

Biodegradation of lignocellulosic residues by wood-rotting fungi

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Abstract: *Biodegradation of lignocellulosic residues by wood-rotting fungi.* Lignocellulosic biomass, consisting of cellulose, hemicellulose and lignin, can be utilized as a substrate in low cost energy recruitment processes e.g. biofuels production. Before application, lignocellulosic residues requires initial treatment based on physical, chemical or biological methods. Biological pretreatment takes of the advantage of the activity of microorganisms, especially bacteria and fungi. Those microorganisms produce cellulolytic and lignin-degrading enzymes which can efficiently degrade lignocellulosic materials. Fungi are able to degrade lignocellulose using two types of extracellular enzymatic systems; the hydrolytic system producing hydrolases that are responsible for polysaccharide degradation and oxidative ligninolytic system, which degrades lignin. The use of wood-rotting fungi for large-scale application in alternative energy production might be attractive given their lignocellulose hydrolysis enzymes.

Keywords: lignocellulose bioconversion, lignocellulosic residues, white-rot fungi

INTRODUCTION

In recent years an increased interest in environmentally friendly recruitment of energy has been observed. Since the industrial revolution our major energy sources: crude oil and coal have been used in great part, causing the excessive release of carbon into the atmosphere. Over the past 250 years atmospheric carbon dioxide level has increased from 280 to 410 ppm and continues to increase (Galbe and Zacchi, 2002; Business Insider, 2018). The increased atmospheric CO₂ level lead to global warming and climate changes, air pollution (Hill et al., 2006; Alonso et al, 2008). On the other hand global crude oil production is predicted to decline five times below its level from 2006 by 2050. Based on World Energy Council (WEC) calculation, the world-wide primary energy consumption is approximately 12 billion tons coal equivalent per year. According to calculation of United Nation the size of the global population will stand between 8.4 and 8.7 billion in 2030, between 9.4 and 10.2 billion in 2050, and between 9.6 and 13.2 billion in 2100. Increase of world's population to about 10 billion people in turn lead to increase energy demands to at least 24 billion tonnes coal equivalent per year depending on economic, social and political developments (United Nation, 2007, 2017; Schiffer, 2008).

Rising energy consumption, depletion of fossil fuels and growing concerns about environmental hazard lead to development of alternative energy technology. World-wide investigations intend to obtain energy from biodegradable materials with simultaneous reduction of energy requirement of these processes (Schneider, 1989). One of the most promising sources of industrial raw material from renewable source is lignocellulosic biomass. Lignocellulosic biomass comprises agricultural and industrial residues, which are sources of cellulose, hemicellulose and lignin (the lignocellulosic fractions). Lignocellulose represents the major component of biomass, since plants can contain high amounts of cellulose (40% to 50% w/w), lignin (18% to 35% w/w), and hemicellulose (10% to 35% w/w) (Hon and Shiraishi, 2001). Each of these types of lignocellulosic fractions has its own particular structural characteristics and chemistry, which can be exploited in chemical analyses (Vaz, 2014a). The high value of lignocellulose as a substrate in the process of obtaining bioenergy is associated with its widespread occurrence among plants, low price obtaining energy, at the expense of obtaining a substrate, low toxicity and the possibility of using waste raw materials (Weng et al., 2008). Nowadays, the estimated worldwide

production of renewable biomass for use in biofuels, fibers and agriculture is currently $210,7 \times 10^6$ tons per year (FAO, 2013). An exact value is difficult to obtain because there is a large variation in production among countries. Biofuel industry can be a good example of an opportunity to develop renewable chemicals from lignocellulosic residues, generating additional profits for the agro-industry. For example, from the production of ethanol from sugarcane and biodiesel from soya we can generate a large diversity of bio-products, such as bioelectricity, bioethanol, biogas, biofertilizer, organic acids, sugars (C5 and C6), materials (fibers, composites), fine chemicals and specialties (Vaz, 2014b).

Bioconversion of lignocellulosic residues to bioproducts is a multi-step process including: 1) pretreatment, 2) hydrolysis of polymers to produce readily metabolize molecules (in biofuels production 5- and 6-carbon chains sugars are converted to bioethanol through fermentation processes), 3) use of obtained molecules to support growth of microorganisms and/or production of chemical products, 5) separation and purification of bioproducts (Smith et al., 1987; Miettinen-Orinonen and Suominen, 2002; Sung and Cheng, 2005). Chemical and physical pretreatment processes partially delignify lignocellulose to allow access to plant polysaccharides (Chen F, Dixon RA, 2007). Lignin, due to its structure is characterized by high resistance to decomposition, and thus constitute a physical and chemical barrier to the degradation of cellulose. Application of chemical or physical pretreatments is expensive, slow and can result in toxic waste streams (Rubin, 2008). Other method for delignification of lignocellulosic residues is biological pretreatment. It uses microorganisms and has advantage over non-biological processes of producing potentially useful by-products and minimal waste (Zimbaridi et al., 1999).

Many microorganisms are capable of degrading and utilizing cellulose and hemicellulose as carbon and energy source. However, only small group of filamentous fungi develop an enzymatic system capable of breaking down lignin. According to recent researches special applicability in biological pretreatments have highly selective lignin degrading white-rot fungi, which possess the unique ability of efficiently degrading lignin to CO_2 . Additionally, white-rot fungi are able to degrade the variety of persistent environmental pollutants, such as chlorinated aromatic compounds, heterocyclic aromatic hydrocarbons, various dyes and synthetic high polymers (Bennet et al., 2002). In this work, the current knowledge about lignocellulosic biomass degradation by wood-rotting fungi has been reviewed.

GENERATION OF LIGNOCELLULOSIC RESIDUES

Lignin-cellulose mass in plants occurs mainly in leaves, stems and shoots. The main sources of lignocellulose in the biofuels production process are energy plants such as: corn, rice, sorghum rape, grass. Large amounts of lignocellulose are produced by various types of industries in addition to municipal and animal wastes (Greene, 2004). Lignocellulosic residues from forestry (e.g. thinnings, sawdust and mill wastes), wood (e.g. poplar trees, pine waste), pulp and paper, agriculture (e.g. corn stover, wheat straw) are abundant in nature and have a promising potential for bioconversion. Table 2 represent the world-wide generation of some lignocellulosic residues.

COMPOSITION OF LIGNOCELLULOSIC RESIDUES

The major component of lignocellulose residues is cellulose, followed by hemicellulose and lignin. In addition, small amounts of other materials such as proteins, pectins, extractives and ash can be found in lignocellulosic residues, in different degrees based on the source (Sanchez, 2009). The composition and proportion of these compounds vary between plants (Stewart et al., 1997; McKendry, 2002; Malherbe and Cloete, 2002; John et al., 2006; Prasad et al., 2007). Hardwoods for example have greater amounts of cellulose, whereas leaves and grasses have more hemicellulose (Table 2). Additionally, the ratios

between various constituents within a single plant vary with stage of growth, age and environment conditions.

Table 1. Examples of lignocellulosic residues produced by different industries

Lignocellulosic wastes	Annual production	References
World Agricultural Wastes	Ton ×10 ⁶ /year	
Wheat straw	354,34	Saini et al., 2015
Rice straw	731,3	
Corn straw	128,02	
Sugarcane bagasse	180,73	
Barley straw	58,45	Kim, 2004
Municipal Solid Waste	Kg/capita ¹	
Poland	249	GIOS, 2014
Denmark	780	
Estonia	270	

¹The amount of municipal waste generated per capita in 2012

Table 2. Cellulose, hemicellulose and lignin contents in some lignocellulosic materials

Lignocellulosic residues	Cellulose (%)	Hemicellulose (%)	Lignin (%)	References
Corn cobs	45	35	15	Mc Kendry, 2002; Prasad et al., 2007
Rice straw	32,1	24	18	Mc Kendry, 2002; Howard et al., 2003; Prasad et al., 2007
Barley straw	31-34	24-29	14-15	Rowell, 1992
Wheat Straw	29-35	26-32	16-21	Rowell, 1992; Mc Kendry, 2002; Prasad et al., 2007
Rye straw	33-35	27-30	16-19	Rowell, 1992; Stewart et al., 1997; Hon, 2000
Hardwood stems	40-55	24-40	18-25	Howard et al., 2003; Malherbe and Cloete 2002
Softwood stems	45-50	25-35	25-35	Howard et al., 2003; Malherbe and Cloete 2002
Leaves	15-20	80-85	0	Howard et al., 2003
Grasses (average values for grasses)	25-40	25-50	10-30	Howard et al., 2003; Malherbe and Cloete 2002
Solid cattle manure	1,6-1,4	1,4-3,3	2,7-5,7	Howard et al., 2003
Waste paper from chemical pulps	60-70	10-20	5-10	Howard et al., 2003
Primary wastewater solids	8-15	NA	24-29	Howard et al., 2003
Banana wastes	13,2	14,8	14	John et al., 2006

NA = Not available

Cellulose is the main constituent of plant cell wall but it is also present in bacteria, fungi and algae. It has structural role giving rigidity to the cells. When existing as unbranched, homopolymer, cellulose is a polymer of beta-D-glucopyranose moieties linked via beta-(1,4)-glycosidic bonds with well documented polymorphs. The degree of polymerization of cellulose chains in nature ranges from 10 000 glucopyranose units in wood to 15 000 in native cotton (Bajpai, 2016). In contrast to other glucan polymers in which repeating unit is glucose cellulose chain consist of disaccharide cellobiose (Desvaux 2005). The cellulose chains (about 20 to 300) are grouped together and coupled by hydrogen bonds, hydrophobic interactions and van der Waals forces to form microfibrils. The last are bundled together to form cellulose fibers. In lignocellulose biomass cellulose appear in two forms: crystalline and amorphous. Crystalline cellulose contains the major proportion of cellulose, whereas a small percentage of unorganized cellulose chains form amorphous cellulose.

Hemicellulose is the second most abundant polymer present in lignocellulose biomass (about 20-50%). The backbone of hemicelluloses is either a homopolymer or a heteropolymer

with short branches linked by beta-(1,4)-glycosidic bonds and occasionally beta-(1,3)-glycosidic bonds. Hemicellulose branches are formed by short lateral chains consisting of various types of monosaccharides including pentoses (arabinose, rhamnose and xylose), hexoses (glucose, galactose and mannose) and uronic acids. Additionally hemicelluloses can have some degree of acetylation e.g. in heteroxylan. Hemicelluloses are found to differ in composition depend on source of lignocellulose materials (Saha, 2003). In agricultural biomass like grasses and straw, hemicelluloses are composed mainly of xylan while softwood hemicelluloses contain mainly glucomannan (Bajpai, 2016).

The third most abundant polymer of lignocellulose biomass is lignin. It is a large chemically complex molecular structure composed of non-phenolic and phenolic structures (80-90%) (Weng et al., 2008). Phenolic monomers (coniferyl alcohol, *p*-coumaryl alcohol and sinapyl alcohol) are cross-linked by alkyl-aryl, alkyl-alkyl and aryl-aryl ether bonds. Presence of lignin in plants cell wall confers a rigid, impermeable resistance to microbial attack. Content of lignin can vary from one plant species to another. Generally herbaceous plants such as grasses have the lowest contents of lignin, whereas softwood have the highest lignin contents (Table 2) (Hendricks and Zeeman, 2009). Lignin acts as a kind of glue that binds component of lignocellulose together, thus making it insoluble in water.

BIODEGRADATION OF LIGNOCELLULOSIC RESIDUES BY WOOD-ROTTING FUNGI

The use of lignocellulose biomass is complicated due to the composition (the presence of hemicellulose and lignin) and due to the variety of structure, size and organization of cells and plant tissues. In addition to the limitations associated with the occurrence of various structures of lignocellulose residues, an additional problem may be the diffusion and transport of cellulolytic and lignolytic enzymes to their place of action. Hemicelluloses and lignin cover the cellulose microfibrils making difficult action of cellulolytic enzymes. Lignin has been identified as a major deterrent to enzymatic and microbial hydrolysis of lignocellulosic residues because of its close association with cellulose microfibrils (Avgerinos and Wang, 1983). Other researchers showed that biomass digestibility is increased with increasing lignin removal (Chang and Holtzaple, 2000). Apart from being a physical barrier lignin cause other difficulties with cellulose hydrolysis by enzymes. These detrimental effect of lignin include: nonspecific adsorption of hydrolytic enzymes to lignin; interference with, and non-productive binding of cellulolytic enzymes to lignin-carbohydrates complexes and toxicity of lignin derivatives to microorganisms. Moreover there has been proposed that at least 50% hemicellulose should be removed from lignocellulose to significantly enhance its digestibility (Bajpai, 2016).

Fungi are predominant group of organisms that are responsible for lignocellulose degradation. They are able to effectively degrade lignocellulose probably due to mycelia growth habit that facilitates transport enzymes and deficient nutrients such as iron and nitrogen, to a distance into the nutrient-poor lignocellulosic substrate which is used as a carbon source. Degradation process takes place exocellularly, either by association of substrate with the outer cell envelope layer or extracellularly, because of insolubility of cellulose, hemicellulose and lignin. Fungi degrade lignocellulose using two types of extracellular enzymatic systems; the hydrolytic system producing hydrolases that are responsible for polysaccharide degradation and oxidative and extracellular ligninolytic system, which degrades lignin and opens phenyl rings.

The use of cellulose is common throughout the entire fungus kingdom from primitive *Chytridiomycetes* to advanced *Basidiomycetes*. The white-rot fungi are the most effective group hydrolyzing the lignocellulosic material, degrading both cellulose and lignin. This degradative ability of white-rot fungi is due to the strong oxidative activity and low substrate

specificity of their ligninolytic enzymes. Other lignocellulose degrading fungi are brown-rot fungi that rapidly depolymerize cellulosic materials while only modifying lignin. Other group of fungi able to degrade lignocellulose are soft-rot fungi. The degradation mechanisms of lignocellulose by soft-rot fungi need to be elusive. It is known that some soft-rot fungi can degrade lignin, because they erode the secondary cell wall and decrease the content of acid-insoluble material (Klason lignin) in angiosperm wood. Soft rot fungi typically attack higher moisture and lower lignin content materials (Shary et al., 2007).

White-rot fungi colonize herbaceous plants and trees taking the advantage of their ability for the enzymatic cleavage of lignin, cellulose and hemicellulose, basic components cell wall of plants (Abdul et al., 1997; Krajewski and Witomski, 2003). Decomposition of wood compounds by white-rot fungi begins with hydrolysis of hemicellulose and cellulose in the so-called primary metabolism. Released monosaccharides are needed to start the process of delignification (Krajewski and Witomski, 2003). Depletion of basic biogenic elements such as nitrogen, sulfur, phosphorus, potassium, and easily accessible carbon sources and energy in the fungus environment induces secondary metabolism in which lignin undergoes degradation (Podgornik et al., 2001, Krajewski and Witomski, 2003). Biosynthesis of lignolytic enzymes by most white-rot fungi is stimulated by a high degree of polymerization and crystallinity of cellulose with simultaneous low content of simple sugars (1%) (Krajewski and Witomski, 2003). Carbohydrates such as: glucose, fructose or xylose are essential in the process of delignification. As a result of their degradation by oxidases H_2O_2 is formed, which is necessary for the activity of lignolytic enzymes (Basu et al., 2002; Khalil, 2002, Krajewski and Witomski, 2003).

Basidiomycetes are the most efficient degraders among white-rot fungi (Bennet et al., 2002; Rabinovich et al., 2004; ten Have and Teunissen, 2001). White-rot *Basidiomycetes* such as *Phanerochaete chrysosporium* and *Trametes versicolor* (Morendo et al., 2003; Wang et al., 2008) have been found to be most efficient lignin-degrading microorganisms studied. Basidiomycetes are considered to be a very interesting group of fungi given their exceptional adjustment abilities to accommodate themselves to the detrimental conditions of the environment where they constantly act as natural lignocellulose destroyers. Basidiomycetes possess the two types of extracellular enzymatic systems necessary to degrade the lignocellulose biomass: a hydrolytic system, consisting mainly of xylanases and cellulases and oxidative ligninolytic system comprises mainly laccases, ligninases, and peroxidases. The most widely studied white-rot fungi from basidiomycota is *Phanerochaete chrysosporium*, which strains simultaneously degrade cellulose, hemicelluloses and lignin. However there are evidences that many species from this genera show different morphological patterns of decay they cause. *Ceriporiopsis subvermispora* tend to remove lignin in advance of cellulose and hemicelluloses.

White-rot fungi produce various enzymes with different specificities, which working together are able to completely degrade lignocellulose residues. Cellulose is hydrolyzed by group of enzymes named cellulases. Cellulase hydrolyze the beta-1,4-glycosidic linkages bonds and can be divided into three major enzyme activity classes: endoglucanases (EC 3.3.1.4), cellobiohydrolase (EC 3.2.1.91) and β -glucosidase (EC 3.2.1.21) (Goyal et al., 1991; Rabinovich et al., 2002). Endoglucanases are supposed to initiate attack randomly at multiple internal site in the amorphous regions of the cellulose fibre which opens-up sites for subsequent attack by the cellobiohydrolases (Lynd et al., 1991). It has been shown that amorphous conformation is more susceptible to enzymatic degradation (Perez et al., 2002). Cellobiohydrolase is principal constituent of the fungal cellulase system and stand for 40-70% of total cellulase proteins. This enzyme is able to hydrolyze cellulose in a crystalline form. (Rowell, 1992). Cellobiohydrolases often called exoglucanases remove monomers and dimers from the end of the glucan chain. Then β -glucosidase hydrolyzes dimers to glucose.

Hemicellulose is degraded to monomeric sugars and acetic acid during cooperative action of a variety of hydrolytic enzymes collectively named hemicellulases. According to type of substrate hemicellulases are classified into two groups of enzymes: endo-1,4- β -xylanase (EC 3.2.1.8), which generates oligosaccharides from the cleavage of xylan, and xylan 1,4- β -xylosidase (EC 3.2.1.37) producing xylose from oligosaccharides (Jeffries, 1994). Moreover, hemicellulose degradation requires accessory enzymes such as xylan esterases, ferulic and p-coumaric esterases, α -1-arabinofuranosidases and α -4-O-methyl glucuronosidases, acting synergistically to efficiently hydrolyze wood xylans and mannans.

Biodegradation of lignin by white-rot fungi is an oxidative process with phenol oxidases as the key enzymes (Leonowicz et al., 1999; Rabinovich et al., 2004). In this group of enzymes lignin peroxidases (EC 1.11.1.14) (LiP), manganese peroxidases (EC 1.11.1.13) (MnP) and phenol laccases (EC 1.10.3.2) from white-rot fungi (e.g. *Phanerochaete chrysosporium*, *Trametes versicolor*, *Pleurotus ostreatus*, *Botrytis cinerea* and *Stropharia coronilla*) have been studied (Howard et al., 2003; Martinez et al., 2004). Lignin peroxidase and manganese peroxidase oxidize the substrate by two consecutive one-electron oxidation steps with intermediate cation radical formation. LiP degrades non-phenolic lignin units (up to 90% of the polymer), whereas MnP generates Mn^{3+} , which acts as a diffusible oxidizer on phenolic or non-phenolic lignin units via lipid peroxidation reactions (Jensen et al., 1996; Cullen and Kersten, 2004). Laccases are blue copper oxidases that catalyze the one-electron oxidation of phenolic and other electron-rich substrates (Hammel, 1997). Other fungal enzymes involved in lignin degradation are alcohol oxidase (AAO) described in *Pleurotus eryngii* (Guillen et al., 1992) glyoxal oxidase found in *Phanerochaete chrysosporium* (Kersten and Cullen, 2007).

CONCLUSIONS

Lignocellulose residues represent the most abundant renewable organic resource on Earth. Only a small amount of cellulose, hemicellulose and lignin produced as by-products in industries such as forestry and wood-processing is used, the rest being considered waste. Accumulation of lignocellulosic materials in large quantities presents a disposal problem which results in deterioration of the environment and also in loss of potentially valuable materials which can be used in biofuels production, paper manufacture, composting, human and animal feed. Taking advantage of broad and diverse groups of microorganisms with the ability to decompose lignocellulose in processes such as alcohol and methane fermentation can be an important means of obtaining biofuels and in result the energy from biochemical processes. The ability of white-rot fungi to break down lignin, the most recalcitrant component of lignocellulose biomass makes them potentially useful in the exploration of the lignocellulosic biomass for the production of bioelectricity, biofuels and other value-added commodity chemicals.

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Streszczenie: *Biodegradacja reszt lignocelulozowych przez grzyby białej zgnilizny.* Biomasa lignocelulozowa jest trudno rozkładalnym odpadem pochodzącym z różnych gałęzi przemysłu m.in. drzewnego, papierniczego oraz rolno-spożywczego. Rozwój technologii wykorzystywania biomasy lignocelulozowej skupia się głównie na biorafinacji, której produktami są: biopaliwa, biomateriały i biochemikalia. Biopaliwa pozyskuje się na drodze degradacji biomasy lignocelulozowej wykorzystując różnorodne grupy mikroorganizmów mające zdolność do rozkładu lignocelulozy w procesach fermentacji alkoholowej, metanowej oraz procesach kompostowania. Wykorzystanie lignocelulozy jest jednak skomplikowane ze względu na obecność hemicelulozy i ligniny, które utrudniają dyfuzję i transport enzymów celulolitycznych do miejsca ich działania. Biologiczna obróbka wstępna wykorzystuje zdolność bakterii i grzybów do wytwarzania enzymów celulolitycznych oraz enzymów rozkładających ligninę, dzięki czemu mogą skutecznie degradować materiały lignocelulozowe. Grzyby białej zgnilizny, jako jedyne mikroorganizmy są zdolne do degradacji lignocelulozy przy użyciu dwóch typów zewnątrzkomórkowych układów enzymatycznych. Układ hydrolityczny wytwarzający hydrolazy, które są odpowiedzialne za degradację polisacharydów oraz oksydacyjny układ ligninolityczny, który rozkłada ligninę.

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