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Research review paper

Lignocellulosic residues: Biodegradation and bioconversion by fungi

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ABSTRACT

The ability of fungi to degrade lignocellulosic materials is due to their highly efficient enzymatic system. Fungi have two types of extracellular enzymatic systems; the hydrolytic system, which produces hydrolases that are responsible for polysaccharide degradation and a unique oxidative and extracellular ligninolytic system, which degrades lignin and opens phenyl rings. Lignocellulosic residues from wood, grass, agricultural, forestry wastes and municipal solid wastes are particularly abundant in nature and have a potential for bioconversion. Accumulation of lignocellulosic materials in large quantities in places where agricultural residues present a disposal problem results not only in deterioration of the environment but also in loss of potentially valuable material that can be used in paper manufacture, biomass fuel production, composting, human and animal feed among others. Several novel markets for lignocellulosic residues have been identified recently. The use of fungi in low cost bioremediation projects might be attractive given their lignocellulose hydrolysis enzyme machinery.

Contents

1. Introduction

Lignocellulose is the major component of biomass, comprising around half of the plant matter produced by photosynthesis (also called photomass) and representing the most abundant renewable organic resource in soil. It consists of three types of polymers, cellulose, hemicellulose and lignin that are strongly intermeshed and chemically bonded by non-covalent forces and by covalent cross-linkages (Pérez et al., 2002). Only a small amount of the cellulose, hemicellulose and lignin produced as by-products in agriculture or forestry is used, the rest being considered waste. Many microorganisms are capable of degrading and utilizing cellulose and hemicellulose as carbon and energy sources. However, a much smaller group of filamentous fungi has evolved with the ability to break down lignin, the most recalcitrant component of plant cell walls. These are known as white-rot fungi, which possess the unique ability of efficiently degrading lignin to CO_2. Other lignocellulose degrading fungi are brown-rot fungi that rapidly depolymerize cellulosic materials while only modifying lignin. Collectively, these wood and litter-degrading fungi play an important role in the carbon cycle. In addition to lignin, white-rot fungi are able to degrade a variety of persistent environmental pollutants, such as chlorinated aromatic

Abbreviations: LiP, Lignin peroxidases; MnP, manganese peroxidases; AAO, Aryl-alcohol oxidase; AAD, Aryl-alcohol dehydrogenases; QR, Quinone reductases.

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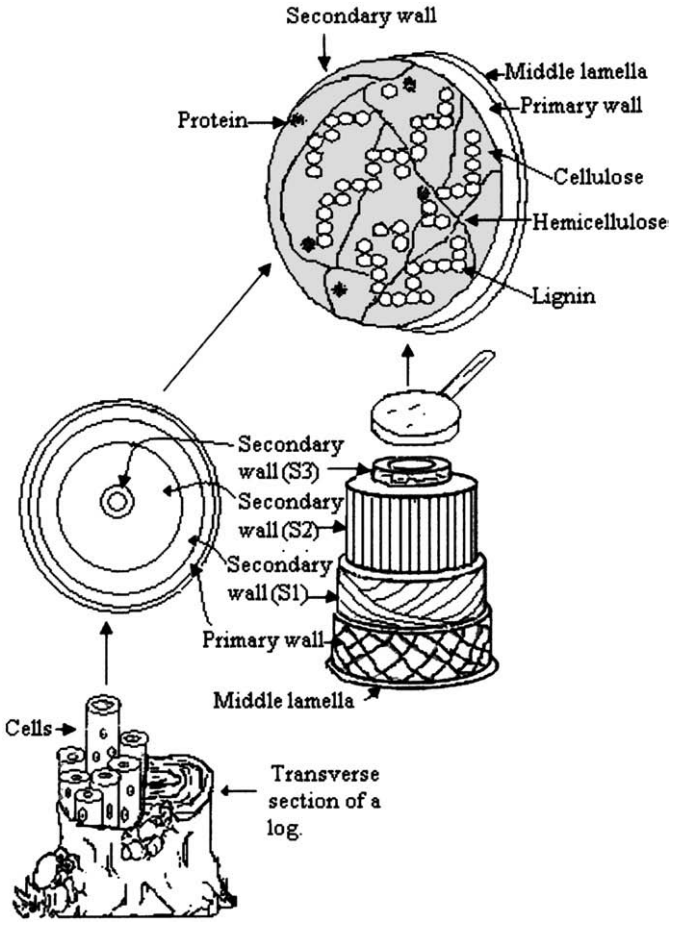

Fig. 1. Composition of lignocellulosic residues. Cellulose, hemicellulose and lignin.

compounds, heterocyclic aromatic hydrocarbons, various dyes and synthetic high polymers (Bennett et al., 2002). This degradative ability of white-rot fungi is due to the strong oxidative activity and low substrate specificity of their ligninolytic enzymes. Little is known about the degradation mechanisms of lignocellulose by soft rot fungi, in contrast to white and brown rot fungi. Nevertheless, it is clear 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). The genome sequences from different fungi such as; *Phanerochaete chrysosporium* strain RP8 (Martinez et al., 2004; http://genome.jgi.psf.org/whiterot1), *Coprinopsis cinerea* (Walti et al., 2006), *Postia placenta* (Stajich, 2007), *Pleurotus ostreatus* (Irie et al., 2000), *Agaricus bisporus* (Challen et al., 2007), *Schizophyllum commune* (Horton and Raper, 1991) and *Serpula lacrymans* (Bruce, 2007) have been revealed and its genomic information may greatly facilitate our understanding of the lignocellulose biodegradation process. World-wide lignocellulosic residue generation every year results in pollution of the environment and in loss of valuable materials that can be bioconverted to several added-value products (Howard et al., 2003). Lignin can be removed by chemical (Chahal, 1991; McMillan, 1994; Gong et al., 1999) or physical pre-treatment which then permits efficient bioconversion. Pre-treatment can also be carried out microbiologically. This has the advantages over non-biological procedures of producing potentially useful by-products and minimal waste (Zimbardi et al., 1999). This review will focus on the use of fungi in the biodegradation of lignocellulose, aspects of bioconversion and world-wide lignocellulosic residues.

2. Composition of lignocellulosic residues

The major component of lignocellulosic materials is cellulose, followed by hemicellulose and lignin (Fig. 1). Cellulose and hemicellulose are macromolecules constructed from different sugars; whereas lignin is an aromatic polymer synthesized from phenylpropanoid precursors. The composition and proportions of these compounds vary between plants (Prassad et al., 2007; McKendry, 2002; Malherbe and Cloete, 2002; John et al., 2006; Stewart et al., 1997; Reguant and Rinaudo, 2000; Pérez-Díaz et al., 2005) (Table 1).

Cellulose is a linear polymer that is composed of D-glucose subunits linked by β-1,4 glycosidic bonds forming the dimer cellobiose. These form long chains (or elemental fibrils) linked together by hydrogen bonds and van der Waals forces. Cellulose usually is present as a crystalline form and a small amount of non-organized cellulose chains forms amorphous cellulose. In the latter conformation, cellulose is more susceptible to enzymatic degradation (Pérez et al., 2002). Cellulose appears in nature to be associated with other plant compounds and this association may affect its biodegradation. Hemicellulose is a polysaccharide with a lower molecular weight than cellulose. It is formed from D-xylose, D-mannose, D-galactose, D-glucose, L-arabinose, 4-O-methyl-glucuronic, D-galacturonic and D-glucuronic acids. Sugars are linked together by β-1,4- and sometimes by β-1,3-glycosidic bonds. The main difference between cellulose and hemicellulose is that hemicellulose has branches with short lateral chains consisting of different sugars and cellulose consists of easily hydrolyzable oligomers. Lignin is linked to both hemicellulose and cellulose, forming a physical seal that is an impenetrable barrier in the plant cell wall. It is present in the cellular wall to give structural support, impermeability and resistance against microbial attack and oxidative stress. It is an amorphous heteropolymer, non-water soluble and optically inactive that is formed from phenylpropane units joined together by non-hydrolyzable linkages. This polymer is synthesized by the generation of free radicals, which are released in the peroxidase-mediated dehydrogenation of three phenyl propionic alcohols: coniferyl alcohol (guaiacyl propanol), coumaryl alcohol (*p*-hydroxyphenyl propanol), and sinapyl alcohol (syringyl propanol). This heterogeneous structure is linked by C–C and aryl-ether linkages, with aryl-glycerol β-aryl ether being the predominant structures.

3. Biodegradation of lignocellulosic residues

The organisms predominantly responsible for lignocellulose degradation are fungi, and the most rapid degraders in this group are basidiomycetes (ten Have and Teunissen, 2001; Bennett et al., 2002; Rabinovich et al., 2004). The ability to degrade lignocellulose efficiently is thought to be associated with a mycelial growth habit that allows the fungus to transport scarce nutrients such as nitrogen and iron, to a distance into the nutrient-poor lignocellulosic substrate that constitutes its carbon source (Hammel, 1997). The fungal degradation occurs exocellularly, either in association with the outer cell envelope layer or extracellularly, because of the insolubility of lignin, cellulose and hemicellulose. Fungi have two types of extracellular enzymatic systems: the hydrolytic system, which produces hydrolases that are responsible for polysaccharide degradation; and a unique oxidative and extracellular ligninolytic system, which degrades lignin and opens phenyl rings. Several microorganisms, mainly fungi, have been isolated and identified as lignocellulolytic organisms (Table 2). The most widely studied white-rot organism is *P. chrysosporium*, which is one of the holobasidiomycetes. *Trichoderma reesei* and its mutants are the most studied ascomycete fungi, and is used for the commercial production of hemicellulases and cellulases (Esterbauer et al., 1991; Nieves et al., 1998; Jørgensen et al., 2003). Not even white-rot fungi are known to be capable of using lignin as a sole carbon and energy source, and it is generally believed that lignin break down is

Table 1
Composition of some lignocellulosic materials

Lignocellulosic residues	Lignin (%)	Hemicellulose (%)	Cellulose (%)	Ash (%)	Reference
Hardwood stems	18–25	24–40	40–55	NA	Howard et al. (2003), Malherbe and Cloete (2002).
Softwood stems	25–35	25–35	45–50	NA	Howard et al. (2003), Malherbe and Cloete (2002).
Nut shells	30–40	25–30	25–30	NA	Howard et al. (2003).
Corn cobs	15	35	45	1.36	Howard et al. (2003), Prassad et al. (2007), McKendry (2002).
Paper	0–15	0	85–99	1.1–3.9	Howard et al. (2003).
Rice straw	18	24	32.1	NA	Howard et al. (2003), Prassad et al. (2007), McKendry (2002).
Sorted refuse	20	20	60	NA	Howard et al. (2003).
Leaves	0	80–85	15–20	NA	Howard et al. (2003).
Cotton seeds hairs	0	5–20	80–95	NA	Howard et al. (2003).
Newspaper	18–30	25–40	40–55	8.8–1.8	Howard et al. (2003).
Waste paper from chemical pulps	5–10	10–20	60–70	NA	Howard et al. (2003).
Primary wastewater solids	24–29	NA	8–15	NA	Howard et al. (2003).
Swine waste	NA	28	6	NA	Howard et al. (2003).
Solid cattle manure	2.7–5.7	1.4–3.3	1.6–4.7	NA	Howard et al. (2003).
Coastal Bermuda grass	6.4	35.7	25	NA	Howard et al. (2003).
Switch grass	12.0	31.4	45	NA	Howard et al. (2003).
S32 rye grass (early leaf)	2.7	15.8	21.3	NA	Howard et al. (2003).
S32 rye grass (seed setting)	7.3	25.7	26.7	NA	Howard et al. (2003).
Orchard grass (medium maturity)	4.7	40	32	NA	Howard et al. (2003).
Grasses (average values for grasses)	10–30	25–50	25–40	1.5	Howard et al. (2003), Malherbe and Cloete (2002).
Sugar cane bagasse	19–24	27–32	32–44	4.5–9	Rowell (1992).
Wheat straw	16–21	26–32	29–35	NA	Rowell (1992), Prassad et al. (2007), McKendry (2002).
Barley straw	14–15	24–29	31–34	5–7	Rowell (1992).
Oat straw	16–19	27–38	31–37	6–8	Rowell (1992).
Rye straw	16–19	27–30	33–35	2–5	Rowell (1992), Stewart et al. (1997), Reguant and Rinaudo (2000), Hon (2000).
Bamboo	21–31	15–26	26–43	1.7–5	Rowell (1992), Stewart et al. (1997), Reguant and Rinaudo (2000), Hon (2000).
Grass Esparto	17–19	27–32	33–38	6–8	Rowell (1992), Stewart et al. (1997), Reguant and Rinaudo (2000), Hon (2000).
Grass Sabai	22.0	23.9	NA	6.0	Rowell (1992), Stewart et al. (1997), Reguant and Rinaudo (2000), Hon (2000).
Grass Elephant	23.9	24	22	6	Rowell (1992), Stewart et al. (1997), Reguant and Rinaudo (2000), Hon (2000).
Bast fiber Seed flax	23	25	47	5	Rowell (1992), Stewart et al. (1997), Reguant and Rinaudo (2000), Hon (2000).
Bast fiber Kenaf	15–19	22–23	31–39	2–5	Rowell (1992), Stewart et al. (1997), Reguant and Rinaudo (2000), Hon (2000).
Bast fiber Jute	21–26	18–21	45–53	0.5–2	Rowell (1992), Stewart et al. (1997), Reguant and Rinaudo (2000), Hon (2000).
Leaf Fiber Abaca (Manila)	8.8	17.3	60.8	1.1	Rowell (1992), Stewart et al. (1997), Reguant and Rinaudo (2000), Hon (2000).
Leaf Fiber Sisal (agave)	7–9	21–24	43–56	0.6–1.1	Rowell (1992), Stewart et al. (1997), Reguant and Rinaudo (2000), Hon (2000).
Leaf Fiber Henequen	13.1	4–8	77.6	0.6–1	Rowell (1992), Stewart et al. (1997), Reguant and Rinaudo (2000), Hon (2000).
Coffee pulp	18.8	46.3	35	8.2	Pérez-Díaz et al. (2005).
Banana waste	14	14.8	13.2	11.4	John et al. (2006).
Yuca waste	NA	NA	NA	4.2	John et al. (2006).

NA = Not available.

necessary to gain access to cellulose and hemicellulose. Although white-rot basidiomycetes have been shown to efficiently mineralize lignin, species differ gross morphological patterns of decay they cause (Blanchette, 1991; Blanchette et al., 1997; Daniel, 1994). *P. chrysosporium* strains simultaneously degrade cellulose, hemicellulose and lignin, whereas others such as *Ceriporiopsis subvermispora* tend to remove lignin in advance of cellulose and hemicellulose. Brown rot mechanism has likely evolved independently multiple times from white rot decay fungi. Presumably, because lignin breakdown is energetically unfavourable, selection has favoured a mechanism which can specifically attack the cellulose and hemicellulose components.

3.1. Lignin biodegradation

Lignin biodegradation by white-rot fungi is an oxidative process and phenol oxidases are the key enzymes (Kuhad et al., 1997; Leonowicsz et al., 1999; Rabinovich et al., 2004)). Of these, lignin peroxidases (EC 1.11.1.14) (LiP), manganese peroxidases (EC 1.11.1.13) (MnP) and laccases (EC 1.10.3.2) from white-rot fungi (especially *Botrytis cinerea*, *P. chrysosporium*, *Stropharia coronilla*, *P. ostreatus* and *Trametes versicolor*) have been studied (Howard et al., 2003; Martinez et al., 2004) (Table 3). LiP and MnP oxidize the substrate by two consecutive one-electron oxidation steps with intermediate cation radical formation. LiP and MnP were discovered in the mid-1980s in *P.chrysosporium* and described as true lignases because of their high potential redox value (Gold et al., 2000; Martínez, 2002). 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). Laccase are blue copper oxidases that catalyze the one-electron oxidation of phenolics and other electron-rich substrates (Hammel, 1997). Recently, other enzymes involved in lignin degradation have been reported. These include aryl-alcohol oxidase (AAO) described in *Pleurotus eryngii* (Guillén et al., 1992) and other fungi, and *P. chrysosporium* glyoxal oxidase (Kersten and Cullen, 2007). Fungal aryl-alcohol dehydrogenases (AAD) and quinone reductases (QR) are also involved in lignin degradation (Guillén et al., 1997; Gutiérrez et al., 1994). As shown in Fig. 2, laccases or ligninolytic peroxidases (LiP and MnP) produced by white-rot fungi oxidize the lignin polymer, thereby generating aromatic radicals (a). These evolve in different non-enzymatic reactions, including C-4-ether breakdown (b), aromatic ring cleavage (c), Cα–Cβ breakdown (d), and demethoxylation (e). The aromatic aldehydes released from Cα–Cβ breakdown of lignin, or synthesized *de novo* by the fungus (f, g), are the substrates for H_2O_2 generation by AAO in cyclic redox reactions also involving AAD. Phenoxy radicals from C4-ether breakdown (b) can repolymerize on the lignin polymer (h) if they are not first reduced by oxidases to phenolic compounds (i). The phenolic compounds formed can be again reoxidized by laccases or peroxidases (j). Phenoxy radicals can also be subjected to Cα–Cβ breakdown (k), yielding *p*-quinones. Quinones from g and/or k contribute to oxygen activation in redox cycling reactions involving oxygen activation in redox cycling reactions with QR, laccases, and peroxidases (l, m). This results in reduction of the ferric iron present in wood (n), either by superoxide cation radical or directly by the semiquinone radicals, and its reoxidation with concomitant reduction of H_2O_2 to a hydroxyl free radical (OH×) (o). The latter is a very mobile and very strong oxidizer that can initiate the attack on lignin (p) in the initial stages of wood decay, when the small size of pores in the still-intact cell wall prevents the penetration of ligninolytic enzymes. Then, lignin degradation proceeds by oxidative attack of the enzymes described

Table 2
Enzymes produced by some lignocellulolytic fungi in several agricultural residues

Fungus	Group	Type of rot fungus	Substrates	Enzyme	Reference
Strobilurus ohshimae	Basidiomycota	White	Sugi Word	LiP, MnP	Homma et al. (2007).
Phanerochaete chrysosporium	Basidiomycota	White	Grape seeds, barley bran and wood shavings	LiP, MnP	Rodríguez et al. (1997), Srinivasan et al. (1995), Kersten and Cullen (2007), Quintero et al. (2006).
Trametes versicolor	Basidiomycota	White	Wood shaving, carozo maize and compost of gardening wheat straw	Laccase	Moredo et al. (2003), Márquez et al. (2007), Dumonceaux et al. (2001), Villagran and Renan (1991), Cabuk et al. (2006), Tong et al. (2007).
			Grape seeds, barley bran and wood shavings	Laccase, xylanases, MnP, cellobiose dehydrogenase	
			Sugar cane bagasse	Laccase, MnP, glucose oxidase, glyoxal oxidase, quinone oxidoreductase, Cellobiose	
Pleurotus ostreatus	Basidiomycota	White	Bagasse of cane maize straw	Xylanases, cellulases, laccase, MnP.	Márquez et al. (2007), Okamoto et al. (2002).
P. ostreatus, P.pulmonarius	Basidiomycota	White	Coffee pulp, used nappy, grass residues, cleaned coffee (substrates analyzed separately and in mixture). Wheat straw, industrial cotton fiber.	Endoglucanase, cellobiohydrolase, laccase, MnP.	Marnyye et al. (2002), Delfin and Duran de bazúa (2003), Okamoto et al. (2002).
Aspergillus niger	Ascomycota	Brown	Sugar cane bagasse	Xylanases, cellulases	Park et al. (2002), Aguiar (2001), Hasan (2000), Keon and Waksman (1990).
Bjerkandera adusta	Basidiomycota	White	Shavings of wood, carozo maize, compost of gardening wheat straw	MnP, LiP	Quintero et al. (2006), Romero et al. (2007), Kimura et al. (1991).
Clonostachys rosea	Ascomycota	White	Clavel leaves, young plant leaves (from *Aster* genus), lamella from oats and maize plants	Endopolygalacturonases galactosidase endo-xylanase, cellulases, arabinofuranosidase, acetylesterase, xylosidase, galactosidase	Mikan and Castellanos (2004), Rezácová et al. (2006).
Fusarium oxysporum	Ascomycota	Brown	Young plant leaves (from *Aster* genus), lamella from oats and maize plants	Endopolygalacturonases galactosidase	Mikan and Castellanos (2004).
Fusarium merismoides	Ascomycota	Brown	Clavel leaves, young plant leaves (from *Aster* genus), lamella from oats and maize plants	Endo-xylanase, cellulases, arabinofuranosidase, acetylesterase, xylosidase	Fernández-Martín et al. (2007).
Streptomyces	Actinomycete (bacterium)	White	Clavel leaves, young plant leaves (from *Aster* genus), lamella from oats and maize plants.	Cellulases, xylanases, arabinofuranosidase xylosidase, acetylesterase	Mikan and Castellanos (2004), Benimelia et al. (2007).
Penicillium sp.	Ascomycota	White	Clavel leaves, young plant leaves (from *Aster* genus), lamella from oats and maize plants	Endo-xylanase, cellulases, arabinofuranosidase, acetylesterase, xylosidase	Mikan and Castellanos (2004).
Pycnoporus cinnabarinus	Basidiomycota	White	Softwood pulp	Laccase, LiP, MnP	Geng and Li (2002), Eggert et al. (1996a,b), Bermek et al. (1998), Alves et al. (2004).
Xylaria hypoxylon	Ascomycota	White		Laccase, endoglucanase, glucosidase, esterase, xylanase	Liers et al. (2006).
X. polymorpha			Wood		Xing-Na et al. (2005).
Fomitopsis palustris	Basidiomycota	Brown	Microcrystalline cellulose	Cellulases (exoglucanases, endoglucanases, β-glucosidase)	Yoon et al. (2007).

above. In the final steps, simple products from lignin degradation enter the fungal hyphae and are incorporated into intracellular catabolic routes (Martínez et al., 2005). Fungal feruloyl and *p*-coumaroyl esterases are capable of releasing feruloyl and *p*-coumaroyl units and play an important role in biodegradation of recalcitrant cell walls in grasses (Kuhad et al., 1997). These enzymes act synergistically with xylanases to disrupt the hemicellulose-lignin association, without mineralization of lignin *per se* (Borneman et al., 1990; Fillingham et al., 1999). Therefore, hemicellulose degradation is required before efficient lignin removal can commence. In *P. chrysosporium*, a co-metabolizable carbon source is essential for lignin degradation (Kirk et al., 1976), and it is produced in response to nitrogen starvation (Keyser et al., 1978). This indicates that the ligninolytic system is formed as part of secondary metabolism in this organism. Carbohydrate starvation likewise leads to a rapid but transient onset of ligninolytic activity (Jeffries, 1987, 1994). Elevated oxygen levels increase the rate of lignin biodegradation through the production of hydrogen peroxide as the extracellular oxidant and the subsequent induction of ligninolytic activity (Kirk and Farell, 1987; Kirk and Cullen, 1998; Faison and Kirt, 1983). The hydrogen peroxide is derived from the co-metabolism of cellulose and/or hemicellulose (Jeffries et al., 1987).

3.2. Cellulose biodegradation

Cellulolytic microorganisms can establish synergistic relationships with non-cellulolytic species in cellulosic wastes; the interaction leads to complete degradation of cellulose. Microorganisms capable of degrading cellulose produce a battery of enzymes with different specificities, working together. Cellulases responsible for the hydrolysis of cellulose, are composed of a complex mixture of enzyme proteins with different specificities to hydrolyze the β-1,4-glycosidic linkages bonds. Cellulases can be divided into three major enzyme activity classes (Goyal et al., 1991; Rabinovich et al., 2002a,b). These are endoglucanases or endo-1-4-β-glucanase (EC 3.2.1.4), cellobiohydrolase (EC 3.2.1.91) and β-glucosidase (EC 3.2.1.21). Endoglucanases, often called carboxymethylcellulases (because of the artificial substrate used for their detection), are thought to initiate attack randomly at multiple internal sites in the amorphous regions of the cellulose fibre which opens-up sites for subsequent attack by the cellobiohydrolases (Lynd et al., 1991). Cellobiohydrolase, often called exoglucanase, is the major component of the fungal cellulase system accounting for 40–70% of the total cellulase proteins, and can hydrolyze highly crystalline cellulose (Esterbauer et al., 1991; Rowell, 1992). Cellobiohydrolases

Table 3
Fungi with the highest specific activity of lignases

Organism	Enzyme	Substrates	Specific activity (μmol min^{-1} mg^{-1})	Opt. *T* (°C)	Opt. pH
Phanerochaete chrysosporium	Diarylpropane peroxidase (ligninase)	1,2-bis(3,4-dimethoxyphenyl)propane-1,3-diol + H_2O_2/1-(3,4-diethoxyphenyl)-1,3-dihydroxy-2-(4-methoxy-phenyl)propane + O_2 + H_2O_2/1-(4-ethoxy-3-methoxyphenyl)-1,2-propane + O_2 + H_2O_2/1-(4-ethoxy-3-methoxyphenyl)-1,2-propene + O_2 + H_2O_2/2-Keto-4-thiomethylbutyric acid + H_2O_2/3,4-dimethoxybenzyl alcohol + H_2O_2	28	23/37	3/4.5
Botrytis cinerea	Laccase	1,2,4-benzenetriol + O_2/1-naphthol + O_2/2-naphthol + O_2/3,5-dimethoxy-hydroxy-benzaldazine + O_2/4,5-dimethyl-o-phenylenediamine O_2/4-amino-N,N`-dimethylaniline + O_2/4-methylcatechol + O_2/ascorbate + O_2/caffeic acid + O_2/catechol + O_2/ferrocyanide + O_2/gallic acid + O_2/guaiacol + O_2	5778	55	4
Stropharia coronilla	manganese peroxidase	Mn^{2+} + H^+ + H_2O_2	692	25	NA

NA = Not available.
Source: Howard et al. (2003).

remove monomers and dimers from the end of the glucan chain. β-glucosidase hydrolyzes glucose dimers and in some cases cellulose-oligosaccharides to glucose. Generally, the endoglucanases and cellobiohydrolases work synergistically in the hydrolysis of cellulose but the details of the mechanisms involved in the process are still unknown (Rabinovich et al., 2002b). Microorganisms generally appear to

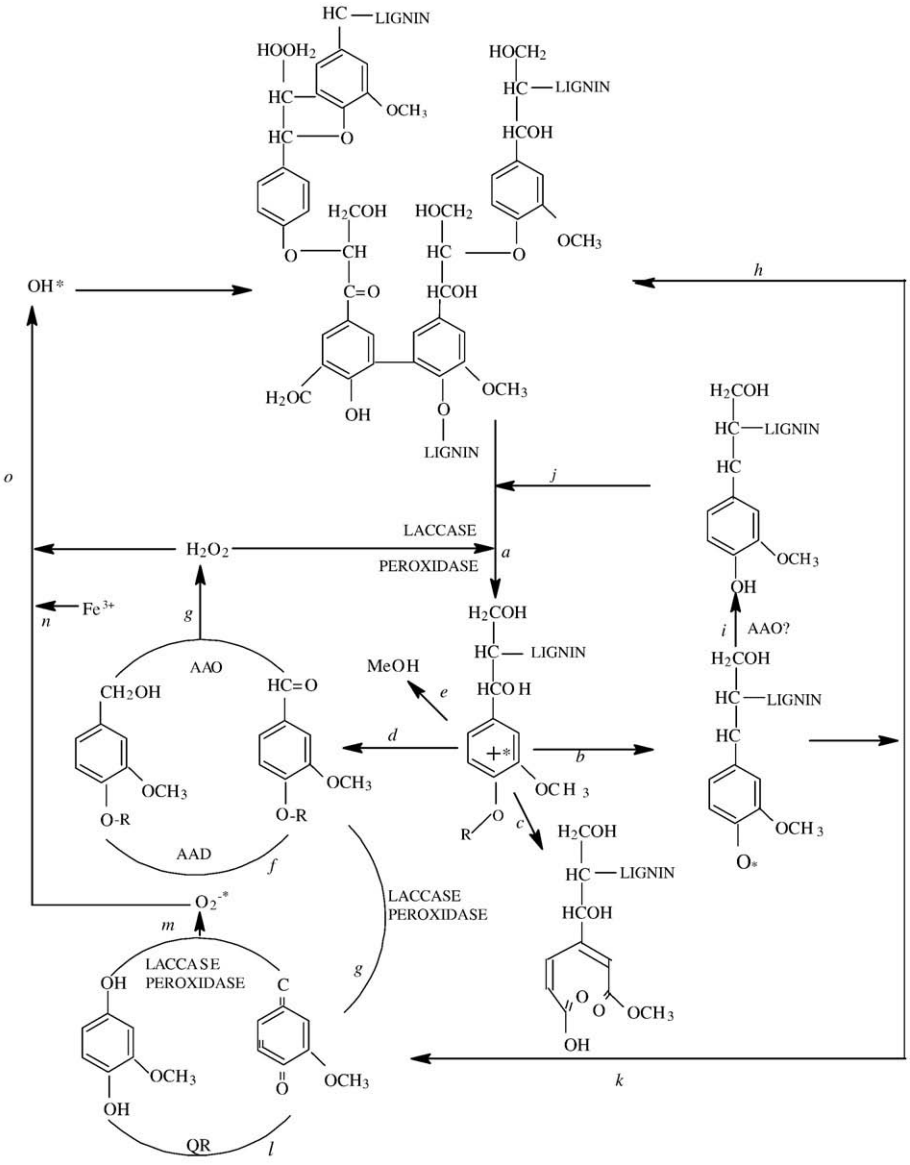

Fig. 2. Lignin biodegradation process by white rot fungi (refer to text).

Table 4
Fungal cellulases with highest specificity activity

Enzyme	Organism	Substrates	Specific activity (μmol min^{-1} mg^{-1})	Opt. *T* (°C)	Opt. pH
Mannnan endo-1,4-β-mannosidase	*Sclerotium rolfsii*	Galactoglucomannan/ galactomannans/ glucomannan/ mannnans	475	72–74	3.3
Cellulase	*Aspergillus níger*	Carboxymethylcellulose/ cellohexaose/ cellopentaose/ cellotetraose/cellotriose/ cellulose	194	70	5
1,3-β-glucan glucohydrolase	*Achlya bisexuales*	Glucan/laminarin/ neutral glucan/ phosphoglucan	7840	30	6
1,3-1,4-β-d-glucan glucanohydrolase	*Orpinomyces* sp.	β-d-glucan/lichenin	3659	45	5.8
1,3-β-d-glucan glucanohydrolase	*Rhizopus chinensis*	β-glucan	4800	NA	NA
1,6-β-d-glucan glucanohydrolase	*Penicillium brefeldianum*	β-glucan/gentiobiose/ pachyman	405	50	4.2

NA = Not available.
Source: Howard et al. (2003).

have multiple distinct variants of endo- and exo-glucanases (Beldman et al., 1987; Shen et al., 1995) (Table 4).

3.3. Hemicellulose biodegradation

Although similar enzymes are involved for cellulose and hemicellulose biodegradation, more enzymes are required for the latter's complete degradation because of its greater heterogeneity compared with cellulose (Malherbe and Cloete, 2002). Hemicelluloses are biodegraded to monomeric sugars and acetic acid. Xylan is the main carbohydrate found in hemicellulose. Its complete degradation requires the cooperative action of a variety of hydrolytic enzymes. Hemicellulases are frequently classified according to their action on distinct substrates, endo-1,4-β-xylanase (EC 3.2.1.8) generates oligosaccharides from the cleavage of xylan and xylan 1,4-β-xylosidase (EC 3.2.1.37) produces xylose from oligosaccharides (Jeffries, 1994). In addition, hemicellulose degradation needs 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. In the case of O-acetyl-4-O-methylglucuronxylan, which is one of the most common hemicelluloses, four different enzymes are required for degradation: endo-1-4-β-xylanase (endoxylanase), acetyl esterase, α-glucuronidase and β-xylosidase. The degradation of O-acetylgalactoglucomannan starts with rupture of the polymer by endomannases. Acetylglucomannan esterases remove acetyl groups, and α-galactosidases eliminate galactose residues. Finally, β-mannosidase and β-glycosidase break down the endomannase-generated oligomeric β-1,4 bonds (Pérez et al., 2002). Table 5 shows the highest specific activity (μmol min^{-1} mg^{-1}) reported for hemicellulases.

4. Generation of lignocellulosic residues

The increasing expansion of agro-industrial activity has led to the accumulation of a large quantity of lignocellulosic residues from wood (e.g. poplar trees), herbaceous (e.g. switchgrass), agricultural (e.g. corn stover, and wheat straw), forestry (e.g. sawdust, thinnings, and mill waste), municipal solid wastes (e.g. waste paper) and various industrial wastes all over the world. Table 6 summarizes the worldwide generation of lignocellulosic residues.

Table 5
Highest specificity activity of fungus hemicellulases

Enzyme	Organism	Substrates	Specific activity (μmol min^{-1} mg^{-1})	Opt. *T* (°C)	Opt. pH
Feruloyl esterase	*Aspergillus níger*	Methyl sinapinate	156	55	5
Endo-1,4-β-xylanase	*Trichoderma longibrachiatum*	1,4-β-d-xylan	6630	45	5
β-1,4-Xylosidase	*Aspergillus nidulans*	ρ-nitrophenyl-β-d-xylopyranoside	107	50	5
Exo-β-1,4-Mannosidase	*Aspergillus níger*	β-d-Man-(1-4)-β-d-GlcNAc-(1-4)-β-d-GlcNAc-Asn-Lys	188	55	3.5
Endo-β-1,4-mannanase	*Sclerotium rolfsii*	Galactoglucomannan/ mannans/ galactomannans/ glucomannans/	380	72–74	2.9/ 3.3
Endo-α-1,5-arabinanase	*Aspergillus Níger*	1,5-α-l-arabinan	90	50–55	4.5–5.0
α-l-Arabinofuranosidase	*Aspergillus Níger*	1,5-α-l-arabinofuranohexaose/ 1,5-α-l-arabinotriose/ 1,5-l-arabinan/α-l-arabinofuranotriose	397	50–60	3.4–4.5
α-Glucuronidase	*Phanerochaete Chrysosporium*	4-O-methyl-glucuronosyl-xylobiose	4.5	50	3.5
α-Galactosidase	*Mortierella vinacea*	Melibiose	2000	60	4
Endo-galactanase	*Aspergillus niger*	NA	6593	50–55	3.5
β-glucosidase	*Humicola insolvens*	(2-hydroxymethylphenyl)-β-d-glucopyranoside	267	50	5
Acetyl xylan esterase	*Schizophyllum commune*	4-methylumbelliferyl acetate/4-nitrophenyl acetate	227	30	7.7

Source: Howard et al. (2003).

5. Bioconversion of lignocellulose into bioproducts

Bioconversion of lignocellulosic residues to useful, higher value products normally requires multi-step processes, which include:

(1) pretreatment (mechanical, chemical or biological);
(2) hydrolysis of polymers to produce readily metabolizable molecules (e. g. hexose or pentose sugars);

Table 6
Lignocellulosic residues generated from different agricultural sources

Lignocellulosic residues	Ton × 10^6/year	Source
Sugar cane bagasse	317–380	Portal Agrario (2005).
Maize straw	159–191	Portal Agrario (2005).
Rice shell	157–188	Portal Agrario (2005).
Wheat straw	154–185	FAO-docrep (2006).
Soja straw	54–65	FRA (2006).
Yuca straw	40–48	FAO (2005).
Barley straw	35–42	SAGPyA-mecom (2005).
Cotton fiber	17–20	SICA (2005).
Sorgoum straw	15–18	SAGPyA-FAO (2004).
Banana waste	13–15	Elnuevodiario (2007).
Mani shell	9.2–11.1	Lorenzati, Ruetsch y Cía, S. A. (2007).
Sunflower straw	7.5–9.0	Horizontea (2008),
Bean straw	4.9–5.9	COFEMERMIR (2006).
Rye straw	4.3–5 2	BCR (2008).
Pine waste	3.8– 4.6	CEDOPEX-FAOSTAT (2004).
Coffee straw	1.6–1.9	FIMARC (2005).
Almond straw	0.4–0.49	Agroalternativo-Argentina (2005).
Hazelnut husk	0.2–0.24	FIA (2005).
Sisal a henequen straw	0.077–0.093	FAO-esc (2008).

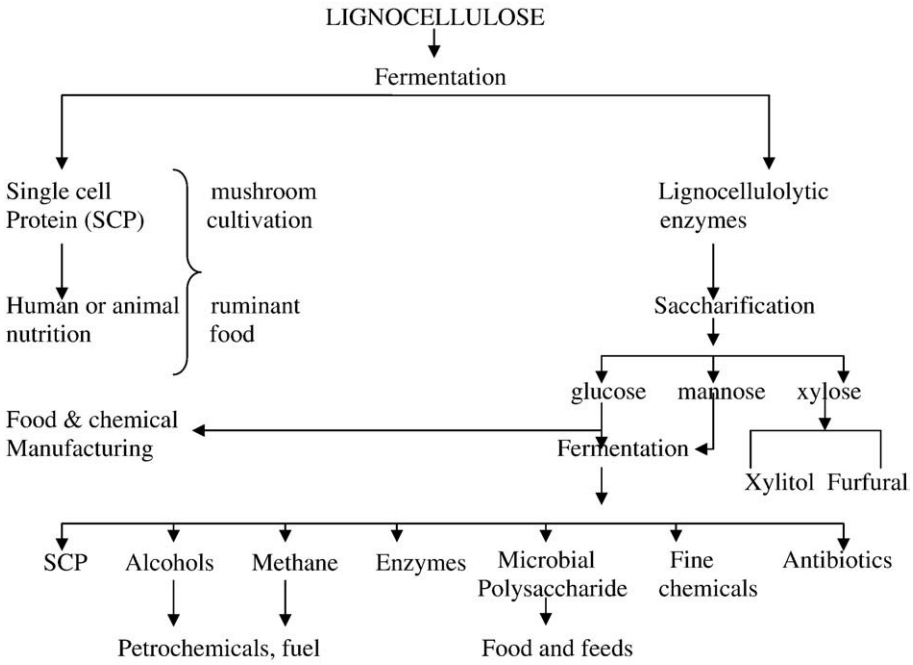

Fig. 3. Generalized process stages in lignocellulosic waste bioconversion.

(3) use of these molecules to support microbial growth or to produce chemical products; and
(4) separation and purification (Smith et al., 1987; Sun and Cheng, 2005; Miettinen-Orinonen and Suominen, 2002).

Several uses have been suggested for biodegrade lignocellulosic wastes; among them are used as raw material for the production of ethanol, for paper manufacturing, for compost making for cultivation of edible mushroom, and directly as animal feed. Much research has been done in finding an alternative fuel using biological methods because of the positive environmental benefits of biofuels. Ethanol is either used as a chemical feedstock or as an additive to gasoline. Softwood, the dominant source of lignocellulose in the Northern hemisphere, has been the subject of interest as a raw material for fuel ethanol production in Sweden, Canada and Western USA (Galbe et al., 2005). Ethanol fuel can reduce greenhouse gas emissions and improve air quality as well as offer strategic or economical advantages (Mosier et al., 2005). Brazil and the USA produce ethanol from the fermentation of sugar cane juice and corn starch respectively. In the US, ethanol has been blended with gasoline as a fuel extender and oxygenate since the 1980's. These gasoline fuels contain up to 20% ethanol by volume (Sun and Cheng, 2002). Over the past two decades, the cost of biological conversion of cellulosic biomass to ethanol has been reduced from around 1.22 USD l^{-1} to the point where it is becoming economically viable. A number of high-value bioproducts such as organic acids, amino acids, vitamins and a number of bacterial and fungal polysaccharides such as xanthans are produced by fermentation using glucose as the base substrate but theoretically these same products could be manufactured from "lignocellulosic residues" (Fig. 3). Ribbons (1987) reported that based on the known metabolism of *P. chrysosporium*, several potential value-added products could be derived from lignin. Cultivation of edible mushrooms using lignocellulosic residues is a value addition process to convert these materials into human food. It is one of the most efficient biological ways by which these residues can be recycled (Royce, 1992; Zhang et al., 2002; Kalm and Sargın, 2004). Mushrooms can be grown successfully on a wide variety of lignocellulosic residues such as cereal straws, banana leaves, sawdust, peanuts hulls, coffee pulp, soybean and cotton stalk, and almost any lignocellulosic substrate that has a substantial cellulose component (Delfin and Duran de bazúa, 2003; Quintero et al., 2006; Rani et al., 2008). Rumen microorganisms convert cellulose and other plant carbohydrates in large amounts to acetic, propionic and butyric acids, which ruminant animals can use as energy and carbon sources (Ezeji et al., 2006; Pérez et al., 2002; Martin et al., 2006; Albores et al., 2006); these microbes also have promise for commercial bioprocessing of lignocellulosic wastes anaerobically in liquid digesters. Cariello et al. (2007) reported that a mixed of endogenous microorganism (*Bacillus subtillis*, *Pseudomonas fluorescens* and *Aspergillus fumigatus*) accelerated the composting process in municipal solid wastes. Studies about a combination of an integrated system of composting, with bioinoculants (strains of *Pleurotus sajor-caju*, *Trichoderma harzianum*, *Aspergillus niger* and *Azotobacter chroococcum*) and subsequent vermicomposting showed an accelerated composting process of wheat straw besides producing a nutrient-enriched compost (Singh and Sharma, 2002). Fig. 4 shows several technologies for converting biomass that are commercial today while others are being piloted or in research and development (UNF Bioenergy, 2006). Biomass pyrolysis is a process by which a biomass feedstock is thermally degraded in the absence of air/oxygen. It is used for the production of solid (charcoal), liquid (tar and other organics) and gaseous products. These products are of interest as they are possible alternate sources of energy. The study of pyrolysis is gaining increasing importance and has many advantages over other renewable and conventional energy sources (Babu, 2008). In the gasification process, the biomass is heated in an environment where the solid biomass breaks down to form a flammable gas. The biogas can be cleaned and filtered to remove problem chemical compounds. The gas can be used in more efficient power generation systems called combined cycles, which combine gas turbines and steam turbines to produce electricity. Anaerobic digestion is a commercially proven technology and is widely used for recycling and treating wet organic waste and waste waters. It is a type of fermentation that converts organic material into biogas, which mainly consists of methane (approximately 60%) and carbon dioxide (approximately 40%) and is comparable to landfill gas. Similar to gas produced via gasification, gas from anaerobic digestion can, after appropriate treatment, be burned

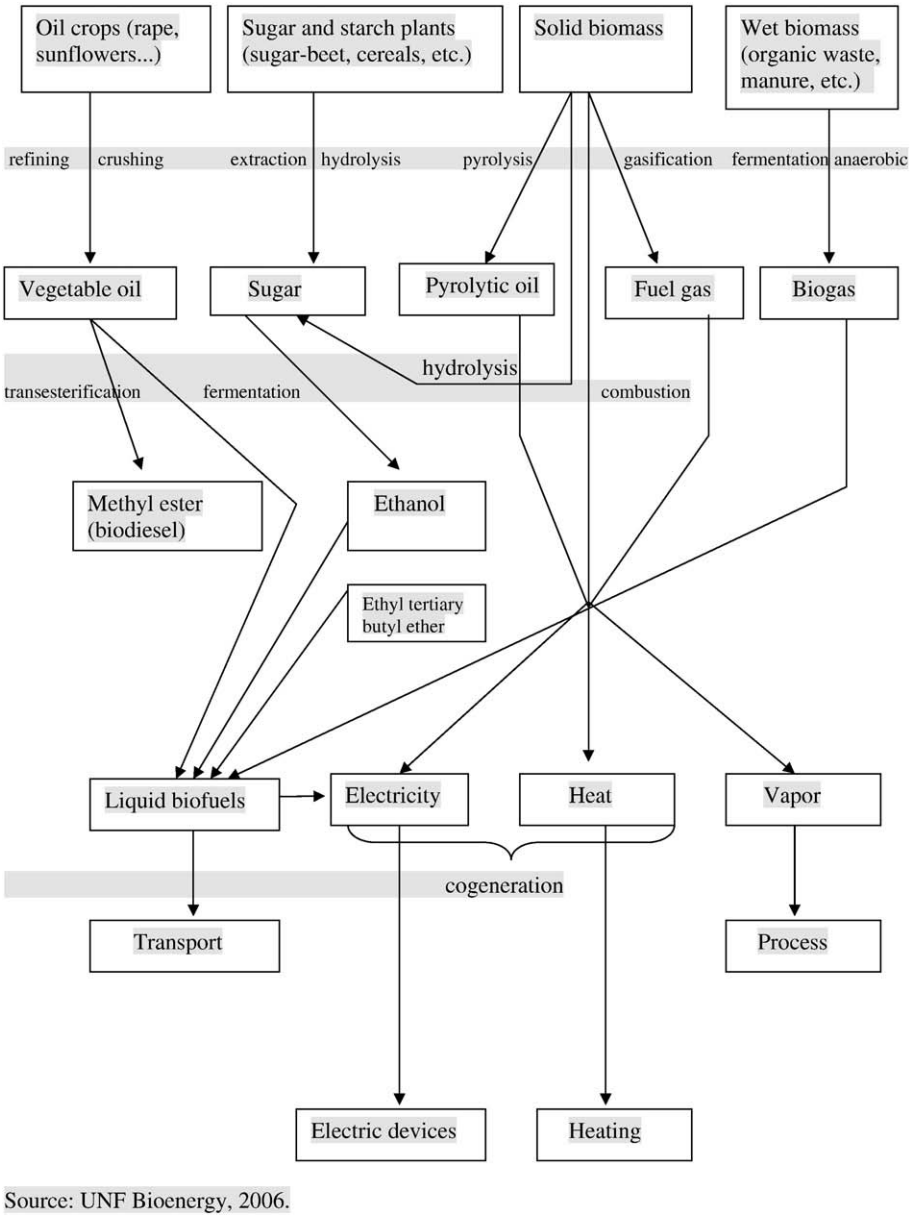

Fig. 4. Biomass energy conversion overview.

directly for cooking or heating. It can be used in secondary conversion devices such as an internal combustion engine for producing electricity or shaft work. (UN Foundation Report, 2008)

6. Conclusions

Lignocellulosic residues from wood, grass, agricultural, forestry wastes and municipal solid wastes are particularly abundant in nature and have a potential for bioconversion. They constitute a renewable resource from which many useful biological and chemical products can be derived. Accumulation of lignocellulose in large quantities in places where agricultural residues present a disposal problem results not only in deterioration of the environment but also in loss of potentially valuable material that can be used in paper manufacture, biomass fuel production, composting, human and animal feed among others. Several novel markets for lignocellulosic residues have been identified recently. The use of fungi in low cost bioremediation projects might be attractive given their highly efficient lignocellulose hydrolysis enzyme machinery.

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