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Review

Oyster mushrooms (*Pleurotus*) are useful for utilizing lignocellulosic biomass

E. A. Adebayo[1,2]* and D. Martínez-Carrera[2]

[1]Department of Pure and Applied Biology, Ladoke Akintola University of Technology, P.M.B. 4000, Ogbomoso, Nigeria.
[2]Biotechnology of Edible, Functional and Medicinal Mushrooms, Colegio de Postgraduados, Apartado Postal 129, Puela 72001, Puebla, Mexico.

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This review shows the biotechnological potential of oyster mushrooms with lignocellulosic biomass. The bioprocessing of plant byproducts using *Pleurotus* species provides numerous value-added products, such as basidiocarps, animal feed, enzymes, and other useful materials. The biodegradation and bioconversion of agro wastes (lignin, cellulose and hemicellulose) could have vital implication in cleaning our environment. The bioprocessing of lignin depends on the potent lignocellulolytic enzymes such as phenol oxidases (laccase) or heme peroxidases (lignin peroxidase (LiP), manganese peroxidase (MnP) and versatile peroxidase) produced by the organism. The cellulose-hydrolysing enzymes (that is, cellulases) basically divided into endo-β-1,4-glucanase , exo-β-1,4-glucanase I and II, and β-glucosidase, they attack cellulose to release glucose, a monomers units from the cellobiose, while several enzymes acted on hemicellulose to give D-xylose from xylobiose. These enzymes have been produced by species of *Pleurotus* from lignocellulose and can also be used in several biotechnological applications, including detoxification, bioconversion, and bioremediation of resistant pollutants.

Key words: Oyster mushroom, lignin, cellulose, hemicellulose.

INTRODUCTION

Lignocellulosic materials are the most promising feedstock as natural and renewable resource essential to the functioning of modern industrial societies (Anwer et al., 2014). A large amount of such materials as waste by-products are being generated through agricultural practices mainly from various agro based industries (Pe´rez et al., 2002).

Large amounts of lignocellulosic waste generated through forestry and agricultural practices, paper-pulp industries, timber industries and many agro-industries, and they are posing serious environmental pollution problems (Howard et al., 2003). Accidentally, much of the lignocellulosic biomass is often disposed of by burning or just lying values without any important used attached to them.

Recently, lignocellulosic biomasses have gained increasing research interests and special importance because of their renewable nature (Asgher et al., 2013; Ofori-Boateng and Lee, 2013). This has attracted the interest of many researchers in the utilization of lignocel-

*Corresponding author. E-mail: eaadebayo@lautech.edu.ng, brogoke2003@yahoo.com. Tel: +2348038099092, +5212221903846.

lulosic wastes. *Pleurotus* are characterized by a white spore print, attached to the gills, often with an essentric stip, or no stip at all, and they are commonly known as Oyster mushrooms (Miles and Chang, 1997). Growing oyster mushroom is becoming more popular throughout the world because of their abilities to grow at a wide range of climate conditions and utilizing various lignocelluloses. In nature, *Pleurotus* species live on parts of plants which are generally poor in nutrients and vitamins.

For spawn running and fruit body development, lignin and cellulose materials such as corn cobs, all cereal straws, paper, wood shavings, sawdust, nutshells and vegetable wastes as well as food industry wastes are sufficient (Baysal et al., 2003). Species of the genus *Pleurotus* (Fr.) P. Kumm known as oyster mushrooms, rank third place in worldwide production of edible mushrooms after *Agaricus bisporus* and *Lentinula edodes*, and comprises various edible species with medical, biotechnological and environmental applications (Cohen et al., 2002). *Pleurotus* species present high adaptability to produce basidiomata within a wide variety of agro-industrial lignocellulosic wastes due to their production of ligninolytic and hydrolytic enzymes (Mikiashvili et al., 2006).

Agro-residues contain three major structural polymers, cellulose, hemicellulose and lignin, which can be easily utilized or broken down by the lignocellulotic enzymes. *Pleurotus* species are the most efficient lignin-degrading organisms, with the ability to produce mainly laccases (EC 1.10.3.2), lignin peroxidase (EC 1.11. 10.14) and manganese peroxidase (EC1.11.1.13) (Adebayo et al., 2012a). These enzymes present a non-specific biocatalyst mechanism and have been used for bioremediation process due to their ability to degrade azo, heterocyclic, reactive and polymeric dyes (Baldrian and Snajdr, 2006; Forgacs et al., 2004). White-rot basidiomycetes are among the most potent organisms to biodegrade and detoxify a wide range of wastes and pollutants. These fungi selectively attack lignin and related compounds by producing one or more of phenol-targeting redox enzymes, namely the peroxidases and laccases/phenol-oxidases (Ntougias et al., 2012). Prospection for fungi is the ability to secret high levels of lignin-degrading enzymes and novel enzyme variants, with desirable properties for biotechnological applications (Adebayo et al., 2012a). Therefore, the huge amounts of lignocellulosic biomass can be potentially bioconverted into different high value raw materials and products such as bio-ethanol, enriched animal feed, cheap energy sources for microbial cultivation (mushrooms included) and enzyme production, biodegradation and bioremediation of toxic organic compounds (Koutrotsios et al., 2014; Anwar et al., 2014; Asgher et al., 2013; Irshad et al., 2013; Ntougias et al., 2012). The objectives of this review are the compilation of the newer achievements in the technologies developed between oyster mushrooms and lignocellulosic materials.

CHEMICAL COMPOSITIONS OF LIGNOCELLULOSE

Lignocellulosic biomass are the most abundant and less utilized biomass, they includes agricultural wastes, forestry residues, grasses and woody materials, which are good source of substrates for oyster mushroom and in turn resulted into valuable products. Agricultural lignocellulosic biomass basically consists of 40 to 50% cellulose, 25 to 30% hemicellulose and 15 to 20% lignin (Malherbe and Cloete, 2002; Iqbal, et al., 2011; Menon and Rao, 2012). Major structural component of plant cell walls is cellulose, which is responsible for its mechanical strength. Hemicelluloses are macromolecules with repeated polymers of pentoses and hexoses, while lignin contains three aromatic alcohols (coniferyl alcohol, sinapyl alcohol and pcoumaryl alcohol) produced through a biosynthetic process and forms a protective seal around the other two components i.e., cellulose and hemicelluloses (Figure 1) (Sanchez, 2009; Menon and Rao, 2012; Anwar et al., 2014). Composition of lignocellulose is generally depends on its source; whether it is derived from the hardwood, softwood, or grasses. Table 1 shows the typical chemical compositions in cellulose, hemicellulose and lignin from various lignocellulosic materials. The variation in chemical compositions may be due to the genetic variability among different sources (Iqbal et al., 2011; Menon and Rao, 2012: Kumar et al., 2009; Malherbe and Cloete, 2002). The chemical formula of cellulose is $(C_6H_{10}O_5)_{n,}$ with structure of single chain polymer shown in Figure 1.

Cellulose is a highly stable polymer consisting of glucose and attached with linear chains up to 12,000 residues. It is majorly com-posed of (1,4)-D-glucopyranose units, which are attached by β-1,4 linkages with an average molecular weight of around 100,000 (Himmel et al., 2007). Cellulose held together by intermolecular hydro-gen bonds in native state, but they have a strong tendency to form intra-molecular and intermolecular hydrogen bonds and this tendency increases the rigidity of cellulose and makes it highly insoluble and highly resistant to most organic solvents. Naturally, cellulose molecules exist as bundles which aggregated together in the form of micro-fibrils order that is, crystalline and amorphous regions (Iqbal et al., 2011; Taherzadeh and Karimi, 2008).

Hemicellulose mainly consists of glucuronoxylan, glucomannan and trace amounts of other polysaccharides. They are majorly found in grasses and straws contain arabinan, galactan and xylan, while mannan is a component of hardwood and softwood (Brigham et al., 1996). Hemicelluloses have sugar backbone which composed xylans, mannans and glucans, with xylans and mannans being the most common (Wyman et al., 2005). Galactans, arabinans and arabinogalactans are also

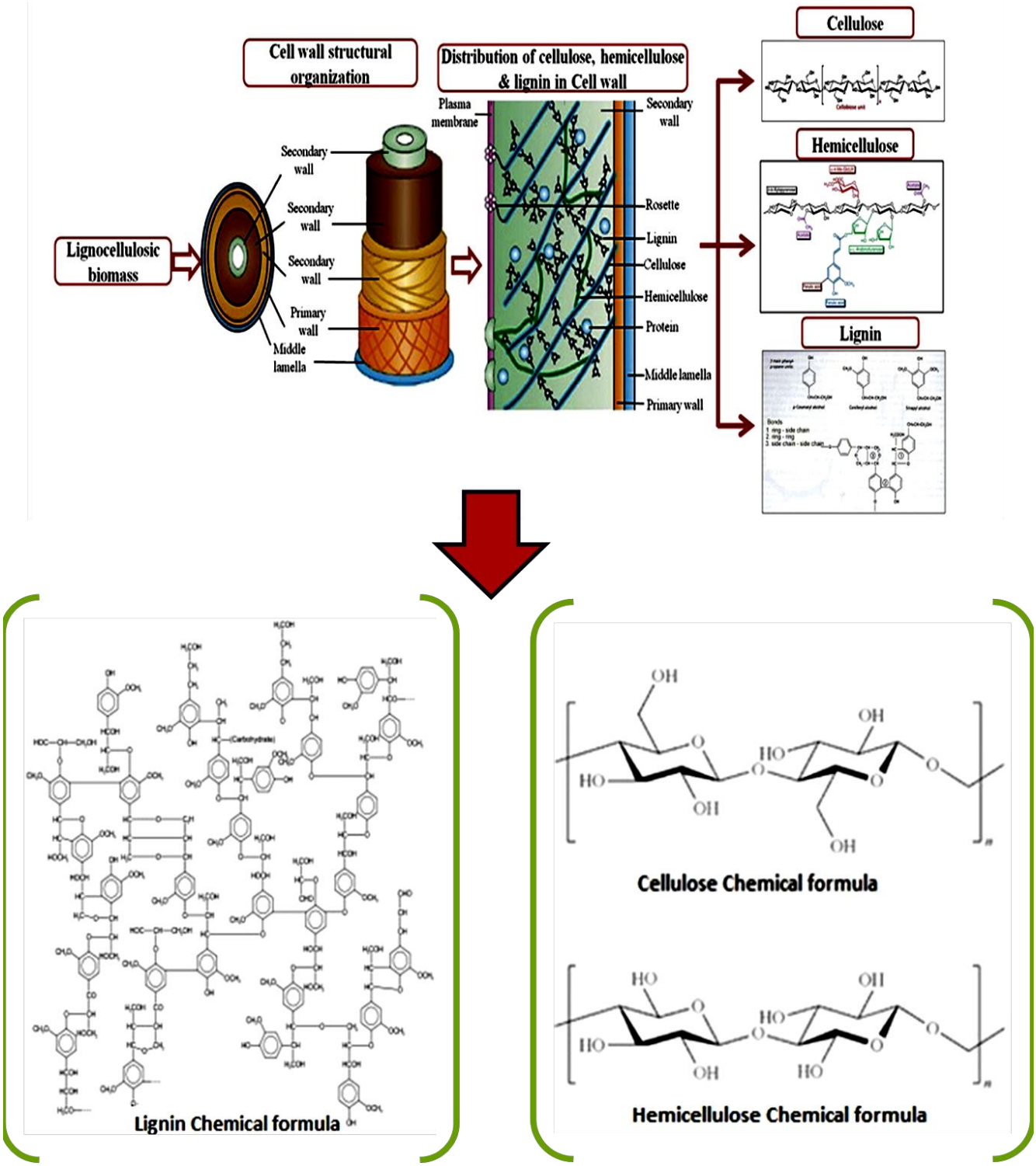

Figure 1. Diagrammatic illustration of the framework of lignocellulose; lignin, cellulose and hemicellulose.

included in the hemicellulose group; however, they do not share the equatorial β-1,4 linked backbone structure. In hardwoods, glucuronoxylan (O-acetyl-4-O-methyl-glucurono-b-Dxylan) is the predominant component, xylospyranose is the backbone of the polymer and connected with β-1,4 linkages. Hemicellulose has average molecular weight of <30,000. Cellulose and hemicellulose binds tightly with non-covalent attractions

Table 1. Composition of representative lignocellulosic feed stocks.

Feedstock	Carbohydrate composition (% dry wt)			References[a]
	Cellulose	Hemicellulose	Lignin	
Barley hull	34	36	19	Kim et al., 2008
Barley straw	36-43	24-33	6.3-9.8	Garda-Aparricio et al., 2006
Bamboo	49-50	18-20	23	Alves et al., 2010
Banana waste	13	15	14	Monsalve et al., 2006
Corn cob	32.3-45.6	39.8	6.7-13.9	Mckendry, 2002
Corn stover	35.1-39.5	20.7-24.6	11.0-19.1	Mosier et al., 2005
Cotton	85-95	5-15	0	Kadolph and Langford, 1998
Cotton stalk	31	11	30	Rubio et al., 1998
Coffee pulp	33.7-36.9	44.2-47.5	15.6-19.1	Perez-Diaz et al., 2005
Douglas fir	35-48	20-22	15-21	Schell et al., 1999
Eucalyptus	45-51	11-18	29	Alves et al., 2010
Hardwood stems	40-55	24-40	18-25	Howard et al., 2003
Rice straw	29.2-34.7	23-25.9	17-19	Prassad et al., 2007
Rice husk	28.7-35.6	11.96-29.3	15.4-20	Abbas and Ansumali, 2010
Wheat straw	35-39	22-30	12-16	Abbas and Ansumali, 2010
Wheat bran	10.5-14.8	35.5-39.2	8.3-12.5	Miron et al., 2001
Grasses	25-40	25-50	10-30	Hon, 2000
Newspaper	40-55	24-39	18-30	Howard et al., 2003
Sugarcane bagasse	25-45	28-32	15-25	Singh et al., 2009
Olive tree biomass	25.2	15.8	19.1	Cara et al., 2008
Sugarcane tops	35	32	14	Jeon et al., 2010
Pine	42-49	13-25	3-29	Pereira, 1998
Poplar wood	45-51	25-28	10-21	Torget and Hsu, 1994
Jutefibres	45-53	18-21	21-26	Mosihuzzaman et al., 1982
Switchgrass	35-40	25-30	15-20	Howard et al., 2003
Grasses	25-40	25-50	10-30	Malherbe and Cloete, 2002
Winter rye	29-30	22-26	16.1	Petersson et al., 2007
Oilseed rape	27.3	20.5	14.2	Petersson et al., 2007
Softwood stem	45-50	24-40	18-25	Howard et al., 2003
Oat straw	31-35	20-26	10-15	Rowell, 1992
Nut shells	25-30	22-28	30-40	Sinner et al., 1979
Sorghum straw	32-35	24-27	15-21	Vazquez et al., 2007
Tamarind kernel powder	10-15	55-65	ND	Menon et al., 2010
Water hyacinth	18.2-22.1	48.7-50.1	3.5-5.4	Aswathy et al., 2010

ND = Not determined, [a]For detailed references: Menon and Rao (2012). Source: Menon and Rao (2012).

to the surface of each cellulose micro-fibril. Hemicelluloses were originally believed to be intermediates in the biosynthesis of cellulose (Vercoe et al., 2005).

Lignin has a long-chain, heterogeneous polymer composed largely of phenyl-propane units, most commonly linked by ether bonds. Lignin acts like a glue by filling the gap between and around the cellulose and hemicellulose complexion with the polymers. It is present in all plant biomass and comprised of complex and large polymer of phenyl-propane, methoxy groups and noncarbohydrate poly phenolic substance, which bind cell walls component together (Hamelinck et al., 2005).

OYSTER MUSHROOMS

Oyster mushrooms are commercially important in the world mushroom market, and several species are grown commercially on a large and small scale in many countries (Adebayo et al., 2012c). *Pleurotus* species have been recognized as mushroom with dual functions to humans; both as food and medicine (Chang and Buswell, 2003). They are nutritive with good quantity of proteins, vitamins and minerals. Medicinally, they are been recommended for obese persons and diabetes patients because of low calorie value (Chang and Buswell, 2003) and very low sugar without starch.

Traditionally, extracts from *Pleurotus* species have been reported to be used in treating some ailments (Osemwegie et al., 2010; Idu et al., 2007). *Pleurotus* are preeminent wood decomposers; they grow on a wider array of forest and agricultural wastes than species of any other group. They thrive on most all hardwoods, on wood by-products (sawdust, paper, pulp sludge), all the cereal straws, corn and corn cobs, on sugar cane bagasse, coffee residues (coffee grounds, hulls, stalks and leaves), banana fronds, cottonseed hulls, agave waste, soy pulp and on other materials too numerous to mention and difficult to imagine possible. In cultivating oyster mushrooms, several valuable by-products are generated. After the crop cycle is complete, the remaining substrate is rendered into a form animal feeds such as cattle, chickens and pigs. Using the spent straw as a nutritious food source could help replace the wasteful practice of feeding grain in the dairy and cattle industry (Stamets, 2000).

Taxonomy of genus *Pleurotus*

Oyster mushrooms are cosmopolitan, and belong to the genus *Pleurotus* (Fungi: Basidiomycetes). Their cap is normally shell-like (about 5 to 20 cm in diameter; 1.9 to 7.8 inches), fleshy, with eccentric or lateral stipe; and their color can be white, cream, yellow, pink, brownish, or dark gray (Martínez-Carrera, 1999). Oyster mushroom was first cultivated by 1917 in Germany by Flank. Evolutionary connection among species in the genus *Pleurotus* is still not clear and many taxonomic issues remain controversial. The genus *Pleurotus* is one of the most diverse groups of cultivated mushrooms. Fungal populations are established and developed through sexual and asexual reproduction (Cohen et al., 2002). Conventional methods for classification (fruit body morphology, microscopic observations, mating studies between populations, biochemical analyses) have not provided clear-cut results (Martínez-Carrera, 1999). This taxonomic confusion has always been associated with the genus *Pleurotus*, especially species belonging to the *Pleurotus ostreatus* complex due to morphological variations of different specimens and similarity of isolates belonging to different species (Asef, 2012). Molecular studies have shown to be more informative; intra and interspecific heterogeneity was determined using ribosomal and mitochondrial DNA analyses, and phylogenetic studies of ribosomal DNA sequences indicated geographic speciation in several groups. Hilber (1982) reported results of mating reactions as well as the microscopic and macroscopic characteristics of many *Pleurotus* isolates and concluded that *Pleurotus pulmonarius* and *P. ostreatus* were different species, *Pleurotus sapidus* is more likely to correspond to *Pleurotus cornucopiae,* and *Pleurotus columbinus* is simply a variety of *P. ostreatus*. There are other disagreements concerning the exact taxonomic position of the cultivar *Pleurotus florida* (considered either as a *P. pulmonarius* or a *P. ostreatus* strain) and whether *Pleurotus cystidiosus* and *Pleurotus abalonus* belong to separate (Han et al., 1974; Bresinsky et al., 1987) or the same species (Jong and Peng, 1975; Moore, 1985). Zervakis and Labarer (1992) classified 23 isolates of genus *Pleurotus* with dendrogram of taxonomic distances demonstrated the suitability of enzyme isoelectric focusing, as it clearly distinguished the four well-defined species *P. cornucopiae, P. cystidiosus, Pleurotus eryngii and Pleurotus flabellatus.* The *P. ostreatus*, whose taxonomy is controversial, was separated from *P. pulmonarius*, and *P. columbinus* was classified as a distinct taxon. The delimitation of *Pleurotus sajor-caju* and *P. sapidus* strains appeared to be more difficult as they seemed to be closely related, the former with *P. pulmonarius* and the latter with *P. ostreatus*. Vilgalys et al. (1993) identified three intersterile groups, *P. ostreatus, P. pulmonarius* and a new species limited to North America: *Pleurotus populinus.* Vilgalys et al. (1996) identified 15 intersterility groups of *Pleurotus* (*ostreatus, pulmonarius, populinus, cornucopiae, djamor, eryngii, cystidiosus, levis, dryinus, tuberregium, agaves, abieticola, brazil, australis, purpureo-olivaceus*) of which some groups have been added in the later time. Oyster mushroom are generally classified as follow; Scientific Name: *Pleurotus* spp.; Phylum: *Basidiomycotina*; Class: *Basidiomycetes*; Subclass: *Holobasidiomycetidae*; Family: *Polyporaceae*; Genus: *Pleurotus;* Species: *sajor caju*, *sapidus, ostreatus, eous, membranaceous, florida, citrinopileatus, flabellatus, pulmonarius* etc.

Life cycle of *Pleurotus* (Oyster mushroom)

Pleurotus mushrooms show the typical life cycle of Basidiomycetes, a major fungal group (Figure 2). It begins with the germination of a basidiospore in a suitable substrate, which gives rise to a monokaryotic mycelium containing genetically identical nuclei (n) and capable of indefinite independent growth. When two compatible monokaryotic mycelia are in close contact, they are able to establish a fertile dikaryon by hyphal fusion or plasmogamy. This dikaryon (n+n), having clamp connexions and binucleate in each hyphal compartment, contains two genetically different nuclei (one from each monokaryon) throughout the mycelium. When environmental conditions are appropriate (temperature, light, relative humidity), the dikaryotic mycelium will differentiate into fruit bodies having specialized structures called basidia. In these club-shaped, binucleate cells, which are formed in the lamellae (hymenium) of each fruit body, karyogamy (fusion of the paired nuclei; 2n) and meiosis (recombination and segregation) take place. The four resulting haploid nuclei move to the sterigmata on the basidium, to form four new basidiospores. When the

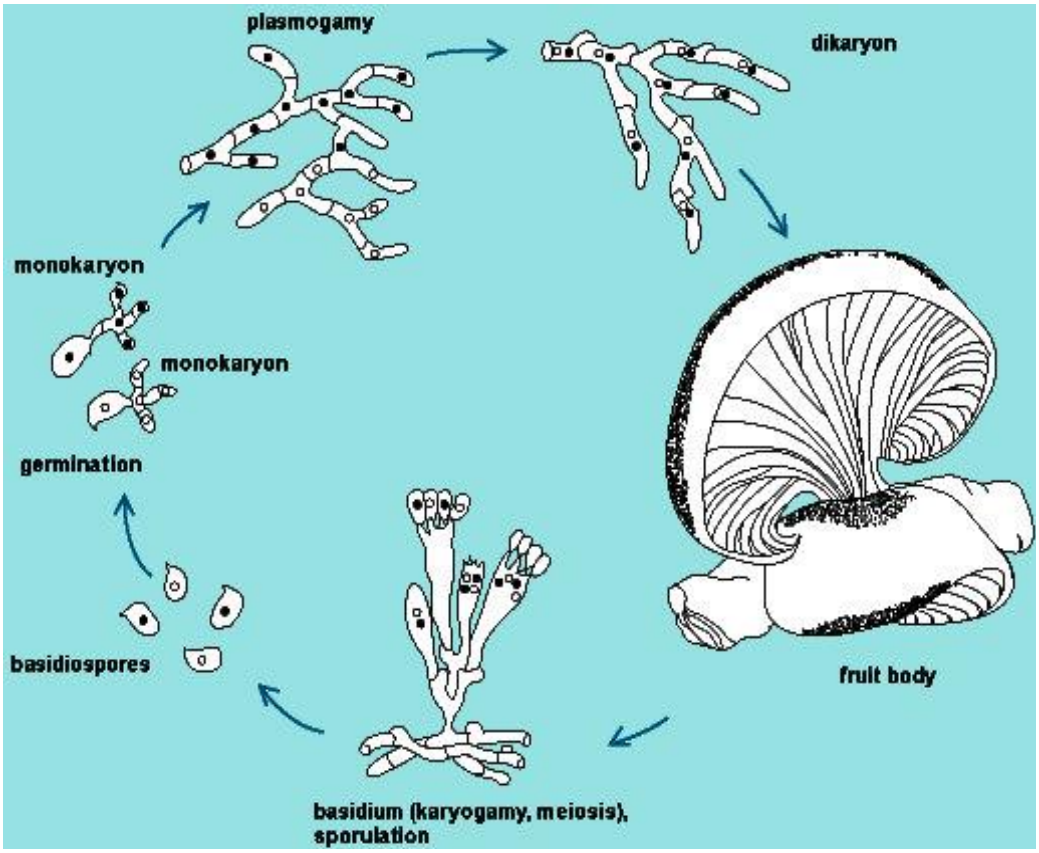

Figure 2. Life cycle of the oyster mushroom *Pleurotus ostreatus*. Source: Martínez-Carrera, 1999.

fruit bodies are mature, basidiospores are discharged, starting the sexual life cycle again.

Lignocellulose biomass as substrate for *Pleurotus* cultivation

In commercial cultivation of mushroom, the availability of good substrates is major limiting factor, which determine mushrooms growth rate and quality of yield produced. The cost of mushroom is directly dependent on the substrate availability and utilizable potential of mushroom species. *Pleurotus* species have been known to grow on a wider array of forest and agricultural wastes than any other mushroom species. Cultivation of edible mushroom with agricultural residues is a value- added process to convert these materials, which otherwise considered to be a wastes, into human and animal food (Zhang et al., 2002). It represents one of most efficient biological ways by which these residues can be recycled (Madan et al., 1987). Oyster mushrooms (*Pleurotus* spp.) are in the third place after the white button and shiitake among the world mushroom production (Gyorfi and Hajdu, 2007). Due to a large variety of non-specific lignocellulosic enzymes produced by them, they can be cultivated on a number of agricultural wastes (Zhang et al., 2002). Varieties of agrowastes have been used in cultivating oyster mushroom, with most of them proved promising and enhanced the yield performance (Table 2). Amongst various cereal straws, paddy straw was reported to be the best substrate for the cultivation of oyster mushroom (Bano and Srivastava, 1962; Jandaik and Kapoor, 1974; Khanna and Garcha, 1982), whereas, next to the paddy straw, wheat straw proved to be the best substrate for the cultivation of *Pleurotus* species (Bano and Rajarathnam, 1982; Bhatti et al., 1987; Thampi et al., 1996; Bonatti et al., 2004). Sorghum straw was also effectively used to cultivate *P. sajor-caju* (Bahukhandi and Munjal, 1989; Patil et al., 1989). Similarly, Garcha et al. (1984) and Diwakar et al. (1989) reported the utility of pearl millet stalks in the cultivation of *P. sajor-caju*. Rye straw waste (Pal and Thapa, 1979), lawn grass (Yamashita et al., 1983), maize cobs (Bhatti et al., 1987), banana waste (Bonatti et al., 2004) and maize straw (Bahukhandi and Munjal, 1989) were reported as suitable substrates for cultivations of different *Pleurotus* species. Bhandari et al. (1991) successfully cultivated *P. sajor-caju* on straws of millets. Many other types of substrates were also reported to be useful for the cultivation of various species of *Pleurotus* species as shown in Table 2.

Table 2. Yield performance of *Pleurotus* spp. on various agro-residues

Substrate	PP (day)	Total yield (g)	BE (%)	References
Paddy straw	29	1,093	109.30	Adebayo et al., 2013
Wheat straw	22	341	68.2	Siddhant et al., 2013
Saw dust	48	205	86.85	Poppe, 1995
Banana leaves	32	770	134.60	Bhavani and Nair, 1989
Guniea grass	36	405	121.04	Kiran and Jandaik, 1989
Coconut leaves	31	585	107.25	Theradi, 1992
Sorghum stalks	29	885	122.45	Patil et al., 2008
Sugarcane bagasse	30	545	125.80	Khan and Ali, 1982
Newspaper	20	1010	193.65	Poppe, 1995
Maize stalks	26	725	139.20	Ruhul Amin et al., 2007
Maize stover	29	ND	89.97	Ragunathan et al., 1996
Coir Pith	27	ND	94.42	Ragunathan et al., 1996
Guar straw	ND	108	11.66	Ragini et al., 1987
Bajra straw	ND	100	7.21	Ragini et al., 1987
Jowar straw	ND	108	7.66	Ragini et al., 1987
Bagasse	ND	97	8.33	Ragini et al., 1987
Sarkanda leaves	ND	73	7.15	Ragini et al., 1987
Mango leaves	ND	61	5.96	Ragini et al., 1987
Coffee pulp	ND	999	159.9	Martínez-Carrera, 2000
Palm oil husk	ND	190	63.3	Adebayo et al., 2014
Cotton Waste	ND	ND	56.41	Martínez-Carrera, 2000

ND = Not determined.

BIOCONVERSION OF AGRO- WASTE INTO USEFUL PRODUCTS

Conversion of lignocellulose into food and feed rich in protein by fungi offers an alternative for developing unconventional source of proteins as food/feed (Mane et al., 2007). Large quantity of lignocellulose materials are produced as by-products and its accumulation in the environment could result to environmental problem. The utilization of waste (reuse or recycle) is very important, in order to keep our environment free of any obnoxious condition. Alternative methods of the utilizing these agricultural wastes are needed to mitigate the environment pollution problems associated with current disposal methods, such as open-field burning and soil incorporation. *Pleurotus* species as primary wood rot fungi are able to colonize different types of agricultural wastes as substrates. Thus, they are cultivated on different lignocellulose wastes. Exploitation of the substrate varies with the species, strain and cultivation technology (Zadrazil and Dube, 1992). In fact, the prospect of utilization of such largely unexploited materials is significant, especially with the cultivation of mushroom to generate new value-added products. 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; Martin et al., 2006; Albores et al., 2006); these microbes also have potential for commercial bioprocessing of lignocellulosic wastes anaerobically in liquid digesters.

Studies on combination of an integrated system of composting, with bio-inoculants (strains of *P. 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). Koutrotsios et al. (2014) reported a high reduction of both fibre and the content of hemicelluloses and cellulose of spent cultivation substrate of *P. ostreatus*, an increase in crude protein of spent substrate is also reported compared to initial substrate (Table 3).

ENZYMES PRODUCED BY *PLEUROTUS* SPECIES IN SEVERAL LIGNOCELLULOSE BIOMASS

Basidiomycetes fungi especially *Pleurotus* species are the most efficient lignin-degrading organisms that produce mainly laccases (EC 1.10.3.2), lignin peroxidase (EC 1.11.10.14) and manganese peroxidase (EC1.11.1.13) (Adebayo et al., 2012a). These enzymes present a non-specific biocatalyst mechanism and have been used for bioremediation process due to their ability to degrade azo, heterocyclic, reactive and polymeric dyes

Table 3. Selected constituents of nine (spent) cultivation substrates by *Pleurotus ostreatus*.

Parameter	AN	BS	CC	GM	OL	OS	PL	PN	WS
N	0.5	0.0	0.5	2.7	1.8	1.1	1.2	2.3	0.5
K	72	ND	424	1057	758	1164	1328	307	364
Na	ND	2.1	12.8	43.6	27.0	21.4	52.6	8.5	14.2
P	46.8	39.5	62.3	193.3	90.9	74.1	121.8	288.8	66.9
Ash	1.7	1.8	3.7	12.5	14.7	4.1	15.0	28.0	13.0
Crude protein	3.1	0.3	3.0	17.1	11.6	6.6	7.5	14.2	2.8
Crude fat	3.7	0.3	0.3	3.2	2.1	0.8	0.2	2.02	0.5
Total carbohydrate	91.6	97.7	93.3	75.2	74.6	78.9	77.7	68.4	68.6
Crude fibre	41.0	50.9	36.7	23.2	25.2	49.5	31.5	11.6	32.9
Hemicellulose	18.4	22.1	20.7	4.1	8.8	15.8	14.3	1.1	12.9
Lignin	16.6	11.0	6.1	39.8	18.3	21.0	14.7	23.8	7.4
Cellulose	28.8	48.7	46.1	11.3	12.7	20.4	26.9	3.9	39.3
Residual biomass	148.3	159	157.4	86.9	103.3	93.1	140	114.9	136.9

ND= Not determined; Source: Koutrotsios et al. (2014). AN, almond and walnut shells 1:1 w/w; BS, beech sawdust; CC, corn cobs; GM, grape marc plus cotton gin trash 1:1 w/w; OL, olive mill by-products (leaves and two phase olive mill waste 1:1 w/w); OS, extracted olive-press cake; PN, pine needles; PL, date palm tree leaves and WS: wheat straw after the production. Values (% d.w., except of the first three parameters) are expressed as means.

(Baldrian and Snajdr, 2006; Forgacs et al., 2004). Fungi prospection is the ability to secret high levels of lignin-degrading enzymes and novel enzyme variants, with desirable properties for biotechnological applications. On the other hand, alternative low cost substrates like agricultural residues for enzyme production using solid state fermentation (SSF) offer economic and environmental advantages. Different types of agro-industrial wastes have been reported from literature as raw materials for diverse value-added products. The cost of raw materials in enzymes production, which translates into 40 to 60% has make enzymes production generally expensive (Hacking, 1987). In this perspective, the utilization of wastes as growth substrates for the production of enzymes is more economical and profitable. Agro-industrial wastes were omnipresence, high biodegradability, and rich in carbon with optimum potential to serve as substrate for enzymes production. Several species of *Pleurotus* have been isolated and identified as producer of lignocellulotic enzymes with better performance on agro waste as substrate (Table 4).

Biodegradation of lignocellulosic biomass

Lignocellulose degrading mushroom species are used in various SSF applications such as biodegradation of hazardous compounds and biological detoxification of toxic agro-industrial wastes (Soccol and Vandenberghe, 2003; Philippoussis and Diamantopoulou, 2011), bio-transformation of agro-industrial residues to mushroom food and animal feed (Philippoussis, 2009), compost and product developments such as biologically active metabolites, enzymes, food, flavour compounds and other added value compounds (Philippoussis and Diamantopoulou, 2011). It has been reported that some species of *Pleurotus* are able to colonize different types of vegetable wastes, increasing their digestibility (Villas-Boas et al., 2002; Zhang et al., 2002; Mukherjee and Nandi, 2004).

Salmones et al. (2005) reported that three species of *Pleurotus* consumed lignocellulose with varied degradation percentage from each strain. In particular *P. ostreatus* efficiently degraded hemicellulose on coffee pulp and wheat straw and lignin on wheat straw, whereas *Pleurotus djamor* showed a preference for the cellulose of coffee pulp. *P. pulmonarius* was distinguished by a high consumption of lignin when grown on coffee pulp. Generally, greater decrease in lignocellulosic compounds was observed for wheat straw samples than for coffee pulp (Salmones et al., 2005). The cellulose has been reported as the most biodegraded component of the lignocellulose by fungi due to its content of the substrate in the production of fruiting bodies (Geetha and Sivaprakasam, 1998; Thomas et al., 1998), followed by the hemicellulose which is less abundant than the cellulose and least is the lignin (Salmones et al., 2005).

Generally, *Pleurotus* species follow the mechanism employed by white-rot fungi in degrading lignocellulose waste. White-rot fungi degrade lignin by secreting enzymes collectively termed “ligninases”. Ligninases can be classified as either phenol oxidases (laccase) or heme peroxidases [lignin peroxidase (LiP), manganese peroxidase (MnP) and versatile peroxidase (VP) (Martinez et al., 2005). Production of lignin peroxidases (EC1.11.1.14) (LiP), manganese peroxidases (EC 1.11.1.13) (MnP) and laccases (EC 1.10.3.2) from *P. ostreatus* and *P. pulmonarius* have been studied (Okamoto

Table 4. Enzymes produced by *Pleurotus* species in several agricultural wastes.

***Pleurotus* species**	**Substrates**	**Enzyme**	**References**
P. ostreatus	Bagasse of cane maize straw	Xylanases, cellulase, Laccase, MnP, LiP.	Marquez at al. (2007) Okamoto et al. (2002)
P. ostreatus, P. pulmonarius	Coffee pulp, used nappy, grass residues, wheat straw, Industrial cotton fiber.	Endoglucanase, cellobiohydrolase, Laccase, MnP, LiP.	Marnyye et al. (2002) Okamoto et al. (2002)
P. ostreatus, P. citrinopileatus	Wheat straw	Laccase, MnP, Endo- β -1,4-glucanase Endo- β -1,4-xylanase β-Glucosidase, β -xylosidase	Carabajal et al. (2012)
P. tuber-regium	Cotton waste, rice straw, cocoyam peels, corncob, groundnut shell, sawdusts of *Khaya ivorensis*, *Mansonia altissima* and *Boscia angustifolia* coffee husks, eucalyptus sawdust, eucalyptus bark, with or without 20 % rice bran	Cellulase, Proteinase, amylase, α-Amylase, Carboxymethylcellulase, Lipase, Peroxidase, Catalase, Polyphenol oxidase, Glucose-6-phosphatase.	Kuforiji and Fasidi (2008)
P. ostreatus		MnP, laccase, LiP, cellulases, xylanases, tanases.	Luz et al. (2012).
P. eryngii	Liquid substrate	Versatile peroxidase Lip, MnP	Camarero et al. (1999)
P. ostreatus, P. eryngii	Liquid substrate	versatile peroxidase Aryl-alcohol oxidase	Ruiz-Duenas et al. (1999) Cohen et al. (2002)
P. sajor-caju, P. florida	Used tea leaves	Aryl-alcohol dehydrogenases Laccase, Lip.	Guillen et al. (1992)
P. ostreatus, P. sajor-caju	saw dust, paddy straw, sugarcane bagasse	Cellobiohydrolase β-glucosidase, CMCase.	Rana and Rana (2011)
P. florida, P. sajor- sajor	Sugarcane leaves, paddy and Wheat straw	Endo-β-1; 4-glucanase, Exo-β-1; 4-glucanase, β-glucosidase, cellulases	Khalil et al. (2011) Ortega et al. (1993)

et al., 2002; Carabajal et al., 2012; Luz et al., 2012), while VPs have been reported to be produced by *P. eryngii* (Camarero et al., 1999; Ruiz-Duenas et al., 1999) and *P. ostreatus* (Cohen et al., 2002) (Table 4).

Lignin biodegradation

Laccase

Laccases are glycosylated blue multi-copper oxidoreductases (BMCO) that use molecular oxygen to oxidize various aromatic and nonaromatic compounds through a radical catalyzed reaction mechanism (Claus, 2004; Baldrian, 2006). Laccases couple the electron reduction of dioxygen into two molecules of water with the oxidation of a vast variety of substrates, such as phenols, arylamines, anilines, thiols and lignins (Figure 3a) (Thurston, 1994). Four copper ions in their catalytic center mediate the redox process. These are classified as being type-1 (T1), type-2 (T2) and two type-3 (T3 and T3'), based on the copper's coordination and spectroscopic properties (Messerschmidt and Huber, 1990). The oxidation reactions catalyzed by laccases lead to the formation of free radicals which act as intermediate substrates for the enzymes (Figure 3b) (Ferraroni et al., 2007). These mediators can leave the enzyme site and react with a broad range of high-redox potential substrates and thus create non-enzymatic routes of oxidative polymerizing or depolymerizing reactions (Figure 1c) (Dashtban et al., 2010). Ultimately, laccase-mediator system (LMS) becomes involved in a range of physiological functions such as lignolysis (Figure 3d), lignin synthesis, morphogenesis, pathogenesis and

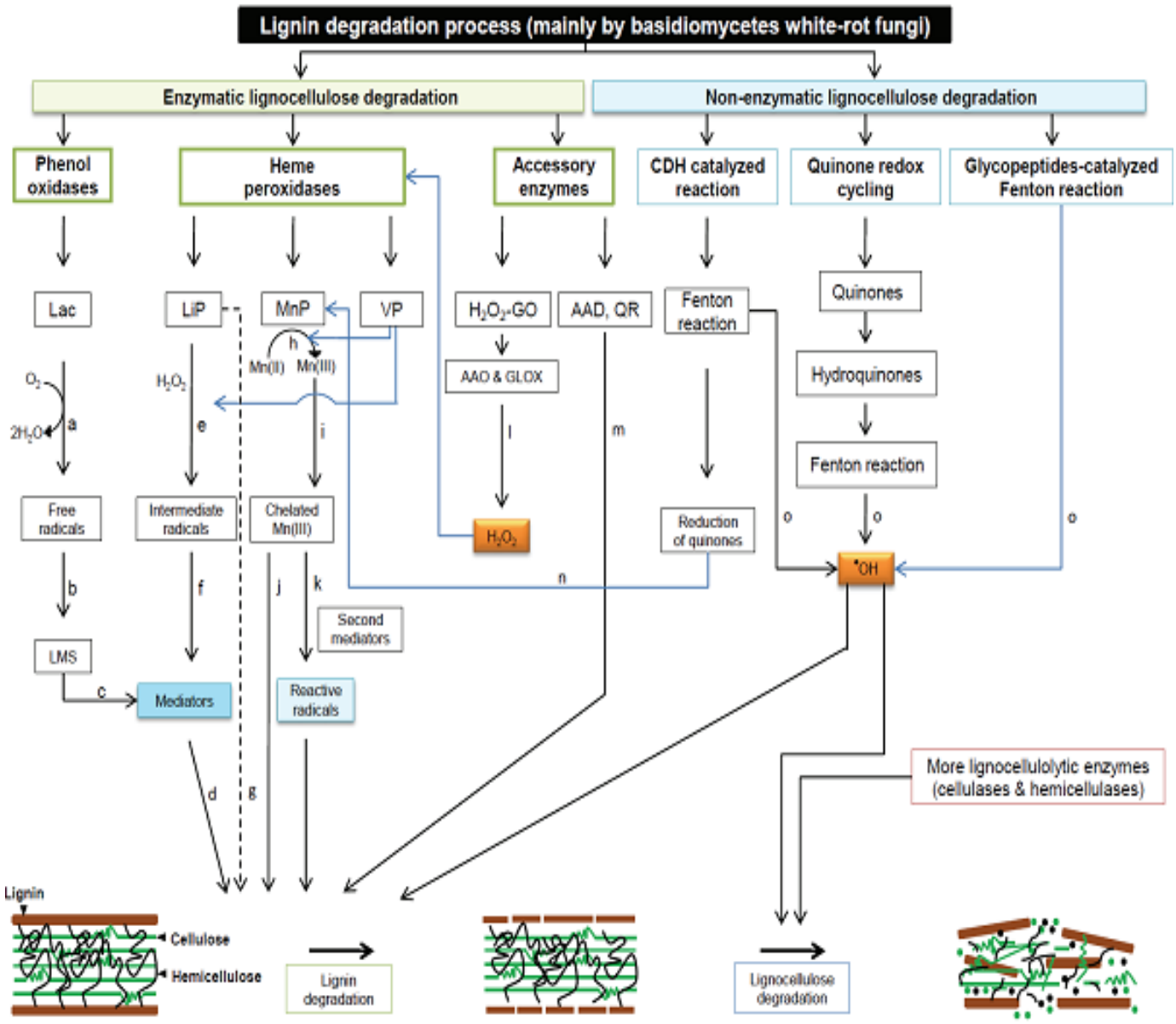

Figure 3. Schematic diagram of lignin degradation by basidiomycetes white-rot fungi: the major steps and enzymes involved (refer to text). Lac: laccase-mediator system, LiP: lignin peroxidase, MnP: manganese peroxidase, VP: versatile peroxidase, H_2O_2-GO: H_2O_2-generating oxidase, AAO: aryl-alcohol oxidase, GLOX: glyoxal oxidase, H_2O_2: hydrogen peroxide, AAD: aryl-alcohol dehydrogenases, QR: quinone reductases and OH: free hydroxyl radicals. Source: Dashtban et al. (2010).

detoxification (Mayer and Staples, 2002).

Heme peroxidase

Lignin peroxidases (LiP): Lignin peroxidase is one of the heme-containing glycoproteins and plays a major role in the biodegradation of lignin cell wall constituent (Piontek, 2001). LiPs catalyze the H_2O_2-dependent oxidative depolymerization of a variety of non-phenolic lignin compounds (diarylpropane), β-O-4 non-phenolic lignin model compounds and a wide range of phenolic compounds (e.g. guaiacol, vanillyl alcohol, catechol, syringic acid, acteosyringone) (Wong, 2009). LiPs oxidize the substrates in multi-step electron transfers and form intermediate radicals, such as phenoxy radicals and veratryl alcohol radical cations (Figure 3e). These intermediate radicals undergo non-enzymatic reactions such as radical coupling and polymerization, side-chain cleavage, demethylation and intramolecular addition and rearrangement (Figure 3f) (Wong, 2009). Unlike the other peroxidises, LiP is able to oxidize non-phenolic aromatic

substrates and does not require the participation of mediators due to its unusually high redox potential (Figure 3g) (Wong, 2009; Wang et al., 2008). The crystal structure of the first LiP has shown that the heme group is buried in the interior of the protein and has access to the outer medium through a channel (Dashtban et al., 2010). Although, the size of the channel is not sufficient to allow the large polymer lignin to access the heme group, small molecule substrates can find a suitable binding site (Piontek, 2001).

Manganese peroxidases (MnP): Manganese Peroxidases are extracellular glycoproteins and are secreted in multiple isoforms which contain one molecule of heme as iron protoporphyrin IX (Asgher et al., 2008). MnP catalyzes the peroxide dependent oxidation of Mn (II) to Mn (III) (Figure 3h), which is then released from the enzyme surface in complex with oxalate or with other chelators (Figure 3i). Chelated Mn (III) complex acts as a reactive low molecular weight, diffusible redox-mediator (Figure 3, j) of phenolic substrates including simple phenols, amines, dyes, phenolic lignin substructures and dimers (Wong, 2009; Wesenberg et al., 2003; Asgher et al., 2008). The oxidation potential of Mn (III) chelator is only limited to phenolic lignin structures. However, for the oxidation of non-phenolic substrates by Mn (III), reactive radicals must be formed in the presence of a second mediator (Figure 3k). Organic acids, such as oxalate and malonate are the primary compounds that act as second mediators in the production of reactive radicals like carbon centered radicals (acetic acid radicals, $COOHC•H_2$), peroxyl radicals ($COOH\text{-}CH_2OO•$), superoxide ($O_2•\text{-}$) and formate radicals ($CO_2•\text{-}$) (Wong, 2009; Wesenberg et al., 2003; Asgher et al., 2008). In the absence of H_2O_2 (e.g. in fungi lacking H_2O_2-generating oxidases), these radicals can be used by MnP as a source of peroxides and increase the lignin-degrading efficiency of the fungi (Wong, 2009; Wesenberg et al., 2003; Asgher et al., 2008).

Versatile peroxidases (VP): Versatile Peroxidases are glycoproteins with combine properties capable of oxidizing typical substrates of other basidiomycetes peroxidases including Mn (II) and also veratryl alcohol (VA), MnP and the typical LiP substrate, respectively (Figure 3) (Wesenberg et al., 2003; Asgher et al., 2008; Ruiz-Duenas et al., 1999). VPs form an attractive ligninolytic enzyme group due to their dual oxidative ability to oxidize Mn (II) and also phenolic and non-phenolic aromatic compounds (Wesenberg et al., 2003). It has been found that VPs can also efficiently oxidize high redox-potential compounds such as dye Reactive Black 5 (RB5) as well as a wide variety of phenols, including hydroquinones (Gomez-Toribio et al., 2001). It has been suggested that VPs can oxidize substrates spanning a wide range of potentials, including low- and high-redox potentials. This is a result of their hybrid molecular structures which provide multiple binding sites for the substrates (Camarero et al., 1999). This makes VPs superior to both LiPs and MnPs, which are not able to efficiently oxidize phenolic compounds in the absence of veratryl alcohol or oxidize phenols in the absence of Mn (II), respectively (Ruiz-Duenas et al., 1999). Similar to the MnP mechanism, Mn (III) is released from VPs and acts as a diffusible oxidizer of phenolic lignin and free phenol substrates (Figure 3h, i and j). Like other members of heme peroxidases, heme is buried in the interior of the protein and has access to the outer medium through two channels (Camarero et al., 1999). The function of the first channel is similar to that described for LiP and is conserved among all heme peroxidases. Conversely, the second channel is found to be specific to VP and MnP and is where the oxidation of Mn (II) to Mn (III) takes place (Ruiz-Duenas et al.,1999).

Other enzymes and mechanisms involved in lignin degradation

In addition to ligninases, other fungal extracellular enzymes which act as accessory enzymes have been found to be involved in lignin degradation. These include oxidases generating H_2O_2, which provide the hydrogen peroxide required by peroxidases, and mycelium-associated dehydrogenases, which reduce lignin-derived compounds (Figure 3l) (Martinez et al., 2005). Oxidases generating H_2O_2 include aryl-alcohol oxidase (AAO) (EC 1.1.3.7) found in *P. eryngii* (Guillen et al., 1992). In addition, aryl-alcohol dehydrogenases (AAD) (a flavoprotein) and quinone reductases (QR) are also involved in lignin degradation by *P. eryngii* (Figure 3, m) (Guillen et al., 1992). Moreover, it has been shown that cellobiose dehydrogenase (CDH), which is produced by many different fungi under cellulolytic conditions, is also involved in lignin degradation in the presence of H_2O_2 and chelated Fe ions (Henriksson et al., 2000). It is proposed that the effect of CDH on lignin degradation is through the reduction of quinones, which can be used by ligninolytic enzymes or the support of a Mn-peroxidase reaction (Figure 3n) (Henriksson et al., 2000). Previous studies have shown the involvement of non-enzymatic mechanisms in plant cell-wall polysaccharide degradation. Mechanisms are mostly assisted by oxidation through the production of free hydroxyl radicals (•OH). Many white and brown-rot fungi have been shown to produce hydrogen peroxide (H_2O_2) which enters the Fenton reaction and results in release of •OH (Figure 3o) (Guillen et al., 1992; Suzuki et al., 2006). By attacking polysaccharides and lignin in plant cell walls in a non-specific manner, these radicals create a number of cleavages which facilitate the penetration of the cell wall by lignocellulolytic enzymes (Call and Mücke, 1997; Wang

et al., 2006). Pathways by which fungi generate free •OH radicals are: cellobiose dehydrogenase (CDH) catalyzed reactions, low molecular weight peptides/quinone redox cycling and glycopeptide-catalyzed Fenton reactions (Renganathan et al., 1990).

Cellulose biodegradation

Cellulose is a homopolysaccharide composed of β-D-glucopyranose units, linked by β-(1→4)-glycosidic bonds. Cellulose contains both nonreducing (NR) and reducing (R) ends. The smallest repetitive unit of cellulose is cellobiose, which can be converted into glucose residues. The cellulose-hydrolysing enzymes (that is, cellulases) have been reported to be produced by species of *Pleurotus* from lignocellulose (Kuforiji and Fasidi, 2008; Carabajal et al., 2012; Luz et al., 2012) (Table 4). The enzyme (cellulases) divided into three major groups: endo-β-1,4-glucanase, exo-β-1,4-glucanase I and II, and β-glucosidase. The endo-β-1,4-glucanase catalyse random cleavage of internal bonds of the cellulose chain, while exo-β-1,4-glucanase I attack the chain at reducing ends to release cellobiose, and exo-β-1,4-glucanase II attack cellulose at nonreducing end chain. β-glucosidases are only active on cellobiose, and release glucose monomers units from the cellobiose (Figure 4A).

Hemicellulose biodegradation

The second most abundant renewable biomass which accounts for 25 to 35% of lignocellulosic biomass is hemicellulose (Saha, 2000). They are heterogeneous polymers built up by pentoses (D-xylose, L-arabinose), hexoses (D-glucose, D-galactose), sugar acids (Ferulic acid and 4-*O*-methyl-D-glucuronic acid and acetyl group. Many enzymes are responsible for the degradation of hemicellulose. The α-D-glucuronidase attack 4-*O*-methyl-D-glucuronic acid, while endo-β-1,4- xylanase break the xylan chains and α-L- arabinofuranosidase attack end chain of L-arabinose. The further reactions are cutting off ferulic acid and removing of the acetyl groups by feruloyl esterase and acetylxylan esterase, respectively. Reduction of xylan to xylobiose is done by α-D-galactosidase. The β-D-xylosidase release D-xylose, a monomers unit from xylobiose (Figure 4B). Like cellulose, hemicellulose is also an important source of fermentable sugars for biorefining applications (Figure 5). Xylanases are being produced and used as additives in feed for poultry and as additives to wheat flour for improving the quality of baked products at the industrial scale.

CONCLUSION

The challenges facing the whole world about the increased production of lignocellulloloses materials from agricultural and forestry practices without efficient utilisation, has informed the alternative uses for this natural and renewable resources through a biotechnological manipulation of oyster mushroom. Majority of developing countries are still grappling with socio economic issues including food security, developing technological solutions in the agriculture, agro-processing and other related issues. Lignocellulolytic fungi, especially *Pleurotus* species, have attracted a great deal of interest as potential biomass degraders for large-scale applications due to their ability to produce vast amounts of valuable products and extracellular lignocellulolytic enzymes. Agro-waste materials which are majorly composed of lignin, cellulose and hemicellulose serves as major source of carbon and energy for *Pleurotus* species cultivation. Oyster mushroom and their enzymes serve as an efficient alternative for the biodegradation and bioconversion of lignocelluloses and other resistant pollutants. Lignocellulose biotechnology by oyster mush-room could produce numerous value-added products such as fruit body, extracellular enzymes, animal feed and other products. The bioprocessing of lignin depends on the potent lignocellulolytic enzymes such as phenol oxidases (laccase) or heme peroxidases (lignin peroxidase (LiP), manganese peroxidase (MnP) and versatile peroxidase) produced by the organism. The cellulose-hydrolysing enzymes (that is, cellulases) basically divided into endo-β-1,4-glucanase, exo-β-1,4-glucanase I and II, and β-glucosidase, they attack cellulose to release glucose, a monomers units from the cellobiose, while several enzymes (α-D-glucuronidase, , endo-β-1,4- xylanase, α-L- arabinofuranosidase, feruloyl esterase, acetylxylan esterase, α-D-galactosidase and β-D-xylosidase) acted on hemicellulose to give D-xylose from xylobiose. The bioconversion of lignocelluloses majorly involves transformation of lignin, hydrolysis of cellulose and hemicellulose to simple sugar, which can then play vital role in fermentation process. This bioprocess sometime refers to as fractionation.

In fact, the prospect of utilisation of such largely unexploited materials is significant, especially when accomplished by combining environmentally sound management with the generation of new value-added products. An indicative case complying with such prerequisites is the controlled solid state fermentation of various plant residues leading to the production of edible mushrooms. The productions of the protein rich foods at low cost could solve the problem of insufficient supply of quantity and quality of the bodybuilding material (protein) in feeding man.

Beside, that the enzymes produced serves in biode-gradation or bioconversion of agro-waste, they can also be used in several biotechnological applications, includ-ing detoxification, bioconversion and bioremedia-tion of resistant pollutants. Several of these enzymes have previously reported of having the ability to degrade and

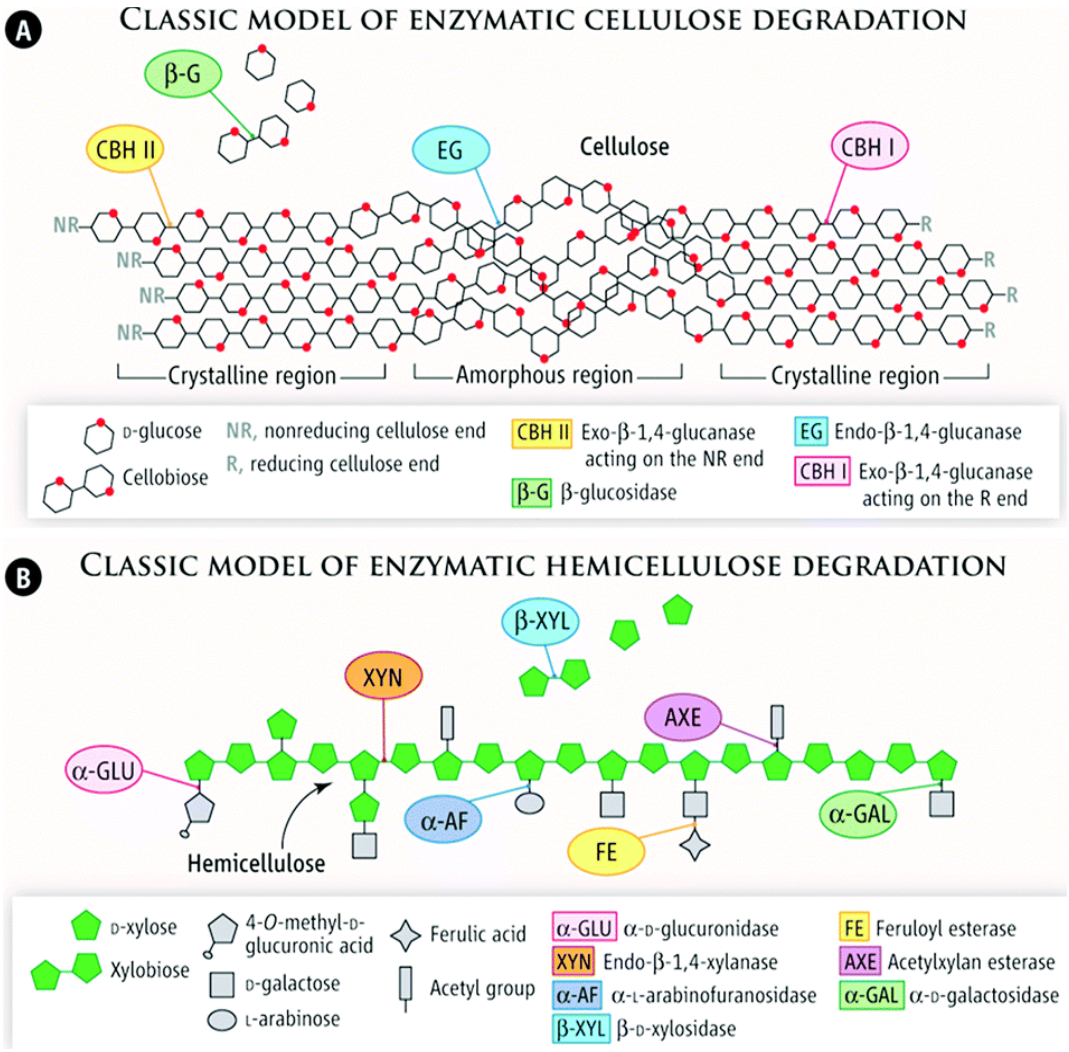

Figure 4. Model of enzymatic degradation with site of action in cellulose and hemicellulose.

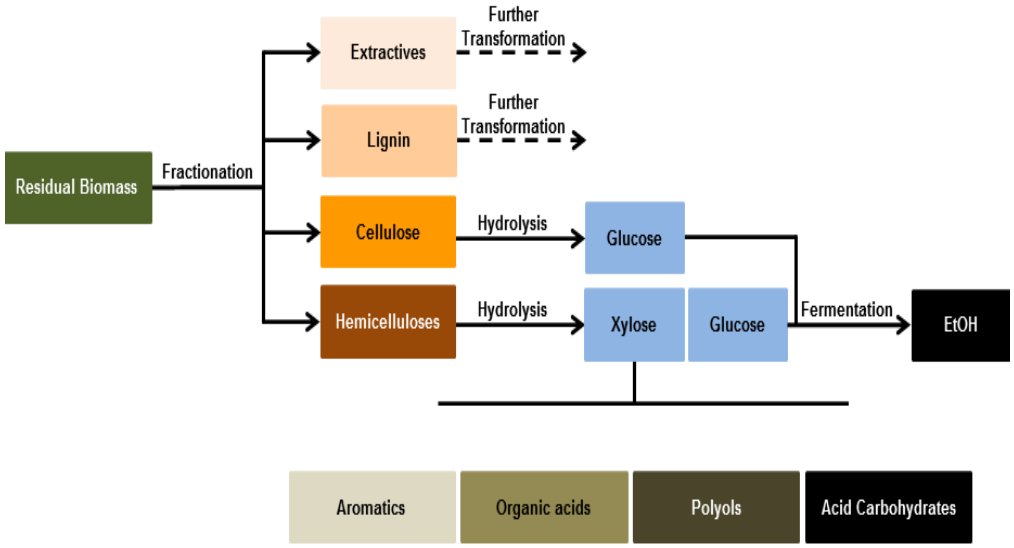

Figure 5. Different chemical reaction in bioconversion of lignocellolosic biomass.

mineralize toxic chemicals, such as polycyclic aromatic hydrocarbons (PAHs), atrazine, organophosphorus and wastewaters.

Conflict of Interests

The author(s) have not declared any conflict of interests.

REFERENCES

Abbas A, Ansumali S (2010). Global potential of rice husk as a renewable feedstock for ethanol biofuel production. Bioenergy Res. 3:328-334.

Adebayo EA, Oloke JK, Yadav A, Barooah M, Bora TC (2013). Improving yield performance of *Pleurotus pulmonarius* through hyphal anastomosis fusion of dikaryons. World J. Microbiol. Biotechnol. 29:1029-1037.

Adebayo EA, Alao MB, Olatunbosun OO, Omoleye EO, Omisakin OB (2014). Yield evaluation of *Pleurotus pulmonarius* (Oyster mushroom) on different Agricultural wastes and various grains for spawn production. Ife J. Sci. 16(3):475-480.

Adebayo EA, Oloke JK, Achana Y, Bora TC (2012a). Improvement of Laccase Production in *Pleurotus pulmonarius*-LAU 09 by Mutation. J. Microbiol. Res. 2(1):11-17.

Adebayo EA, Oloke JK, Majolagbe ON, Ajani RA, Bora TC (2012c). Antimicrobial and anti-inflammatory potential of polysaccharide from *Pleurotus pulmonarius* LAU 09. Afr. J. Microbiol. Res. 6(13):3315-3323.

Alborés S, Pianzzola MJ, Soubes M, Pía Cerdeiras M (2006). Biodegradation of agroindustrial wastes by *Pleurotus* spp for its use as ruminant feed. Electronic J. Biotechnol. 9(3):0717-3458.

Alves FF, Bose SK, Francis RC, Colodette JL, Iakovlev M, Heiningen AV (2010). Carbohydrate composition of eucalyptus, bagasse and bamboo by a combination of methods. Carbohydr. Polym. 82:1097-10101.

Anwar Z, Muhammad G, Muhammad I (2014). Agro-industrial lignocellulosic biomass a key to unlock the future bio-energy: A brief review. J. Rad. Res. Appl. Sci. 7: 163-173.

Asef MR (2012). Intersterility groups of *Pleurotus ostreatus* complex in Iran. Mycology 3(2):147-152.

Asgher M, Ahmad Z, Iqbal HMN (2013). Alkali and enzymatic delignification of sugarcane bagasse to expose cellulose polymers for saccharification and bio-ethanol production. Ind. Crops Prod. 44:488-495.

Asgher M, Bhatti HN, Ashraf M, Legge RL (2008). Recent developments in biodegradation of industrial pollutants by white rot fungi and their enzyme system. Biodegradation 19:771-783.

Aswathy US, Sukumaran RK, Devi GL, Rajasree KP, Singhania RR, Pandey A (2010). Bio-ethanol from water hyacinth biomass: an evaluation of enzymatic saccharification strategy. Bioresour. Technol. 101:925-930.

Bahukhandi D, Munjal RL (1989). Cultivation of Pleurotus sp. on different agricultural residues. Indian Phytopathol. 42(4): 492-495.

Baldrian P (2006). Fungal laccases - occurrence and properties. FEMS. Microbiol. Rev. 30:215-242.

Baldrian P, Snajdr J (2006). Production of ligninolytic enzymes by litter-decomposing fungi and their ability to decolorize synthetic dyes. Enzyme Microbiol. Technol. 39: 1023-1029.

Bano Z, Rajarathnam S (1982). Studies on cultivation of *Pleurotus sajor-caju*. Mushroom J. 115:243-245.

Bano Z, Srivastava HC (1962). Studies in the cultivation of *Pleurotus sp*. on paddy straw. Food Sci. 12: 363-368.

Baysal E, Peker H, Mustafa KY, Ali T (2003). Cultivation of oyster mushroom on waste paper with some added supplementary materials. Bioresour. Technol. 89:95-97.

Bhandari TPS, Singh RN, Verma BL (1991). Cultivation of oyster mushroom on different substrates. Indian Phytopathol. 44(4):555-557.

Bhatti M, Mir FA, Siddiq M (1987). Effect of different bedding material on relative yield of oyster mushroom in successive flushes. Pak. J. Agric. Res. 8:256-259.

Bhavani D, Nair M (1989). Observation of the biology and cultivation of *Volvariella volvacea*. Mushroom Sci. 12(2): 517-531.

Bonatti M, Karnopp P, Soares HM, Furlan SA (2004). Evaluation of *Pleurotus ostreatus* and *P. sajor-caju* nutritional characteristics when cultivated on different lignocellulosic wastes. Food Chem. 88: 425-428.

Bresinsky A, Fischer M, Mbixner B, Paulus W (1987). Speciation in *Pleurotus*. Mycology 79: 234-245.

Brigham JS, Adney WS, Himmel ME (1996). Hemicellulases: diversity and applications. In C. E. Wyman (Ed.), Bioethanol: Production and utilization. pp. 119-141.

Call HP, Mücke I (1997). History, overview and applications of mediated lignolytic systems, especially laccase-mediator-systems (Lignozyme®-process). J. Biotechnol. 53: 163-202.

Camarero S, Sarkar S, Ruiz-Duenas FJ, Martinez MJ, Martinez AT (1999). Description of a versatile peroxidase involved in the natural degradation of lignin that has both manganese peroxidase and lignin peroxidase substrate interaction sites. J. Biol. Chem. 274: 10324-10330.

Cara C, Ruiz C, Ballesteros M, Manzanares P, Negro MJ, Castro E (2008). Production of fuel ethanol from steam-explosion pretreated olive tree pruning. Fuel 87: 692-700.

Carabajal M, Levin L, Albertó E, Lechner B. (2012). Effect of co-cultivation of two *Pleurotus* species on lignocellulolytic enzyme production and mushroom fructification. Int. Biodeterior. Biodegrad. 66: 71-76.

Chang ST, Buswell JA (2003). Medicinal mushrooms—as prominent source of nutriceuticals for the 21st century Curr. Top. Nutraceutical Res. 1: 257-280.

Claus H (2004). Laccases: structure, reactions, distribution. Micron 35: 93-96.

Cohen R, Persky L, Hadar Y (2002). Biotechnological applications and potential of wood-degrading mushrooms of the genus *Pleurotus*. Appl. Microbiol. Biotechnol. 58:582-594.

Dashtban M, Heidi S, Tarannum AS, Wensheng Q (2010). Fungal biodegradation and enzymatic modification of lignin. Int. J. Biochem. Mol. Biol. 1(1): 36-50.

Ezeji TC, Qureshi N, Karcher PM, Blaschek HP (2006). Production of butanol from corn. In: Alcoholic Fuels for today and tomorrow, edited by S.D. Minteer, New York: Marcel Dekker. pp. 99-122.

Ferraroni M, Myasoedova NM, Schmatchenko V, Leontievsky AA, Golovleva LA, Scozzafava A, Briganti F (2007). Crystal structure of a blue laccase from Lentinus tigrinus: evidences for intermediates in the molecular oxygen reductive splitting by multicopper oxidases. BMC Struct. Biol. 7: 60.

Forgacs E, Cserháti T, Oros G (2004). Removal of synthetic dyes from wastewaters: A review. Environ. Int. 30: 953-971.

Garda-Aparicio MAP, Ballesteros I, Gonzalez A, Oliva JWM, Ballesteros M, Negro MAJ (2006). Effect of inhibitors released during steam-explosion pretreatment of barley straw on enzymatic hydrolysis. Appl. Biochem. Biotechnol. 129(32): 278-288.

Geetha D, Sivaprakasam K (1998). Enzyme and sporophore production potential of oyster mushroom (*Pleurotus* spp.). Mushroom Res. 7: 39-42.

Gomez-Toribio V, Martinez AT, Martinez MJ, Guillen F (2001). Oxidation of hydroquinones by the versatile ligninolytic peroxidase from *Pleurotus eryngii*, H_2O_2 generation and the influence of $Mn2^+$. Eur. J. Biochem. 268: 4787-4793.

Guillen F, Martinez AT, Martinez MJ (1992). Substrate specificity and properties of the arylalcohol oxidase from the ligninolytic fungus *Pleurotus eryngii*. Eur. J. Biochem. 209: 603-611.

Gyorfi J, Hajdu CS (2007). Casing-material experiments with *P. eryngii*. Int. J. Hortic. Sci. 13: 33-36.

Hacking AJ (1987). Economic Aspects of Biotechnology, Cambridge University Press, Cambridge. p. 317.

Hamelinck CN, Hooijdonk V, Faaij APC (2005). Ethanol from lignocellulosic biomass: techno-economic performance in short, middle and long-term. Biomass Bioenergy 28: 384-410.

Han Yh, Chbn KM, Cheno S (1974). Characteristics and cultivation of a

new *Pleurotus* in Taiwan. Mushroom Sci. 9: 167-174.
Henriksson G, Johansson G, Pettersson G (2000). A critical review of cellobiose dehydrogenases. J. Biotechnol. 78: 93-113.
Hilber O (1982). Die Gattung *Pleurotus*. Biblioth. Mycol. 87: 448.
Himmel ME, Ding SY, Johnson DK, Adney WS, Nimlos MR, Brady JW (2007). Biomass recalcitrance: engineering plants and enzymes for biofuel production. Science 315: 804-807.
Hon DNS (2000). In: Natural polymers and agrofibers composites. New York: Marcel Dekker Inc.
Howard RL, Abotsi E, Van Rensburg EJ, Howard S (2003). Lignocellulose biotechnology: issues of bioconversion and enzyme production. Afr. J. Biotechnol. 2(12): 602-619.
Idu M, Osemwegie O, Timothy O, Onyibe HI (2007). A survey of plants used in traditional healthcare by Waja tribe Bauchi State, Nigeria. Plant Arch. 7(2): 535- 538.
Iqbal HMN, Asgher M, Bhatti HN (2011). Optimization of physical and nutritional factors for synthesis of lignin degrading enzymes by a novel strain of *Trametes versicolor*. BioResources 6: 1273-1278.
Irshad M, Anwar Z, But HI, Afroz A, Ikram N, Rashid U (2013). The industrial applicability of purified cellulose complex indigenously produced by *Trichoderma viride* through solid-state bio-processing of agro-industrial and municipal paper wastes. BioResources 8(1): 145-157.
Jandaik CL, Kapoor JN (1974). Studies on cultivation of *Pleurotus sajor-caju* (Fr.) Singer. Mushroom Sci. 9(1): 667-672.
Jeon YJ, Xun Z, Rogers PL (2010). Comparative evaluations of cellulosic raw materials for second generation bioethanol production. Lett. Appl. Microbiol. 51: 518-24.
Jong SC, Peng JT (1975). Identity and cultivation of a new commercial mushroom in Taiwan. Mycology 67: 1235-1238.
Kadolph SJ, Langford AL (1998). Textiles. 8th ed. Upper Saddle River, N.J: Prentice Hall, Inc.
Khalil MI, Hoque MM, Basunia MA, Alam N, Khan MA (2011). Production of cellulase by *Pleurotus ostreatus* and *Pleurotus sajor-caju* in solid state fermentation of lignocellulosic biomass. Turk. J. Agric. 35: 333-341.
Khan S, Ali M (1981). Cultivation of Oyster mushroom *Pleurotus* on ball locules. Mushroom Sci. 11(1): 691-695.
Khanna P, Garcha HS (1982). Utilization of paddy straw for cultivation of *Pleurotus* species. Mushroom Newsl. Trop. 2(1): 5-9.
Kim TH, Taylor F, Hicks KB (2008). Bioethanol production from barley hull using SAA (soaking in aqueous ammonia) pretreatment. Bioresour. Technol. 99: 5694-702.
Kiran BM, Jandaik CL (1989). Cultivation of Pleurotus sapidus in India. Mushroom Sci. 12(2):179-185.
Koutrotsios G, Konstantinos CM, Iordanis C, Georgios IZ (2014). Bioconversion of lignocellulosic residues by *Agrocybe cylindracea* and *Pleurotus ostreatus* mushroom fungi- Assessment of their effect on the final product and spent substrate properties. Food Chem. 161: 127-135.
Kuforiji OO, Fasidi IO (2008). Enzyme activities of *Pleurotus tuber-regium* (Fries)Singer, cultivated on selected agricultural wastes. Bioresour. Technol. 99: 4275-4278.
Kumar P, Barrett DM, Delwiche MJ, Stroeve P (2009). Methods for pretreatment of lignocellulosic biomass for efficient hydrolysis and biofuel production. Ind. Eng. Chem. Res. 48: 3713-3729.
Luz JMR, Nunes MD, Paes SA, Torres DP, Silva MCS (2012). Lignocellulolytic enzyme production of *Pleurotus ostreatus* growth in agroindustrial wastes. Braz. J. Microbiol. 43: 1508-1515.
Madan M, Vasudevan P, Sharma S (1987). Cultivation of *Pleurotus sajor-caju* on different wastes. Biol. Waste. 22: 241-250.
Malherbe S, Cloete TE (2002). Lignocellulose biodegradation: fundamentals and applications. Rev. Environ. Sci. Biotechnol. 1: 105-114.
Mane VP, Patil SS, Syed AA. Baig MMV (2007). Bioconversion of low quality lignocellulosic agricultural waste into edible protein by *Pleurotus sajor-caju* (Fr.) Singer. J. Zhejiang Univ. Sci. B 8: 745-751.
Marnyye A, Velásquez C, Mata G, Michel SJ (2002). Waste-reducing cultivation of *Pleurotus ostreatus* and *Pleurotus pulmonarius* on coffee pulp: changes in the production of some lignocellulolytic enzymes. World. J. Microb. Biotechnol. 18: 201-207.
Márquez ATA, Mendoza MGD, González MSS (2007). Actividad fibrolitica de enzimas producidas por *Trametes* sp. EUM1, *Pleurotus ostreatus* IE8 y Aspergillus niger AD96.4 en fermentación sólida. Interciencia 32: 780-785.
Martin C, López Y, Plasencia Y, Hernández E (2006). Characterization of agricultural and agroindustrial residues as raw materials for ethanol production. Chem. Biochem. Eng. 20: 443-447.
Martinez AT, Speranza M, Ruiz-Duenas FJ, Ferreira P, Camarero S, Guillen F, Martinez MJ, Gutierrez A, del-Rio JC (2005).Biodegradation of lignocellulosics: microbial, chemical, and enzymatic aspects of the fungal attack of lignin. Int. Microbiol. 8: 195-204.
Martínez-Carrera D (1999). Oyster mushrooms. McGraw-Hill Yearbook of Science and Technology. Ed.: M. D. Licker. McGraw-Hill, Inc.,New York. ISBN 0-07-052625-7 (447 pp.) [http://books.mcgraw-hill.com]. pp. 242-245.
Martínez-Carrera D (2000). Mushroom biotechnology in tropical America. Int. J. Mushroom Sci. 3: 9-20.
Mayer AM, Staples RC (2002). Laccase: new functions for an old enzyme. Phytochemistry 60: 551-565.
McKendry P (2002). Energy production from biomass (part 1): overview of biomass. Bioresour. Technol. 83: 37-43.
Menon V, Prakash G, Rao M (2010). Enzymatic hydrolysis and ethanol production using xyloglucanase and *Debaromyces hansenii* from tamarind kernel powder: galactoxyloglucan predominant hemicellulose. J. Biotechnol. 148: 233-239.
Menon V, Rao M (2012). Trends in bioconversion of lignocellulose: biofuels, platform chemicals and biorefinery concept. Prog. Energy Combust. Sci. 38(4): 522-550.
Mikiashvili N, Wasser S, Nevo E, Elisashvili V (2006). Effects of carbon and nitrogen sources on*Pleurotus ostreatus* ligninolytic enzyme activity. World J. Microbiol. Biotechnol. 22: 999-1002.
Miles PG, Chang ST (1997). Mushroom Biology: Concise Basics and Current Developments. World scientific. Singapore. 194p.
Miron J, Yosef E, Ben-Ghedalia D (2001). Composition and in vitro digestibility of monosaccharide constituents of selected byproduct feeds. J. Agric. Food Chem. 49: 2322-2326.
Monsalve G, John F, Medina PIV, Ruiz CAA, Adriana A (2006). Ethanol production of banana shell and cassava starch. Dyna, Universidad Nacional de Colombia 73:21-27.
Moore RT (1985). Mating type factors in *Pleurotus cystidiosus*. Trans. Br. Mycol. Soc. 85: 354-358.
Mosier NS, Wyman C, Dale B, Elander R, Lee YY, Holtzapple M (2005). Features of promising technologies for pretreatment of lignocellulosic biomass. Bioresour. Technol. 96: 673-686.
Mosihuzzaman M, Theander O, Aman P (1982). Comparative study of carbohydrates in the two major species of jute (Corchorus capsularis and Corchorus olitorius). J. Sci. Food Agric. 33: 1207-1212.
Mukherjee R, Nandi B (2004). Improvement of *in vitro* digestibility through biological treatment of water hyacinth biomass by two *Pleurotus* species. Int. Biodeterior. Biodegrad. 53(1): 7-12.
Ntougias S, Baldrian P, Ehaliotis C, Nerud F, Antoniou T, Merhautova V (2012). Biodegradation and detoxification of olive mill wastewater by selected strains of the mushroom genera *Ganoderma* and *Pleurotus*. Chemosphere 88: 620-626.
Ofori-Boateng C, Lee KT (2013). Sustainable utilization of oil palm wastes for bioactive phytochemicals for the benefit of the oil palm and nutraceutical industries. Phytochem. Rev. 1-18.
Okamoto K, Narayama S, Katsuo A, Shigematsui I, Yanase H (2002). Biosynthesis of p-anisaldehyde by the white-rot basidiomycete *Pleurotus ostreatus*. J. Biosci. Bioeng. 93: 207-210.
Ortega GM, Marttinez PC, Betancourt, Ortega MA (1993). Enzyme activities and substrate degradation during white rot fungi growth on sugarcane straw in a solid state fermentation. World J. Microb. Biotechnol. 9: 210-212.
Osemwegie OO, Okhuoya JA, Akpaja EO, Oghenekaro AO, Ihayere CA (2010). Nigeria Mushrooms:Underutilized Non- Wood Forest Resources. J. Appl. Sci. Environ. Manage.14 (1): 43-54.
Patil BD, Jadhav SW, Kakade SS (1989). Studies on cultivation of Pleurotus sajor-caju on different substrates. J. Maharashtra Agric. Univ. 14(1):156-158.
Patill SS, Kadam RM, Shinde SI, Deshmukh SA (2008). Effect of different

substrates on productivity and proximate composition of *P.florida*. Int. J. Plant Sci. 3(1):151-153.
Pe´rez J, Mun ˜oz-Dorado de la Rubia T, Martı´nez J (2002). Biodegradation and biological treatments of cellulose, hemicellulose and lignin: an overview. Int. Microbiol. 5:53-63.
Pereira H (1988). Variability in the chemical composition of plantation eucalyptus. Wood Fiber Sci. 20: 82-90.
Pérez-Díaz N, Márquez-Montesinos F, Autíe PM (2005). Pinar del Río: CIGET, www. ciget.pinar.cu/No.2005-2/beneficio.htm.
Petersson A, Thomsen MH, Hauggaard-Nielsen H, Thomsen A-B (2007). Potential bioethanol and biogas production using lignocellulosic biomass from winter rye, oilseed rape and faba bean. Biomass Bioenergy 31:812-819.
Philippoussis A (2009). Production of mushrooms using agro-industrial residues as substrates. In: Biotechnology for Agro-industrial Residues Processing. P. Sing Nigam and Pandey A. Eds. Springer. pp.163-196.
Philippoussis A, Diamantopoulou P (2011). Agro-Food Industry Wastes and Agricultural Residues Conversion into High Value Products by Mushroom Cultivation. Proceedings of the 7th International Conference on Mushroom Biology and Mushroom Products (ICMBMP7). pp. 339-351.
Piontek K, Smith AT, Blodig W (2001). Lignin peroxidase structure and function. Biochem. Soc. Trans. 29: 111-116.
Poppe J (1995). Cultivation of Edible Mushrooms on tropical agricultural wastes. Biennial Training course. ABOS & VLIR. University Gent.
Prassad S, Singh A, Joshi HC (2007). Ethanol as an alternative fuel from agricultural, industrial and urban residues. Resour. Conserv. Recycl. 50: 1-39.
Ragini B, Madan M, Bisaria VS (1987). Biological Efficiency and Nutritive Value of *Pleurotus sajor-caju* Cultivated on Different Agro-wastes. Biol. Waste. 19:239-255
Ragunathan R, Gurusamy R, Palaniswamy M, Swaminathan K (1996). Cultivation of *Pleurotus* spp. on various agro-residues. Food Chem. 55:139-144.
Rana IS, Rana AS (2011). Lignocellulolytic Enzyme Profile of Agaricus and Pleurotus Species Cultured on used Tea Leaves Substrate. Adv. Biotechnol. 11(6):10-14
Renganathan V, Usha SN, Lindenburg F (1990). Cellobiose oxidizing enzymes from the lignocellulose-degrading basidiomycete *Phanerochaete chrysosporium* - interaction with microcrystalline cellulose. Appl. Microbiol. Biotechnol.32: 609-613.
Rowell MR (1992). Emerging technologies for material and chemicals from biomass. Proceedings of symposium. Washington, DC: American Chemical Society. pp. 26-31.
Rubio M, Tortosa JF, Quesada J, Gomez D (1998). Fractionation of lignocellulosics: solubilization of corn stalk hemicelluloses by autohydrolysis in aqueous medium. Biomass Bioenergy 15:483-491.
Ruhul Amin SM, Rahman MM, Hossain MM (2007). Effect of Different Substrates on the Growth and Yield of Five Selected Oyster Mushrooms. Banglad. J. Mushroom 1(2):21-25.
Ruiz-Duenas FJ, Guillen F, Camarero S, PerezBoada M, Martinez MJ, Martinez AT (1999). Regulation of peroxidase transcript levels in liquid cultures of the ligninolytic fungus *Pleurotus eryngii*. Appl Environ. Microbiol. 65:4458-4463.
Saha BC (2000). Alpha-L-arabinofuranosidases: Biochemistry, Molecular Biology and Application in Biotechnology. Biotechnol. Adv. 18:403-423.
Salmones D, Mata G, Waliszewski KN (2005). Comparative culturing of *Pleurotus spp.* on coffee pulp and wheat straw: biomass production and substrate biodegradation. Bioresour. Technol. 96(5):537-544.
Sanchez C (2009). Lignocellulosic residues: Biodegradation and bioconversion by fungi. Biotechnol. Adv. 27:185-194.
Schell DJ, Ruth MF, Tucker MP (1999). Modeling the enzymatic hydrolysis of dilute acid pretreated douglasfir. Appl. Biochem. Biotechnol. 77-79:67-81.
Siddhant, Swapanil Y, Aquil A, Singh CS (2013). Effect of wheat straw components on the yield of Pleurotus eous. Int. J. Curr. Microbiol. Appl. Sci. 2(8):221-225.
Singh A, Sharma S (2002). Composting of a crop residue through treatment with microorganisms and subsequent vermicomposting. Bioresour. Technol. 85:107-111.
Singh R, Varma AJ, Laxman RS, Rao M (2009). Hydrolysis of cellulose derived from steam exploded bagasse by *Penicillium* cellulases: comparison with commercial cellulase. Bioresour. Technol. 100:6679-6681.
Soccol CR, Vandenberghe LPS (2003). Overview of applied solid-state fermentation in Brazil. Biochem. Eng. J. 13: 205-218.
Stamets P (2000). Chapter 21: Growth Parameters for Gourmet and Medicinal Mushroom Species". Growing gourmet and medicinal mushrooms (3rd ed.). Berkeley, California, USA: Ten Speed Press. pp. 316-320. ISBN 978-1-58008-175-177.
Suzuki MR, Hunt CG, Houtman CJ, Dalebroux ZD, Hammel KE (2006). Fungal hydroquinones contribute to brown rot of wood. Environ. Microbiol. 8:2214-2223.
Taherzadeh MJ, Karimi K (2008). Pretreatment of lignocellulosic wastes to improve ethanol and biogas production: a review. Int. J. Mol. Sci. 9:1621-1651.
Thampi SC, Wani PV, Bachchhav MB, Sawant DM (1996). Studies on Different *Pleurotus* Species: Spawn Production and Morphological Features. Nat. Symp. On Integrated Disease Manag. Indian Soc. Plant Pathol. Rahuri, India. pp. 53-54.
Theradi M (1992). Cultivation of *Pleurotus* and *Volvariella* on coconut waste in India. Mushroom Res. 27-31.
Thomas GV, Prabhu SR, Reeny MZ, Bopaiah BM (1998). Evaluation of lignocellulosic biomass from coconut palm as substrate for cultivation of *Pleurotus sajor-caju* (Fr.) Singer. World J. Microbiol. Biotechnol. 14: 879-882.
Thurston CF (1994). The structure and function of fungal laccases. Microbiol (UK) 140: 19-26.
Torget R, Hsu TA (1994). Two temperature dilute-acid prehydrolysis of hardwood xylan using a percolation process. Appl. Biochem. Biotechnol. 45-46: 5-22.
Vázquez M, Oliva M, Téllez-Luis SJ, Ramírez JA (2007). Hydrolysis of sorghum straw using phosphoric acid: evaluation of furfural production. Bioresour. Technol. 98: 3053-3060.
Vercoe D, Stack K, Blackman A, Richardson D (2005). A study of the interactions leading to wood pitch deposition. In 59th Appita annual conference and exhibition: Incorporating the 13th ISWFPC (international symposium on wood, fibre and pulping chemistry), Auckland, New Zealand, 16-19: Proceedings. p. 123.
Vilgalys R, Moncalvo JM, Liou SR, Volovcek M (1996). Recent advances in molecular systematics of the genus *Pleurotus*. In Mushroom Biology and Mushroom Products, Edited by D. J. Royse. Penn State: Penn State University. pp. 91-102.
Vilgalys R, Smith A, Sun BL, Miller OK (1993). Intersterility groups in the *Pleurotus ostreatus* complex from the continental United States and adjacent Canada. Can. J. Bot. 71: 113-128.
Villas-Boas SG, Esposito E, Mitchell DA (2002). Microbial conversion of lignocellulosic residues for production of animal feeds. Anim. Feed Sci. Technol. 98: (1-2):1-12.
Wang L, Yan W, Chen J, Huang F, Gao P (2008). Function of the iron-binding chelator produced by *Coriolus versicolor* in lignin biodegradation. Sci. China. C. Life Sci. 51: 214-221.
Wang W, Huang F, Mei Lu X, Ji Gao P (2006). Lignin degradation by a novel peptide, Gt factor, frombrown rot fungus Gloeophyllum trabeum. Biotechnol. J. 1: 447-453.
Wesenberg D, Kyriakides I, Agathos SN (2003). White-rot fungi and their enzymes for the treatment of industrial dye effluents. Biotechnol. Adv. 22: 161-187.
Wong DW (2009). Structure and action mechanism of ligninolytic enzymes. Appl. Biochem. Biotechnol. 157: 174-209.
Wyman CE, Dale BE, Elander RT, Holtzapple M, Ladisch MR, Lee YY (2005). Coordinated development of leading biomass pretreatment technologies. Bioresour. Technol. 96: 1959-1966.
Zadrazil F, Dube HC (1992). The Oyster mushroom. Importance and prospects. Mushroom Res. 1: 25-32.
Zervakis G, Labarer J (1992). Taxonomic relationships within the fungal genus *Pleurotus* as determined by isoelectric focusing analysis of enzyme patterns. J. Gen. Microbiol. 138: 635-645
Zhang R, Li X, Fadel JG (2002). Oyster mushroom cultivation with rice and wheat straw. Bioresour. Technol. 82: 277-284.