REVIEW

Fungal Glycoside Hydrolases of White-Rot Fungi for Cellulosic Biofuels Production: A Review

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The second generation bioethanol production from lignocellulose materials through environmental friendly methods is one of the biggest challenges on industrial application. Enzymatic hydrolysis of cellulose has more benefits compared with the acid hydrolysis This method has the good specificity, low consumption of energy and chemicals and is more environmental friendly. However, the utilization of lignocellulose for bioethanol production through enzymatic methods is still confronting several difficulties for commercialization. Cellulose hydrolysis step has been reported to be the bottleneck of bioethanol production by enzymatic process, and the major barrier of this process is high price of enzymes, which making the process less economically feasible. For this reason, many developments are still needed in cellulase production from various organisms for cellulose saccharification. White-rot fungi have received much consideration for their valuable enzyme systems which can effective degrade lignocellulose biomass. These fungi could secrete extracellular oxidative and hydrolytic enzymes that degrade lignin, hemicellulose, and cellulose. This review provides a complete overview of the glycoside hydrolases enzymes production by white-rot fungus, such as endoglucanase, exoglucanase, β-glucosidase, cellobiose dehydrogenase and lytic polysaccharide monooxygenase. The use of white-rot fungus for low cost glycoside hydrolases enzymes production might be fascinating for second generation bioethanol production.

Keywords: White-rot fungi, Biofuels, Glycoside hydrolases, Enzymatic hydrolysis, Enzymes.

INTRODUCTION

Biomaterials, biofuels and chemicals derived from lignocellulose biomass have received extensive interest to reduce dependence on petroleum-based products [1,2]. In the converting process of lignocelluloses into bioethanol and other valuable chemicals, hydrolysis of cellulose and hemicelluloses to corresponding sugars is a crucial stage [3]. Enzymatic hydrolysis of cellulose by cellulases is accepted as one of the hopeful and general techniques compared with conventional hydrolysis by acid catalyst [4,5]. Enzymatic hydrolysis is considered as an environmental friendly method with good specificity and sensitivity, low energy and chemical consumption, smaller amount of byproducts, and time efficiency [2,5,6]. However, to date, the high cost of cellulases for cellulose hydrolysis is the main obstacle of bioethanol production [5,7-9].

White-rot fungi have received much consideration for their valuable enzyme systems that are effective to degrade lignocellulose biomass. The fungi have powerful extracellular oxidative and hydrolytic enzymes which can degrade biopolymer, such as lignin and cellulose biopolymer [3,10,11]. Nowadays, significant attentions have been dedicated to researches on the cellulases from white-rot fungi.

Overview of the current situation on bioethanol production: Increasing energy demands and consumption, depletion in the reserve of fossil fuels and global warming issue have caused a paradigm shift towards sustainable and clean production of biofuels and bioproducts from renewable sources [5,12-14]. Presently, bioethanol is considered as the most common alternative, renewable, sustainable, clean and economically feasible fuel. The first generation bioethanol is produced from starch and sugar commonly derived from corn (*Zea mays*) and

sugar cane (*Saccharum officinarum*). However, these bioethanol sources also have to be used for human food and animal feed, causing negative effects if the demand of bioethanol increases [5,13]. A potential source for low-cost, abundant and renewable bioethanol production is lignocellulose materials, such as forestry and agricultural residues, as feedstock for the second generation bioethanol [9,13,15]. Even though temporary fossil fuel prices have currently decreased, it probably will increase rapidly in the future due to the disparity between the crude oil demand and the total production [5]. The current gap condition in fossil fuel consumption and limited resources has brought a global challenge for cellulosic biofuel production to replace energy sources.

Presently, effective conversion of lignocellulose biomass to bioethanol and other chemicals is still a challenging problem [15]. To estimate the prospective for lignocelluloses biomass, International Energy Agency (IEA) presented two scenarios in which 10% and 25% of total forestry and agricultural residues are available for biofuel production, while the remaining residues for other utilization [16]. According to IEA report, lignocellulose biomass residues will be enhanced by approximately 28% for crop sources and approximately 50% for roundwood in year 2030. It is resumed that approximately 10% of total lignocellulose could produce about 155 billion liter of gasoline equivalent (5.2 EJ) bioethanol or approximately 4.1% of the projected transport fuel demand in year 2030 and that 25% of total lignocellulose converted to either bioethanol, biodiesel, or syngas could supply 385-554 billion liter of gasoline equivalent (13.0-23.3 EJ) totally [16].

Bioethanol production from lignocellulose through environmental friendly and sustainable methods, where converting cellulose into fermentable sugars is main step, is one of the biggest challenges on industrial application [17]. The common methods to convert cellulose to fermentable sugars are chemical method using acids and biological methods using enzymes (bioconversion). Compared with acid hydrolysis, enzymatic hydrolysis of cellulose has more benefits [5]. This method has the good specificity, low consumption of energy and chemicals, and is more environmental friendly. In biological methods, enzymes can cleave from the β-1,4-glycosidic bond of cellulose selectively and the methods can avoid the unwanted products from glucose, such as furfurals which are inhibitors at the fermentation step for producing bioethanol [17]. Enzymatic hydrolysis of cellulose into glucose unit, therefore, requires cooperative actions of cellulase complex enzymes, at least *endo*-1,4-β-D-glucanases, *exo*-1,4-β-D-glucanases and β-glucosidase [18,19]. The endoglucanase acts on glycosidic bonds randomly, preferentially in non-crystalline cellulose regions, resulting in the production of oligosaccharides consisting of reducing and non-reducing ends. The produced oligosaccharides are attacked progressively by exoglucanase which produces cellobiose as a main product. The existence of β-glucosidase is important in cellulose saccharification, because this enzyme not only produces glucose, but also reduces cellobiose, which is an inhibitor of enzymatic depolymerization of cellulose [14]. However, the utilization of lignocellulose for bioethanol production through enzymatic methods is still confronting several difficulties for commercialization. Cellulose hydrolysis step has been

reported to be the bottleneck of bioethanol production by enzymatic process, and the major barrier of this process is high price of enzymes [17], which making the process less economically feasible. For this reason, many developments are still needed in cellulase production from various organisms for cellulose saccharification.

Chemical characteristics of lignocellulose biomass: Lignocellulose is the major structural component of biomass, comprising about half of the plant matter produced by photosynthesis and it represents the most abundant renewable resource in the world. It mainly consists of cellulose, hemicelluloses, and lignin which are chemically bonded by non-covalent forces and covalent crosslinkages [15,20]. In nature, lignocellulose is derived from grass, forestry and agricultural residues in various compositions and proportions [21].

Cellulose composes about 40-50% of wood biomass in dry weight. Native cellulose has complex physical structure and morphology [22]. However, the chemical composition is simple: the linear polysaccharide consists of D-glucose subunit, linked by β-1,4 glycosidic bond (Fig. 1a). The individual chains bond to each other to form long chain polymer by hydrogen bond and van der Waals force. Although cellulose has usually highly crystalline form, the structure is not uniform. Physical and chemical evidences of cellulose also show a small amount of non-organized cellulose chains forming amorphous cellulose [20,23]. Hemicelluloses and lignin masks many of cellulose microfibril to form very complex morphologies. Degradation of cellulose, therefore, requires multiple enzyme system [23].

Hemicelluloses are complex carbohydrate polymers and make up 25-30% of the wood biomass in dry weight [20]. Hemicelluloses are polysaccharides with several sugar units and substituted side chains in the form of a low molecular weight linear or branched structures (Fig. 1b). These polymers are named in accordance with their main sugar residues in the backbone, such as D-xylose, D-mannose, D-galactose, D-glucose and L-arabinose. Hemicelluloses have different compositions between softwoods and hardwoods. The main hemicelluloses of softwoods and hardwoods are galactoglucomannan and 4-*O*-methylglucuronoxylan, respectively. Galactoglucomannan is composed of β-1,4-linked D-glucose and D-mannose, which can be substituted by D-galactose. 4-*O*-Methylglucuronoxylan is composed of β-1,4-linked xylose that can be substituted 4-*O*-methyl glucuronic acid [24]. Branched polymers in hemicelluloses contain neutral and/or acidic side groups. These groups provide hemicelluloses as non-crystalline or poorly crystalline form and make them more easily to be hydrolyzed than cellulose chains. In primary cell walls, hemicelluloses build a matrix jointly with pectins and proteins and with lignin in secondary cell walls. Interactions between hemicelluloses and lignin in covalent bonds containing ester or ether linkages form lignin-carbohydrate complexes. Cleaving these covalent bonding in lignin-carbohydrate complexes has been suggested to be crucial for lignin degradation by white-rot fungi [25].

Lignin is also the abundant polymer in nature, being about 18-35% of wood biomass in dry weight. Functions of lignin are structural support, impermeability and resistance against oxidative stresses and microbial attacks [20]. Lignin is an amorphous
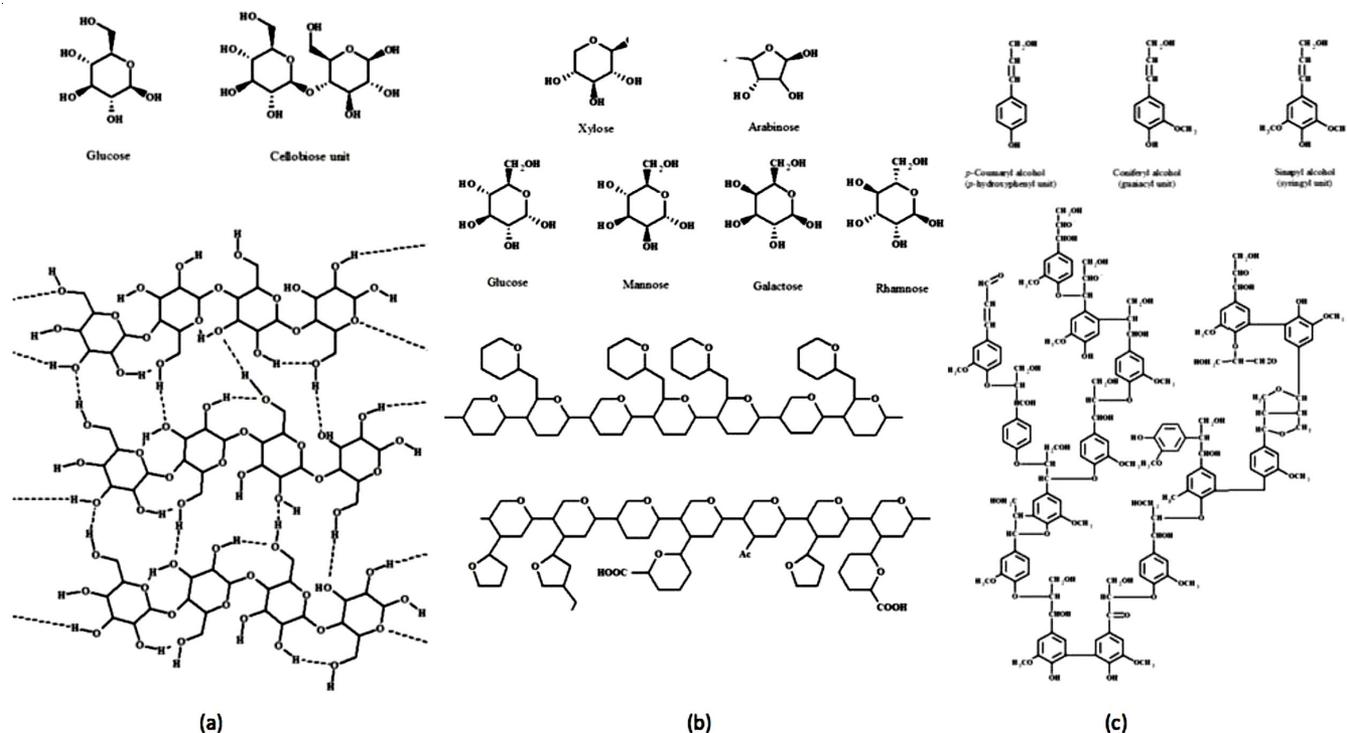
Fig. 1. Suggested chemical structures of wood chemical components (a) cellulose chains with hydrogen bonds, (b) hemicelluloses, (c) softwood lignin

heteropolymer, non-soluble in water and optically inactive. Lignin consists of phenylpropane units joined together by different types of linkages (Fig. 1c). Lignin is synthesized by free radicals, which are released by the peroxidase-mediated dehydrogenation of cinnamic alcohols, such as coniferyl alcohol, p-coumaryl alcohol and sinapyl alcohol leading to guaiacyl lignin, p-hydroxyphenyl lignin and syringyl lignin, respectively. Lignins have different compositions between softwoods and hardwoods. Guaiacyl lignin, predominantly consists of coniferyl alcohol with some p-coumaryl subunits, is the main component of softwood lignin. On the other hand, guaiacyl-syringyl lignin, composed of guaicyl and syringyl with a few amount of p-hydroxyphenyl units, is the main constituent of hardwood lignin [26]. Syringyl (S) units of lignin are preferentially degraded by fungi, whereas guaiacyl (G) units are more resistant to degradation [27]. Laccase and peroxidases can cleave linkages in polymeric lignins and disrupt β-aryl ether bond, which represents the most dominant linkage in syringyl lignin [28].

Degradation of lignocellulose by white-rot fungi: The biological degradation of lignocellulose biomass has drawn the attention of researchers for many years [20]. Generally, lignocellulose biomass degradation by wood-rot fungi should not be regarded as only a damaging process. It also has a positive effect on nutrient cycling processes in natural environment [29-31]. This process can be applied for lignocellulose based industries [32]. Fundamentally, lignocellulose degradation by fungi and bioethanol production have similar objectives: to break down lignocellulose structures into small molecules, such as glucose, xylose, mannose, galactose, rhamnose and arabinose [28]. Wood-rot fungi have evolved a large variety of hydrolytic and oxidative enzymes for depolymerization of cellulose, hemicelluloses and lignin. Enzymatic processes in lignocellulose

degradation observed in nature have been reproduced under laboratory conditions and at an industrial scale, such as in bioethanol production [33,34].

Wood-rot fungi are classified by type of degradation *viz*. white-rot fungi, brown-rot fungi and soft-rot fungi. Both white- and brown-rot fungi belong to the basidiomycetes, while soft-rot fungi to ascomycetes [35]. White-rot fungi mainly degrade the lignin, resulting that remaining wood after decay shows more bright color (white). Some of these fungi degrade both lignin and cellulose simultaneously by powerful extracellular oxidative and hydrolytic enzymes [36]. Based on the ability of white-rot fungi, the pattern of white-rot fungi was sub-divided into selective delignification and simultaneous white-rot fungi [35-39]. Brown-rot fungi degrade cellulose and hemicelluloses, while partially modify lignin. Consequently, the decayed wood reduces in size and its colour becomes a brown color because of lignin modification, such as demethylation and oxidation [40]. Soft-rot fungi secrete cellulases for degrading cellulose but not lignin degrading enzymes, leading to the formation of microscopic holes/cleft within the wood, the occasional discoloration and the cracking similar to that by brown-rot fungi [36,41].

White-rot fungi have obtained great interest for their useful enzyme systems which can efficiently degrade the lignocellulose. These fungi have potent extracellular oxidative and hydrolytic enzymes. Of many enzymes, ligninolytic enzymes, such as lignin peroxidase, manganese(II)-dependent peroxidase and laccase, are responsible for depolymerizing and modifying lignin and for opening phenyl rings [11,42]. Cellulolytic enzymes, such as endoglucanase, exoglucanase, β-glucosidase, cellobiose dehydrogenase and lytic polysaccharide monooxygenases, are responsible for cellulose degradation [11,43-45]. However, more researches are still required to completely understand the

relationships between degradation process and enzymes or other metabolites secreted by white-rot fungi during degradation process. The obtained information could facilitate to clarify the biochemical mechanisms of lignocellulose degradation by white-rot fungi and simplify the fungal strain selection for biotechnological applications [11,38].

Glycoside hydrolases (GHs): Lignocellulose represents an enormous and sustainable natural polymer source that requires several enzymatic approaches to rearrange or depolymerize polysaccharide structures [46]. Enzymatic decomposition of cellulose primarily depends on glycoside hydrolases (GHs) and oxidative enzymes. A variety of organisms produce various enzymes, in which though various proteins distribute separately, work synergistically to degrade lignocellulose. The decomposition of lignocellulose to fermentable sugars involves the coordinated actions of GHs and non-catalytic proteins [47]. GHs, such as cellulases, xylanases and other glucosidase, cleave the glycosidic bonds between carbohydrates or carbohydrate and noncarbohydrate part [48].

A sequence-based classification system for carbohydrate-active enzyme has developed in 1991 by Henrissat [49], namely the CAZy database (CArbohydrate enZyme database). The exponentially growing genomic database has provided an alternative classification system of enzymes based on amino acid sequence similarities of their catalytic domains [50-52]. This enzyme classification system enables prediction of the main catalytic part and the catalytic mechanism because these are conserved in GH families [48]. A classification system of GHs into families has been suggested based on amino acid sequence similarities, developing the direct correlation of amino acid sequence with enzyme folding [52,53]. The larger number of 3D-structure of GHs validated similarities in protein folding properties in the member of GHs families [53].

Cellulases mostly contain the modular structures, composed of catalytic domain attached to one or several associated non-catalytic domains. While catalytic domain can be classified into several families based on their amino acid sequence similarities and structure, the classification of non-catalytic domain, independent and admiring to their catalytic domain, is not yet to be completed. Presently, the CAZy database (www.cazy.org) categorizes GHs into 135 families with more than 150,000 protein sequences and 71 carbohydrate-binding module (CBM) families with more than 32,000 protein sequences [50].

Fungal cellulases: Fungal cellulases take part in crucial functions by providing easily digestible carbon source to fungal metabolism and growth [54]. The great capability of white-rot fungi to degrade all wood components is mainly based on the activity of various complexes of extracellular enzymes. The fungi secrete oxidative enzymes, such as lignin peroxidase (LiP), manganese peroxidase (MnP) and laccase to oxidize, modify, and degrade lignin. On the other hand, these fungi also secrete hydrolytic enzymes, such as cellulase, hemicellulase and pectinase, which are typically induced by their substrates [55]. Simultaneous degradation type of white-rot fungi significantly degrades cellulose due to their high cellulolytic activity [54]. Many white-rot fungi can secrete various types of cellulase enzyme mixtures (Table-1).

Cellulase refers to a group of complex enzymes, which act together to hydrolyze cellulose at the β-1,4 glycosidic bond, leading to production of soluble oligosaccharides [2]. Cellulases distribute throughout the biosphere, such as plants, animals and microorganisms. For efficient and complete hydrolysis of cellulose, cellulolytic enzyme system needs at least three fundamental types of cellulases: endoglucanase, exoglucanase and β-glucosidases. These enzymes lead to synergistic interactions, an improvement of activity, which shows more activity than those of added individual enzymes [56]. All cellulase enzymes contribute to cleavage of β-1,4 glycosidic bond, often referred to GH family enzymes. Though cellulose structure is quite uncomplicated, there is an enormous native variety of cellulases with catalytic component and classified into more than 14 GH families to adapt the reaction types and diverse synergisms [2]. A general characteristic of most cellulases in various fungal genera is a domain structure with a catalytic function linked with a binding module, namely cellulose-binding domain (CBD) [57]. The CBDs are non-catalytic part and clearly necessary for efficient hydrolysis of crystalline cellulose, but not for soluble substrates, such as cellobiose [57].

Exoglucanases or cellobiohydrolases are exo-type enzymes that mainly degrade crystalline cellulose. Some exoglucanase are also active on cellotriose, cellotetraose or higher cellodextrins [58,59]. Exoglucanases belong to the GH6, GH7 and GH48 families with GH6 and GH7 exoglucanases being archetypical [2]. According to secretome and genome sequence, GH6 and GH7 exoglucanase are found in many cellulolytic fungi, up to 70% wt level [60-62]. There are two specificity types of exoglucanases, GH7 exoglucanase, also known as CBH I (E.C. 3.2.1.176), performing uni-directionally on the long chain oligomers either from the reducing end of a cellulose chain. On the contrary, GH6 exoglucanase, known as CBH II (E.C. 3.2.1.91), can be specific toward the non-reducing end, liberating cellobiose or cellulo-oligosaccharides [57]. GH7 and GH6 exoglucanases show greatly synergistic and collaborative actions in degrading cellulose as substrate. In addition to catalytic module, many exoglucanase posses CBD as non-catalytic domains that considered to be important in exoglucanase actions on crystalline cellulose. Exoglucanases have been reported from several white-rot fungi, such as *Sporotricum thermophile*, *Pleurotus ostreatus*, *Agaricus arvensi*, *Trametes hirsuta*, *Irpex lacteus*, *Auricularia polytricha*, *Phanerochaete chrysosporium*, *Lentinus edodes* and *Armillaria gemina, Porodaedalea pini* [63-71].

Endoglucanases (EG, E.C. 3.2.1.4) are *endo*-type enzymes that cleavage glycosidic bonds at the amorphous region of the cellulose, producing new long chain oligomers (non-reducing end), cellobiose or cello-oligosaccharides [11]. A small number of endoglucanases also can perform on crystalline cellulose [72,73] and collaborate with exoglucanase for highly useful enzymatic process on cellulose degradation. Endoglucanases distribute among various organisms and are classified into more than ten GH families with different performance mechanisms toward cellulose, such as GH5, GH7, GH9, GH12, GH45 and GH48. Among secreted proteins and enzymes of cellulolytic fungi, up to 20% wt may be endoglucanases [60-62]. A few endoglucanase may be act on crystalline cellulose as a substrate,

TABLE-1
LIST OF CELLULASES SECRETED BY VARIOUS WOOD-ROT FUNGI

Name of fungi	Family	Secreted cellulase	Ref.
Agaricus arvensis	Agaricaceae	Endoglucanase, exoglucanase, β-glucosidase	[77]
Agaricus bisporus	Agaricaceae	Endoglucanase	[96]
Armillaria gemina	Physalacriaceae	Endoglucanase, exoglucanase, β-glucosidase, xylanase	[69]
Auricularia polytricha	Auriculariaceae	Endoglucanase, exoglucanase, β-glucosidase, xylanase	[97]
Ceriporiopsis subvermispora	Phanerochaetaceae	β-glucosidase, endoglucanase, exoglucanase	[39,98,99]
Chrysosporium lignorum (*Sporotrichum poulverulentum*)	Fomitopsidaceae	Endoglucanase, exoglucanase, xylanase, β-glucosidase; cellobiose dehydrogenase	[36,100,101]
Coriolopsis rigida	Polyporaceae	Endoglucanase, xylanase	[55]
Dichomitus squalens	Polyporaceae	Endoglucanase, exoglucanase, β-glucosidase, xylanase, cellobiose dehydrogenase	[44,102]
Flammulina velutipes	Physalacriaceae	Endoglucanase, β-glucosidase, cellobiose dehydrogenase	[75,103]
Fomes fomentarius	Polyporaceae	Endoglucanase, exoglucanase, xylanase, β-glucosidase	[10,104]
Funalia trogii	Polyporaceae	Endoglucanase, xylanase	[76,105]
Ganoderma applanatum	Ganodermataceae	Endoglucanase, xylanase	[10,106]
Ganoderma capense	Ganodermataceae	Endoglucanase, xylanase, cellobiose dehydrogenase	[75]
Ganoderma gibbasum	Ganodermataceae	Endoglucanase, xylanase, cellobiose dehydrogenase	[75]
Ganoderma lucidum	Ganodermataceae	Endoglucanase, exoglucanase, xylanase	[107]
Hericium erinaceus	Hericiaceae	Endoglucanase, xylanase, cellobiose dehydrogenase	[75]
Heterobasidion annosum	Bondarzewiaceae	Endoglucanase, exoglucanase, xylanase, cellobiose dehydrogenase	[84,108]
Hypholoma fasciculare	Hypholoma	Endoglucanase, exoglucanase, xylanase, β-glucosidase	[104]
Irpex lacteus	Steccherinaceae	Endoglucanase, xylanase, β-glucosidase, exoglucanase	[66,67,109]
Lentinus edodes	Pleurotaceae	Endoglucanase, xylanase, β-glucosidase, exoglucanase	[76,68,110]
Lentinus tigrinus	Pleurotaceae	Endoglucanase, xylanase, β-glucosidase	[79]
Merulius tremellosus	Meruliaceae	Endoglucanase, exoglucanase, xylanase	[108]
Peniophora sp.	Peniophoraceae	Endoglucanase, xylanase	[55]
Phanerochaete chrysosporium	Pleurotaceae	Endoglucanase, exoglucanase, β-glucosidase, xylanase, cellobiose dehydrogenase	[68,81,101,105,110,111]
Phlebia tremellosa	Meruliaceae	Endoglucanase, exoglucanase, xylanase, β-glucosidase,	[38]
Picnoporus cinnabarinus	Polyporaceae	Cellobiose dehydrogenase	[86,112]
Pycnoporus coccineus	Polyporaceae	Endoglucanase, exoglucanase, xylanase, β-glucosidase,	[38]
Pleurotus dryinus	Pleurotaceae	Endoglucanase, exoglucanase, xylanase	[76]
Pleurotus ostreatus	Pleurotaceae	Endoglucanase, exoglucanase, xylanase, β-glucosidase,	[64,68,104,113]
Pleurotus tuberregium	Pleurotaceae	Endoglucanase, exoglucanase, xylanase	[76]
Rhodocollybia butyracea	Rhodocollybia	Endoglucanase, exoglucanase, xylanase, β-glucosidase	[104]
Poria medulla-panis	Polyporaceae	Endoglucanase, exoglucanase, xylanase, β-glucosidase	[38]
Porodaedalea pini	Hymenochaetaceae	Endoglucanase, exoglucanase, β-glucosidase, xylanase, cellobiose dehydrogenase	[70,71]
Schizophyllum commune	Schizophyllaceae	Endoglucanase, cellobiose dehydrogenase, β-glucosidase	[75,108,114]
Sporotricum thermophile	Fomitopsidaceae	Endoglucanase, exoglucanase, β-glucosidase,	[63,115]
Stereum hirsutum	Stereaceae	Endoglucanase, exoglucanase, xylanase	[108]
Trametes gibbosa	Polyporaceae	Endoglucanase, xylanase	[10]
Trametes hirsuta	Polyporaceae	Endoglucanase, exoglucanase, β-glucosidase	[65,89]
Trametes ochracea	Polyporaceae	Endoglucanase, xylanase	[10]
Trametes pubescens	Polyporaceae	Endoglucanase, xylanase	[10,88]
Trametes versicolor	Polyporaceae	Endoglucanase, xylanase, β-glucosidase, cellobiose dehydrogenase	[10,38,85,108,116]
Trametes villosa	Polyporaceae	Endoglucanase, xylanase	[55,88]
Trametes biforme	Polyporaceae	Endoglucanase, xylanase	[10]
Volvariella volvacea	Pluteaceae	Endoglucanase, exoglucanase, β-glucosidase	[117,118]
Xylaria polymorpha	Xylariaceae	Endoglucanase, xylanase β-glucosidase,	[119]

followed by numerous successive cuts in a single cellulose which is grooved *via* the active site [74]. In addition to the catalytic center, endoglucanase may have CBD or other domains as host for endoglucanase but is not a requirement for endoglucanase performing [2]. Several white-rot fungi secrete fungal endoglucanase, such as *Pleuratus ostreatus*, *Auricularia polytrica*, *Ganoderma* sp., *Funalia trogii*, *Lentinus edodes*, *P. drynus*, *P.*

tuberregium, *Coriolopsis rigida*, *Trametes* sp., *T. hirsuta*, *Agaricus arvensis*, *Phanerochaete chrysosporium*, *Irpex lacteus*, *Armillaria gemina* and *Porodaedalea pini* [55,64,65,67-71, 75-77].

β-Glucosidases (E.C 3.2.1.21) are enzymes that hydrolyze the products of exoglucanase action, cellobiose or glucooligo-saccharides and produce glucose molecules [33]. β-Glucosidases

cleavage the *O*-glycosyl linkage of terminal, non-reducing β-D-glucosyl residues, such as the bond in cellobiose to liberate β-D-glucose. According to substrate specificity, the enzymes perform on soluble substrates and can be categorized into cellobiases (specificity against cellobiose) or aryl-β-glucosidases (specificity against *p*-nitrophenyl-β-D-glucopyranoside), although most of β-glucosidases have specificity for both substrates [78]. β-Glucosidases have catalytic cores belonging to the GH1, GH3 and GH9 families, with GH1 and GH3 β-glucosidases being archetypical [2,78]. Unlike the cellulases mention above, β-glucosidases have no CBD as non-catalytic domain [2]. Although several cellulolytic fungi produce β-glucosidases only in a small level (about 1% of total secreted proteins), the enzymes play an important role in the efficiency of cellulose degradation by cellulase [60-62]. The degradation of cellobiose by β-glucosidases can remove the inhibitor (cellobiose) of exoglucanase and endoglucanase in cellulose conversion for industrial applications. β-Glucosidases have been characterized from many white-rot fungi, such as *Sporotricum thermophile*, *Pleurotus ostreatus*, *Auricularia polytricha*, *Ganoderma* sp., *Lentinula tigrinus*, *Agaricus arvensis*, *Trametes hirsuta*, *Irpex lacteus*, *Phanerochaete chrysosporium*, *Armillaria gemina*, *L. edodes* and *Porodaedalea pini* [63-71,75,77,79].

Cellobiose dehydrogenase (CDH, E.C. 1.1.3.25/E.C.1.1.99.18) is an extracellular oxidative enzyme participating in cellulose degradation. CDH generates hydroxyl radical that is able to degrade cellobiose, mannobiose, carboxymethyl cellulose and soluble xylan [80,81], although the biological function is still not understood. CDH also acts as an electron acceptor that diminishes phenoxy radical, cytochrome c, complexed Fe^{3+}, manganese and molecular oxygen, leading to the hydrogen peroxide production [82,83]. In addition, CDH also contributes to lignin degradation process [80,81].

The function of CDH in degradation process of lignocellulose was considered from a Fenton reaction concept [82], until a new paradigm of oxidative cleavage of cellulase was proposed after cellulose-active GH61 family has discovered, namely, lytic polysaccharide monooxygenase (LPMO) [8]. CDH is needed for improvement of cellulose degradation because the heme domain of this enzyme can stimulate LPMO enzyme activity. This enzyme has been identified from many white-rot fungi, such as *Heterobasidion annosum*, *Trametes versicolor*, *Auricularia polytrica*, *Pycnoporus cinnabarinus*, *Ganoderma* sp., *Phanerochaete chrysosporium*, *Grifola frondosa*, *T. hirsuta*, *Phlebia lidnteri*, *T. pubescens*, *T. villosa* and *Porodaedalea pini* [70,71,75,82,84-91].

Lytic polysaccharide monooxygenase (LPMO) is a new family of carbohydrate degrading enzymes that exposed a totally novel mechanism for breaking down glycosidic bonds in cellulose [57]. These enzyme has been discovered in year 2010 and the hypothesis was verified on its mechanism to disorder crystalline structure of cellulose, reversing the traditional degrading cellulose concept using oxidation mechanism [92] (Fig. 2). LPMOs can be synergistic with the other cellulases. Interactions of LPMOs and CDH naturally significantly increase catalytic activity on cellulose degradation [93,94]. CDH is believed to work as a reducing agent for LPMOs. CDH consists of two domains: (i) aflavin adenine dinucleotide (FAD) domain
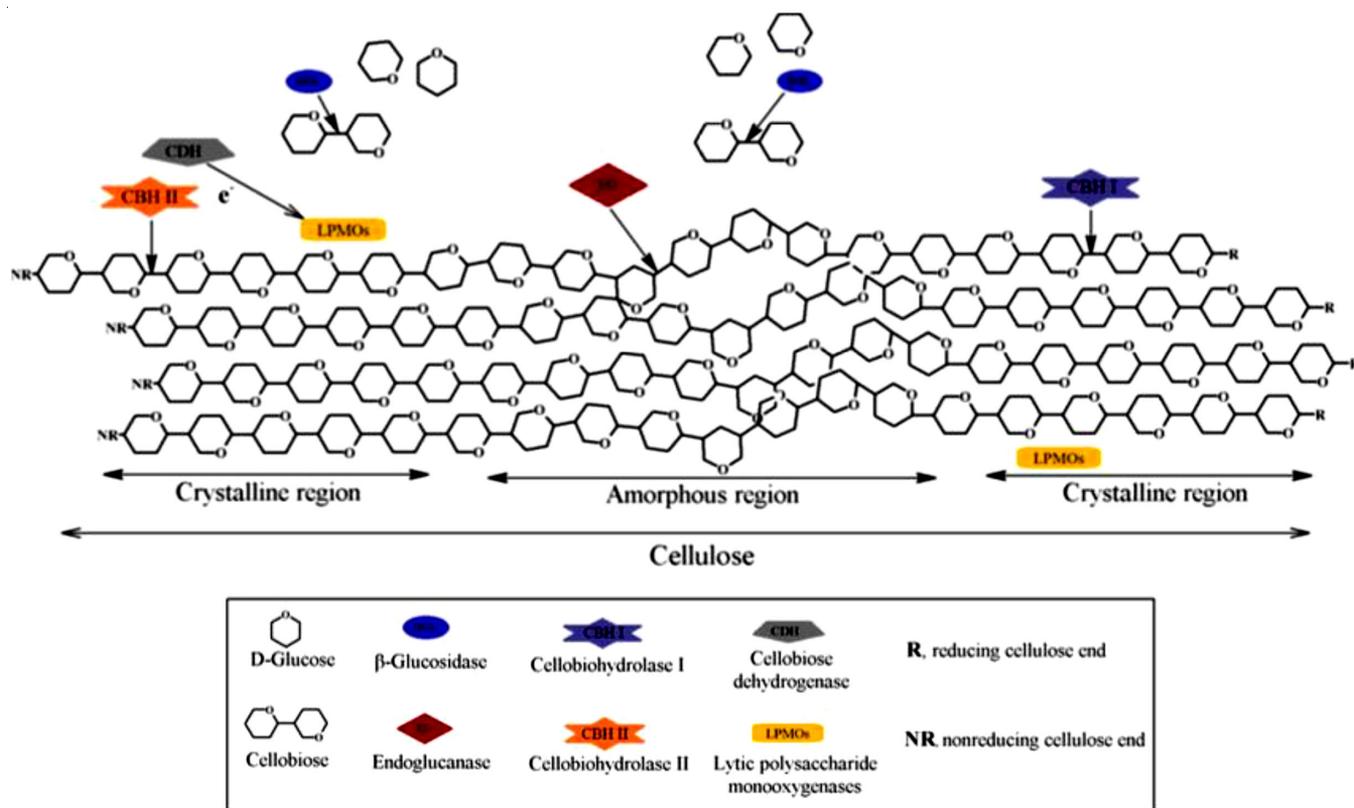

Fig. 2. Hypothetical mechanism of enzymatic degradation of cellulose by cellobiohydrolase, endoglucanase, β-glucosidase, cellobiose dehydrogenase and lytic polysaccharide monooxygenases

and (ii) a heme domain. The FAD domain is responsible for oxidation of cellobiose and the heme domain for transfering the electron from FAD domain to another electron acceptor including LPMOs [57]. Presently, many white-rot fungi have been reported to produce LPMOs for enhancing cellulose depolymerization by opening the crystalline cellulose oxidatively, indicating a vital function of LPMOs together with conventional cellulases [95]. Fungal LPMOs have been reported from many white-rot fungi, such as *Dichomitus squalens, Schizophyllum commune, Phanerochaete chrysosporium, Heterobasidion irregular, Plicaturopsis crispa, Omphalotus olearius, Hypholoma sublateritium, Fomitiporia mediterranea, Stereum hirsutum, Trametes versicolor, Pleurotus ostreatus, Armillaria mellea, Gymnopus luxurians, Auricularia subglabra, Galerina marginata* [43-45].

Conclusion

Lignocellulose degradation by white-rot fungi should not be viewed as only a negative process. It can also have an advantageous effect on carbon cycling processes in natural environment. It can be used in biotechnological applications, such as lignocellulosic biorefineries and lignocellulolytic enzyme production. Lignocellulose degradation by enzymatic processes, which is observed in nature, has been applied for industries, such as biopulping processes in pulp and paper industries or bioethanol production in biofuel industries. Presently, utilization both of lignocellulose materials and fungal enzymes has also enlarged to respond the fossil energy crises and the global warming issues. Bioethanol and chemicals derived from lignocellulose have received extensive interest to reduce dependence on petroleum based products. In the converting process of cellulose into bioethanol and valuable chemicals, hydrolysis of cellulose and hemicellulose into sugars is a crucial step. Enzymatic hydrolysis is considered as an environmentally friendly methods with high specificity and sensitivity, low energy and chemical consumption, fewer byproduct and time efficiency. However, to date, cellulases still being the most expensive part of hydrolysis cellulose processing, it would be of enormous interest to produce glycoside hydrolases enzyme from white-rot fungi for bioethanol production. In conclusion, based on these review, it is proposed that white-rot fungi could be used as a novel alternative sources of glycoside hydrolases enzymes, to solve the bottleneck of cellulosic bioethanol production.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interests regarding the publication of this article.

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