanol production [444]. The activities and thermostabilities of the four PPP enzymes (transaldolase: TAL1, transketolase: TKL1, ribose-5-phosphate ketol-isomerase: RKI1, and d-ribulose-5-phosphate 3-epimerase: RPE1) can affect the efficiency of cellulosic ethanol production. Strains that

overexpressed *S. cerevisiae* TKL1 exhibited the highest rate of xylose consumption [445].

Disruption of the alkaline phosphatase gene PHO13 enhances ethanol production by a strain expressing the xylose reductase (XR) and xylitol dehydrogenase (XDH) gene [446]. *S. cerevisiae* strain co-expressing genes for several cell surface cellulases and the cellodextrin transporter was constructed to improving the efficiency of direct ethanol fermentation [447]. A novel xylose-fermenting yeast strain, FSC1, was developed for ethanol production by intergeneric hybridization between *S. cerevisiae* and *Candida intermedia* mutants by using a protoplast fusion technique [448]. Ethanolic xylose fermentation is controlled by the XR activity. Xylose transport also plays an important role in ethanol production [449]. A novel *Clostridium thermocellum* cellulolytic recombinant cellulase is expressed in *Escherichia coli* cells [23].

Overexpression or deletion of genes enhances acetic acid tolerance. Strains overexpressing ASC1 and GND1 displayed enhanced tolerance to acetic acid [450]. Multifunctional β-glucosidase/β-xylosidase/α-arabinosidase (Bgxa1) is found as an interesting candidate for the saccharification of lignocellulosic material [451]. Overexpression of GRE2 gene from *Scheffersomyces stipitis* to *Saccharomyces cerevisiae* as an aldehyde reductase contributes tolerance to aldehyde inhibitors produced from lignocellulosic biomass. GRE2 can reduce furfural to FM and reduce hydroxymethyl furfural to FDM [452]. Expression of dehydrin gene from Arctic *Cerastium arcticum* increases abiotic stress tolerance and fermentation capacity of a genetically engineered *Saccharomyces cerevisiae* [453]. It has been demonstrated that *S. cerevisiae* has the ability of in situ detoxification of aldehydes (furan, aliphatic, and phenolic) to their corresponding less toxic alcohols by the action of NAD(P)H-dependent aldehyde reductases [454].

Heterologous genes for xylose utilization were introduced into an industrial *Saccharomyces cerevisiae* [455]. Overexpression of PMA1 enhances tolerance to various types of stress and constitutively activates the SAPK pathways in *Saccharomyces cerevisiae* [456]. Restitution of the NAD$^+$/NADH redox balance plays a vital role in ethanol stress response [457]. Multiple gene-mediated NAD(P)H-dependent aldehyde reduction is a mechanism of in situ detoxification of furfural and 5-hydroxymethylfurfural by *Saccharomyces cerevisiae* [458]. Overexpression of native *Saccharomyces cerevisiae* exocytic SNARE genes increased cellulase secretion. SNAREs (soluble NSF [N-ethylmaleimide-sensitive factor attachment receptor proteins) are required for fusion events under intracellular membrane transport and facilitate protein trafficking between the various membrane-enclosed organelles and the plasma membrane [407]. Co-expression of TAL1 and ADH1 in recombinant *Saccharomyces cerevisiae* improves ethanol production from lignocellulosic hydrolysates [459].

Deletion of the PHO13 gene in *Saccharomyces cerevisiae* improves ethanol production from lignocellulosic hydrolysate in the presence of acetic and formic acids, and furfural [460]. PRS3, RPB4, and ZWF1 were identified as key genes for yeast tolerance to lignocellulose-derived inhibitors or multiple stresses [461]. Ethanol production is improved through decreased glycerol synthesis in *Saccharomyces cerevisiae* by metabolic and genetic engineering approaches. Glycerol production was hindered by the deletion of the most important GPD genes involved in glycerol production [462]. The Msn2 overexpression of various antioxidant enzyme genes in microbial strain showed tolerance to oxidative stress during ethanol production [463].

A recombinant *S. cerevisiae* strain (SK-NY), overexpressing GRE3-encoded NADPH-dependent aldose reductase and NADP$^+$-dependent xylulokinase, was constructed for efficient bioethanol production [464]. The redox balance between xylose reductase (XR) and xylitol dehydrogenase (XDH) is an important parameter for effective xylose fermentation. Xylitol accumulation is reduced and ethanol production is improved by reversing the dependency of XDH from NAD$^+$ to NADP$^+$ [465]. Efficient xylose-fermenting *Saccharomyces cerevisiae* is constructed through a synthetic isozyme system of xylose reductase from *Scheffersomyces stipites*. The xylose-metabolic genes (XYL1, XYL2 and XYL3) from *Scheffersomyces stipitis* have been engineered into *S. cerevisiae* [466].

Ethanol production from xylose in the presence of acetic acid is improved by the overexpression of HAA1 gene and the deletion of PHO13 gene in *Saccharomyces cerevisiae* [467]. Improved sucrose metabolism by overexpressing invertase is an attractive strategy to improve ethanol yields. The promoter and 5′ coding sequences of SUC2 are engineered, resulting in (94%) cytosolic localization of invertase [468]. Co-consumption of multiple sugars can be attained by modulating phosphotransferase system (PTS); this may be improved by amplifying the non-PTS pathway genes such as galP and glk [469]. The xylose utilization capability of *Saccharomyces cerevisiae* was enhanced by applying the concept of inverse metabolic engineering to identify the factors involved in improving xylose utilization. It has been observed that deletion of molecular chaperone-encoding genes HSP26, SSA1, and HSP104 facilitates the protein folding of xylose isomerase and enhancing xylose isomerase activity [470]. Saitoh et al. [471] constructed the triple auxotrophic strain OC2-HUT and introduced cell surface–displaying β-glucosidase (BGL) gene and a xylose-assimilating gene to generate the final strain OC2-ABGL4Xyl for efficient ethanol production. Improved xylose isomerase activity, upregulation of glycolysis and glutamate synthesis enzymes, and downregulation of trehalose and glycogen synthesis altogether contribute to the effective xylose utilization by the strain [472].

Co-fermentation of cellulose/xylan was investigated by the engineered industrial yeast strain OC-2 displaying both β-glucosidase and β-xylosidase [473]. *Saccharomyces cerevisiae* strain was engineered for xylose assimilation by the constitutive overexpression of the *Orpinomyces* xylose isomerase, *S. cerevisiae* xylulokinase, and the *Pichia stipitis* SUT1 sugar transporter genes [474]. To enhance heterologous cellulase protein production in yeast, a plasmid embracing the endoglucanase gene from *Clostridium thermocellum* (Ctcel8A) was used to transform a homozygous diploid yeast [475]. *Saccharomyces cerevisiae* strain was engineered with a three-plasmid SUMO yeast expression system by utilizing the portable small ubiquitin-like modifier (SUMO) vector set combined with the efficient endogenous yeast protease Ulp1 [476]. Transaldolase and transketolase are the key enzymes responsible for non-oxidative pentose phosphate pathway–based xylose utilization in recombinant *Saccharomyces cerevisiae*. Overexpression of TAL1 (transaldolase gene) and TKL1 (transketolase gene) increases the flux from the pentose phosphate pathway into the glycolytic pathway [477].

Improvement in cellulase production can also be done by modifying regulator expression in *T. harzianum* [478]. PfMig188, a catabolically derepressed engineered strain of the hyper-cellulolytic fungus *Penicillium funiculosum* NCIM1228, was investigated. Results demonstrated that the PfMig188 secretome has relatively broad substrate specificity and acts as an efficient substitute for *T. reesei*–based secretomes for diverse biomass saccharification [479].

Deletion of the HXK2 gene (a moonlighting protein) in *Saccharomyces cerevisiae* enables mixed sugar fermentation of glucose and galactose (major sugar components of red seaweeds) in oxygen-limited conditions [480]. Overexpression of native PSE1 and SOD1 genes under the transcriptional control of the constitutive PGK1 promoter in *Saccharomyces cerevisiae* improved heterologous cellulase secretion. The effect of these genes on heterologous protein secretion of three cellulases—an exoglucanase encoded by cel6A of *Neocallimastix patriciarum*, a β-glucosidase encoded by cel3A of *Saccharomycopsis fibuligera*, and an endoglucanase encoded by cel7B of *Trichoderma reesei*—was investigated by integrating the PGK1P/T–PSE1 and PGK1P/T–SOD1 cassettes into *S. cerevisiae* strains to produce the relevant cellulases [481]. A novel β-glucosidase gene encoding a protein (BglA) of 446 amino acid, belonging to the glycoside hydrolase family 1 (GH1), was cloned from a hyperthermophilic bacterium *Thermotoga naphthophila* RKU-10T and overexpressed in *Escherichia coli* BL21CodonPlus. All these significant features make BglA an appropriate candidate for biotechnological and industrial applications [482].

6.4 Attachment on cell surface aspects

Yeast cell surface engineering enables more than 100 enzymes to be displayed on the surface of a yeast cell. The displaying yeast can be used as a whole-cell biocatalyst without requiring enzyme separation and purification processes [483]. Construction of a new system for endoglucanases exhibiting carbohydrate-binding modules using yeast cell surface engineering. *Saccharomyces cerevisiae* BY4741 (Δ sed1) exhibiting 3 cellulases (*Trichoderma reesei* endoglucanase II [EG], *T. reesei* cellobiohydrolase II [CBH], and *Aspergillus aculeatus* β-glucosidase I [BG]) was constructed by yeast cell surface engineering [484]. For making more efficient bioethanol production, the endoglucanase gene endo753 of *Aspergillus flavus* NRRL3357 was introduced on the cell surface of *Saccharomyces cerevisiae* EBY100 strain by the C-terminal fusion using Aga2p protein as an anchor attachment tag [485].

Heterologous cellulolytic enzymes were expressed on the *Z. palmae* cell surface by cell surface display motif of the *Pseudomonas* ice nucleation protein N-terminal anchoring [486]. Yeast strain was engineered by codisplaying several hemicellulolytic enzymes on the surface of xylose-utilizing *Saccharomyces cerevisiae* cells [487]. A recombinant was developed by expressing three cellulases from *Clostridium cellulolyticum*—endoglucanase (Cel5A), exoglucanase (Cel9E), and β-glucosidase—on the surface of the *Escherichia coli* LY01 [488].

6.5 By checking bacterial contamination

The presence of bacterial contaminants reduces alcoholic fermentation. Antibiotics are currently used to control contamination, but their residues may be detected; therefore the antimicrobial activity of the natural compounds such as hops extract, 4-hydroxybenzoic acid, nisin Z, and lysozyme were investigated and found their great potential for the substitute of antibiotics used conventionally in the ethanol industry [489]. Bioethanol fermentation is usually suppressed by lactic acid bacteria (LAB), thereby leading to a decrease in bioethanol yield. Nisin-loaded P4VP microspheres were added into the simulated contaminative fermentation system for controlling the *L. plantarum* contamination in bioethanol fermentation [490].

Bacteriophage can be used as a potential alternative agent for controlling *Lactobacillus plantarum* contamination during bioethanol production. Moreover, increased concentrations of monounsaturated fatty acids due to bacteriophage treatment might lead to more membrane fluidity and promote the cell viability of *S. cerevisiae* [491]. Bacteriocins, bacteriophages, and beneficial bacteria are used as a non-conventional antimicrobial agents to reduce bacterial contamination in the bioethanol industry [492]. *Brettanomyces/Dekkera*

bruxellensis–based microbial contamination of ethanol fermentation has been controlled by saccharomycin (biocide composed of antimicrobial peptides) secreted by *Saccharomyces cerevisiae* [493]. Transcriptional profile (genes with significantly repressed or induced expression) of a bioethanol production contaminant can provide information on antimicrobials, to combat yeast contamination during industrial bioethanol production [494].

6.6 To develop ethanol and acetate tolerance

Alcohol toxicity is a more serious problem for bioproduction using bacteria. Alcohols interact directly with the lipid bilayer because of their amphiphilicity and thereby, membrane fluidity is altered. These changes in fluidity increase membrane permeability and induce conformational changes in membrane proteins. Ethanol-induced membrane induces the expression of heat-shock and phage-shock proteins. Transcriptomic analyses identified important roles of the groESL chaperone system and the global regulator of sporulation in alcohol tolerance [495]. Higher ethanol concentration in *Saccharomyces cerevisiae* leads to cell growth inhibition and ultimately cell death. Several mechanisms, viz. changes in gene expression, membrane composition, and increment in chaperone proteins, help stabilize other denatured proteins [496].

Ethanol and acetate accumulation under the fermentation process affects ethanol yield by stressing the metabolic capabilities of the microorganisms. Such conditions can be regulated by overexpression of the iron-sulfur cluster (ISC) in the *E. coli* KO11 strain [497, 498]. Green tea polyphenols (GTP) enhance the ethanol tolerance of *S. cerevisiae* may be due to the significantly differentially expression of large amounts of genes related to the cell wall, cell membrane, basic metabolism, and redox regulation [499]. Amend effect of *Cyclocarya paliurus* (*C. paliurus*) triterpenoids on *S. cerevisiae* under the ethanol stress was explored. It has been observed that the treatment of triterpenoids enhances ethanol tolerance of *S. cerevisiae* [500].

Bacterial signals of N-acyl homoserine lactones induce the changes of *S. cerevisiae* morphology, thus making it more ethanol tolerant. Bacterial signals QSMs (quorum signal molecules) of N-acyl homoserine lactones induce the changes of morphology and ethanol tolerance in *Saccharomyces cerevisiae*. Microbes communicate with each other using chemical signal molecules, termed autoinducers (AI) or quorum sensing molecules (QSM). When the signal molecules accumulate a threshold, the communicating microbes begin to alter gene expression and therefore behavior in response. *Saccharomyces cerevisiae*, exposed to short-chain 3-OC6-HSL and long-chain C12-HSL, showed obvious changes in morphology and ethanol tolerance [501]. *Issatchenkia orientalis*, a non-*Saccharomyces* yeast that can resist a wide

variety of environmental stresses (ethanol stress), has potential use in bioethanol production [502]. The metabolic differences of diploid (α/a) and haploid (α, a) yeasts in response to ethanol stress were recently studied. It was found that the haploid genotype being more susceptible to ethanol stress as compared to diploid may be due to its higher content of protective metabolites including polyols [503]. Antiseptics such as hydrogen peroxide, potassium metabisulfite, and 3,4,4-trichlorocarbanilide have been shown to inhibit and control bacterial contamination in ethanol fermentations [504].

Stress-tolerant *Saccharomyces cerevisiae* strains are developed by metabolic engineering through cell flocculation and zinc supplementation [505]. Metabolically engineered *Saccharomyces cerevisiae* strain showed tolerance for acetic and formic acids. Improved activities of transaldolase (TAL) and formate dehydrogenase (FDH) through metabolic engineering successfully deliberated resistance to weak acids in a recombinant xylose-fermenting *Saccharomyces cerevisiae* strain [506]. Plasma membrane proteins Yro2 and Mrh1 are required for acetic acid tolerance in *Saccharomyces cerevisiae* [507]. Creation of yeasts with acid tolerance was successful using yeast cell surface engineering. The cell wall of *Saccharomyces cerevisiae* plays a crucial role in the biophysical characteristics of the cell surface. The modification of the cell wall property is an important factor for adaptation under a stressful environment. A novel peptide, Scr35, that provides acid tolerance in yeasts was obtained [508].

Expression of a salt-induced 2-Cys peroxiredoxin from *Oryza sativa* improves stress tolerance in the recombinant yeast *Saccharomyces cerevisiae*. Peroxiredoxins (Prxs) are a thiol-specific antioxidant enzymes that are seriously involved in cell defense and protect cells from oxidative damage [509]. Adaptive laboratory evolution (ALE) was used for the development of furfural and acetic acid–tolerant strain [510]. Rpn4 and proteasome-mediated yeast resistance to ethanol includes regulation of autophagy. It has been suggested that Rpn4 affects the autophagic system activity upon ethanol stress through the PRB1 regulation [511]. One approach to alleviate the inhibition problem is to use genetic engineering to introduce increased tolerance by overexpression of *Saccharomyces cerevisiae* Pad1p. The overexpressing transformants showed approximately tenfold higher activity [512].

Acetate is an effective agent for the prevention of bacterial contamination, but it negatively affects the fermentation ability of *S. cerevisiae*. Overexpression of the organic acid–tolerant HAA1 gene, which encodes a transcriptional activator, could be a useful molecular breeding method for acetate-tolerant yeast strains [513].

7 Future prospects

To develop a successful and commercially viable technology for bioethanol production, novel strategies for generating enzyme cocktails for lignocellulose hydrolysis in biorefineries would be developed by enzyme engineering, reconstitution of enzyme mixtures, and bioprospecting for superior enzymes. The current situation warrants the need for integrated research and development of lignocellulosic biomass utilization [514]. Understanding of the complexity of lignocellulose feedstock, their chemical compositions, and the knowledge of pretreatment methods are required [19].

Functional metagenomic strategies for the finding of novel enzymes for biomass hydrolysis and biofuel production such as new-generation sequencing and mining the metagenome are becoming more efficient [515]. In recent years, postgenomic approaches such as metabolomics in combination with other omics such as genomics, chemogenomics, transcriptomics, and proteomics were studied to boost the use of systems metabolic engineering tools in industrial settings. It provides insights of the mechanisms and interactions of genes and allowed to better understand under severe environments, overexpression and downregulation of multiple genes, and construction of synthetic regulatory proteins and other components such as ethanol and acetic acid tolerance [495, 498, 516–518].

Permeases are directly involved in the utilization of and regulatory response to nutrient sources. Permease regulatory mechanisms on yeast metabolic engineering provide important insights for the elimination of harmful substances in *S. cerevisiae* [519]. *S. cerevisiae* is frequently challenged by bacterial contamination and a combination of lignocellulosic inhibitors formed during the pretreatment so it can be checked [520]. Required robust *Saccharomyces cerevisiae* strains with improved capacity to cope with the toxic compounds formed during the biomass pretreatment, among which are 5-hydroxymethylfurfural (HMF), furfural, weak organic acids, and phenolic compounds generated [399].

Recently, global transcription machinery engineering (gTME) has been applied as an effective technique to enhance the target specific phenotype of microbes for enhanced ethanol production. The gTME uses random mutagenesis libraries of global transcription factors generated by error-prone PCR to reprogram transcription and obtain specific phenotypes. Ep-PCR is a fast and cheap molecular biology method for the random mutation in a particular piece of DNA [495, 521]. Microorganisms have great potential for the engineering and/or incorporation of complete metabolic pathways for the over production of value-added chemicals. Despite the wide capability of microorganisms, there is still a lack of knowledge about the metabolic networks responsible for such processes. Metabolomics are used for microbial strain selection

and engineering novel biochemical pathways strictly responsible for efficient biomass conversion [503, 522].

Xylose acts as the second most prevalent sugar after glucose in lignocellulosic biomass utilization; therefore, extensive research efforts have been made and still needed to introduce heterologous genes for xylose metabolism into *S. cerevisiae*. For this reason, detailed studies about naturally xylose-fermenting yeasts species (*Scheffersomyces stipitis* or *Pachisolen tannophilus*), comparative genomics, and evolutionary analysis are needed as effective approaches to determine the limiting steps in pentose metabolism. Overexpression of genes encoding enzymes of nonoxidative pentose phosphate pathway (PPP) and replacement of a small amount of enzymes of xylose metabolism, as well as isolation of xylose transporters were pointed out as crucial factors for the adequate function of this pathway [522, 523].

The combination of metabolomics, fluxomics, and synthetic biology is used as a powerful tool for prospecting novel metabolic routes [524, 525]. Designer cellulosomes (also known as chimeras) unlike native cellulosomes are artificial constructs, composed of chimeric scaffoldin and enzymes with cohesins and dockerins of divergent specificities, thus providing interdomain flexibility in the enzyme complex for effective utilization [21]. Recent trends in ligninolytic green biotechnology by immobilization engineering processes suggest the potential industrial applications of ligninolytic enzymes in various sectors of the modern industry [526].

Nanoparticles are gaining increasing interest among researchers due to their exquisite properties. They are also being explored in biofuels to improve the performance of bioethanol production. Different types of nanomaterials (metallic, nanofibers, and nanotubes) have been used and they can effectively suppress inhibitory compounds under certain conditions [527]. Metabolic engineering is used of microorganisms for biofuel production. Metabolically engineered yeasts in surface displaying various hydrolytic enzymes appear to hold the greatest potential. The bacterium *Zymomonas mobilis* metabolically engineered to make bioethanol from pentose sugars is already being commercialized [51, 415, 528].

Chromosomal integration of genetic material is the preferred method to overcome gene loss that may occur by homologous recombination. The use of CRISPR/Cas9 provides a marker-free genome-editing tool and thereby, it should open a new avenue in creating microbial biorefineries for enhanced bioethanol production by engineering the microbial genomes for desired traits such as enhancing the biofuel tolerance, inhibitor tolerance, and thermotolerance as well as modifying the cellulases and hemicelluloses enzymes [415, 529].

However, more research on the metabolic pathways, regulation of end-product formation, and construction of genetically engineered thermophilic/thermotolerant microorganisms with high tolerance to ethanol is required for industrial fermentations. Evolutionary engineering is another approach for

development. It uses laboratory evolution for selecting industrially relevant traits. By integrating whole genome sequencing, bioinformatics, classical genetics, and genome-editing techniques, evolutionary engineering has also become a powerful approach for the identification and reverse engineering of molecular mechanisms that underlie industrially relevant traits [524].

Adaptive laboratory evolution (ALE) is a powerful tool for analyzing phenotypic and genotypic changes during bacterial evolution. In this approach, cells are cultured under a selective environment for many generations, leading to adaptive evolution [495]. DNA microarrays can also be used in detecting transcription factor binding sites and single-nucleotide polymorphisms. Target genes for genetic manipulation should be identified to confer useful phenotypes, such as stress tolerance and high fermentation activity, and to improve the production of the target product [530]. It is possible to evaluate the effects of specific mutations on alcohol tolerance using genome-editing technology [495].

Genome shuffling is an efficient way to improve complex traits or phenotypes under the control of multiple genes. Genome shuffling is the best way for strain improvement in very high-gravity (VHG) fermentation [531, 532]. A better perception of the yeast adaptation under multiple stresses is of critical importance to develop strategies to improve yeast robustness and bioconversion capacity from lignocellulosic biomass [533]. Design and engineer a strain with a high secretory phenotype, bioethanol-specific stressors, including tolerance to products formed during hydrolysis of lignocellulosic substrates [534]. Industrial yeast strains with better xylose fermentation ability and stress tolerance are important for economical lignocellulosic bioethanol technology [535]. Isolated strains of *Saccharomyces* c*erevisiae* from different sources display extensive genetic and phenotypic diversity. To better understand how genomic changes influence phenotypes is more important for developing strategies. Whole genome sequencing was carried out based on single-nucleotide variations and small insertions/deletions/annotations in the genome. Phylogenetic analysis also recommended the unique genes, obtained through horizontal gene transfer from other species. RNA-Seq analysis also suggests that sometimes unique genes are not functional due to unidentified intron sequences [376].

As an efficient ethanol-producing bacterium, *Zymomonas mobilis* has created special attention due to several properties, viz. high sugar uptake, ethanol yield, and tolerance. Different metabolic engineering strategies have been used to create a new metabolic pathway for *Z. mobilis* to broaden its application range [51]. Expressing hydrolase in the lignocellulosic feedstock is a favorable alternative, due to the large availability of biomass [5]. The mixed feedstock approach to lignocellulosic ethanol production has shown that their use can bring about significant cost savings as compared to single feedstock

utilization [536]. Stress tolerance in industrial yeast strains is an important point for cost-effective bioprocessing. It optimizes microbial systems to adapt under environmental stresses and thus has a huge power of the creation of robust stress-tolerant yeasts [537]. The future of lignocellulosic biomass would be based on improvements of plant biomass, metabolic engineering of ethanol production pathway and hydrolytic enzyme-producing microorganisms, and the fullest exploitation of waste biomass and process integration of the individual steps involved in bioethanol production [538].

8 Conclusions

Lignocellulosic biomass, as a waste material, offers an attractive alternative for its valorization into valuable products. However, the recalcitrance of these materials and the inability of microorganisms to efficiently ferment each sugar present as well as lignocellulosic hydrolysates still lower the production of bioethanol. The viability of lignocellulosic material for ethanol production has been still searched around the world depending upon its availability. More attention is required on the development of sustainable and scalable fuels from renewable biomass, viz. agricultural and industrial residues, as a means to curb global warming. There is an intense emphasis on lowering the costs of renewable bioethanol production by overcoming the challenges connected to high substrate costs, limited microbial capacity, stress tolerance, low titers, and low production rates.

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