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Industrial and biotechnological applications of ligninolytic enzymes of the basidiomycota: A review

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Abstract Ligninolytic enzymes of the basidiomycetes play a crucial role in the global carbon cycle. The demand for application of ligninolytic enzymes complexes of white-rot fungi in industry and biotechnology is ever increasing due to their use in a variety of processes. Ligninolytic enzymes have potential applications in a large number of fields, including the chemical, fuel, food, agricultural, paper, textile, cosmetic industrial sectors and more. This ligninolytic system of white-rot fungi is also directly involved in the degradation of various xenobiotic compounds and dyes. Their capacities to remove xenobiotic substances and produce polymeric products make them a useful tool for bioremediation purposes. This paper reviews the applications of ligninolytic enzymes of basidiomycetes within different industrial and biotechnological area.

Keywords: laccase, lignin peroxidase, manganese peroxidase, white-rot fungi

INTRODUCTION

Basidiomycetes species are considered to be a very interesting group of fungi given their exceptional adjustment abilities to accommodate detrimental conditions of the environment where they continue to act as natural lignocellulose destroyers and include very different ecological groups such as white rot, brown rot, and leaf litter fungi (Cho et al. 2009). Lignin is the most abundant natural aromatic polymer on earth and degradation of this recalcitrant aromatic polymer is caused in nature by white rot fungi through a process that was defined as an enzymatic combustion (Kirk and Farrell, 1987). The ligninolytic system is an extracellular enzymatic complex that includes peroxidases, laccases and oxidases responsible for the production of extracellular hydrogen peroxide (H_2O_2) (Ruiz-Dueñas and Martinez, 2009). Those enzyme systems exhibit differential characteristics depending on the species, strains and culture conditions (Kirk and Farrell, 1987). The fungi absorb nutrients available in the ambient when the molecules are small, and when they are bigger the fungi uses their enzymes (Esposito and de Azevedo, 2004). The enzymes responsible for lignin degradation are mainly: lignin peroxidase (LiP), manganese peroxidase (MnP) and a copper containing phenoloxidase, known as laccase (Table 1). The potential application of ligninolytic enzymes in biotechnology has stimuled their investigation (Vikineswary et al. 2006) and the understanding of physiological mechanisms regulating enzyme synthesis in lignocellulose bioconversion could be useful for improving the technological process of edible and medicinal mushroom production (Songulashvili et al. 2007). Ligninolytic enzymes have a potential in several industrial and biotechnological processes (Figure 1) within a wide variety of organic and inorganic specific substrates (Esposito and de Azevedo, 2004; Rodríguez and Toca, 2006). Consequently, the aim of this review is to highlight the potential industrial and biotechnological applications of ligninolytic enzymes.

GENERAL FEATURES (CLASSIFICATION, DISTRIBUTION, STRUCTURE AND MODE OF ACTION)

Laccases (benzenediol: oxygen oxidoreductase EC 1.10.3.2) belong to multicopper oxidase family (Hoegger et al. 2006; Alcalde, 2007). These copper-containing enzymes catalyze the oxidation of various substrates with the simultaneous reduction of molecular oxygen to water (Yaropolov et al. 1994). Yoshida first discovered laccases in 1883 after observing that latex from the Japanese lacquer tree (*Rhus vernicifera*) hardened in the presence of air (Call and Mücke, 1997; Gianfreda et al. 1999). Since then, laccase activity has been found in other plants, some insects, and few bacteria (Kramer et al. 2001; Claus, 2003; Claus, 2004; Dittmer et al. 2004). However, most laccases were reported from fungal organisms and most biotechnologically useful laccases are also of fungi origin (Kalmiş et al. 2008). Probably the first report on the presence of laccase in fungi was from Laborde in 1897 (Mayer and Harel, 1979). Over 60 fungal strains belonging to the phyla Ascomycota, Zygomycota and especially Basidiomycota show laccase activities (Kiiskinen et al. 2004; Baldrian, 2006). The catalytic site of laccase is quite conserved among different species of fungi, but the rest of the enzyme structure shows high diversity (Gochev and Krastanov, 2007). Fungal laccases are mostly inducible, extracellular, monomeric glycoproteins with carbohydrate contents of 10-20% which may contribute to the high stability of laccases (Mayer and Staples, 2002). The amino acid chain contains about 520-550 aminoacids including a N-terminal secretion peptide (Gianfreda et al. 1999). Laccases are multinuclear enzymes (Gayazov and Rodakiewicz-Nowak, 1996; Heinzkill et al. 1998; Bertrand et al. 2002; Piontek et al. 2002). The active site of laccase comprises four copper atoms in three groups, referred to as T1, T2 and T3 (Yaropolov et al. 1994; Solomon et al. 1996). Copper atoms differ from each other in their paramagnetic resonance (EPR) signals (Gianfreda et al. 1999). The T1 copper is responsible for the blue colour of the enzyme and has a characteristic absorbance around 610 nm. The T2 copper is colourless and cannot be detected spectrophotometrically, but EPR detectable (Solomon et al. 1996; Leontievsky et al. 1997; Koroljova-Skorobogat'ko et al. 1998). The bi-nuclear T3 copper is diamagnetic. It displays a spectral absorbance shoulder in the region of 330 nm and also displays a characteristic

Table 1. Ligninolytic enzymes produced by white rot fungi.

Enzyme	EC No	Catalyzed reactions	Fungi	References
Laccase	1.10.3.2	Phenol oxidation	*Trametes versicolor*	Yaropolov et al. 1994
Lignin peroxidase	1.11.1.14	Phenol polymerization	*Phanerochaete chrysosporium*	Gold and Alic, 1993 Haglund, 1999 Piontek et al. 2001 Erden et al. 2009
Manganese peroxidase	1.11.1.13	Phenol oxidation; Oxidize Mn^{2+} to Mn^{3+}	*Phanerochaete chrysosporium*	Hofrichter, 2002
Cellobiose-quinone oxireductase	1.1.5.1	Quinone reduction; Celobiose degradation	*Phanerochaete chrysosporium*	Soares, 1998
Aryl alcohol oxidase	1.1.3.7	H_2O_2 production	*Pleurotus sabor-caju*	Martínez et al. 2009
Glyoxal oxidase	1.2.3.5	H_2O_2 production	*Phanerochaete chrysosporium*	Martínez et al. 2009
Manganese independent peroxidase	1.11.1.7	Activity on aromatic substrates	*Phanerochaete chrysosporium*	Wyatt and Broda, 1995 Ruiz-Dueñas and Martínez, 2009
Versatile peroxidase	1.11.1.16	Oxidizes Mn^{2+}; High redox-potential aromatic compouds	*Pleurotus sp.*	Ruiz-Dueñas et al. 2009
Cellobiose dehydrogenase	1.1.99.18	Lignin degradation; Unite the hydrolytic and oxidative systems; Dispose manganese (MnII) for MnP through precipitate reduction from manganese oxide (MnO_2)	*Phanerochaete chrysosporium*	Henriksson et al. 2000a Henriksson et al. 2000b Kersten and Cullen, 2007 Carvalho et al. 2009

fluorescence spectrum (Shin and Lee, 2000). The yellow laccase had no blue maxima in the absorption spectrum. The yellow laccase was suggested to be formed as a result of blue laccase modification by products of lignin degradation, which might play a role as natural electron-transfer mediators for the oxidation of non-phenolic substances (Higuchi, 2004). Almost all fungi that have been examined produce more than one isoform of laccase (Hoshida et al. 2001). Laccases are usually the first ligninolytic enzymes secreted to the surrounding media by the fungus that normally oxidizes only those lignin model compounds with a free phenolic group, forming phenoxy radicals as the mediators that are a group of low molecular-weight organic compounds. Many artificial mediators have been studied, being ABTS [2.2-azino-bis-(3-ethylbenzothiazoline-6-sulphonic acid)] the first described laccase mediator (Bourbonnais and Paice, 1990; Call and Mücke, 1997). There are natural compounds acting as mediator in laccase oxidation such p-hydroxycinnamic acids (Gianfreda et al. 1999; Moreira Neto, 2006; Gochev and Krastanov, 2007; Camarero et al. 2008).

Lignin peroxidases (EC 1.11.1.14) belong to the family of oxidoreductases (Higuchi, 2004; Martínez et al. 2005; Hammel and Cullen, 2008). Lignin peroxidases (LiPs) were first described in the basidiomycete *Phanerochaete chrysosporium* Burdsall (order Corticiales) in 1983 (Glenn et al. 1983; Tien and Kirk, 1988). This enzyme has been recorded for several species of white-rot basidiomycetes (Buswell et al. 1987; Kirk and Farrell, 1987; Pointing et al. 2005) and in actinomycetes (Périé and Gold, 1991; Périé et al. 1996; Niladevi and Prema, 2005). LiP is an extracellular hemeprotein, dependent of H_2O_2, with an unusually high redox potential and low optimum pH (Gold and Alic, 1993; Haglund, 1999; Piontek et al. 2001; Erden et al. 2009). LiP is capable of oxidizing a variety of reducing substrates including polymeric substrates (Oyadomari et al. 2003). Due to their high redox potentials and their enlarged substrate range LiPs have great potential for application in various industrial processes (Erden et al. 2009). LiP shows little substrate specificity, reacting with a wide variety of lignin model compounds and even unrelated molecules (Barr and Aust, 1994). It has the distinction of being able to oxidise methoxylated aromatic rings without a free phenolic group, generating cation radicals that can react further by a variety of pathways, including ring opening, demethylation, and phenol dimerisation (Haglund, 1999). LiP in contrast with laccases does not require mediators to degrade high redox-potencial compounds but it needs hydrogen peroxide to initiate the catalysis.

Manganese peroxidases (EC 1.11.1.13) belong to the family of oxidoreductases (Higuchi, 2004; Martínez et al. 2005; Hammel and Cullen, 2008). Following the discovery of LiP in *Phanerochaete chrysosporium*, Manganese peroxidase (MnP) secreted from the same fungus was found as another lignin degrading enzyme (Glenn and Gold, 1985; Paszczyński et al. 1985), and subsequent investigations have shown that MnP is distributed in almost all white-rot fungi (Hofrichter, 2002). Manganese peroxidases (MnP) seem to be more widespread among white rot fungi than lignin peroxidase (Hammel and Cullen, 2008). Manganese peroxidase (MnP) oxides Mn^{2+} to Mn^{3+}, which oxides phenolic structures to phenoxyl radicals (Hofrichter, 2002). The product Mn^{3+} is highly reactive and complex with chelating organic acid, as oxalate or malate, which are produced by the fungus (Kishi et al. 1994; Galkin et al. 1998; Mäkëla et al. 2002). The redox potential of the Mn peroxidase system is lower than that of lignin peroxidase and it has shown capacity for preferable oxidize *in vitro* phenolic substrates. On the other hand, studies indicate that contrary to LiP, MnP may oxidize Mn(II) without H_2O_2 with decomposition of acids, and concomitant production of peroxyl radicals that may affect lignin structure (Hofrichter et al. 1999). Due to their Mn-oxidizing activity, the *Pleurotus* Versatile peroxidase

Table 2. Biological functions of ligninolytic enzymes.

Enzyme	Applications	References
Laccase	Spore resistance Rhizomorph formation Pathogenesis Fruit bodies formation Pigments synthesis Lignin degradation	Mayer and Staples, 2002; Claus, 2004; Minussi et al. 2007
Lignin Peroxidase	Biodegradation of lignin Defense of fungi against pathogens	Score et al. 1997; Piontek et al. 2001; Trejo-Hernandez et al. 2001
Manganese Peroxidase	Degradation of lignin Interespecific fungal interactions	Score et al. 1997; Trejo-Hernandez et al. 2001

(VP) enzymes were first described as MnP enzymes, but they were later recognized as representing a new peroxidase type. VP is also able to efficiently oxidize phenolic compounds and dyes that are the substrates of generic peroxidases and related peroxidases, or the well-known horse-radish peroxidase (HRP). Versatile Peroxidase (EC 1.11.1.16) oxidizes Mn^{2+}, as MnP does, and also high redox potential aromatic compounds, as LiP does. The interest on VP has increased during the last years, both as a model enzyme and as a source of industrial/environmental biocatalysts (Martínez et al. 2005; Martínez et al. 2009; Ruiz-Dueñas et al. 2009).

BIOLOGICAL FUNCTIONS OF LIGNINOLYTIC ENZYMES

The enzymes are used for the degradation of many compounds, and it's used for biological functions too, having many functions in the fungi organism, as shown in Table 2.

POTENTIAL INDUSTRY AND BIOTECHNOLOGICAL APPLICATIONS OF LIGNINOLYTIC ENZYMES

Food Industry

Laccases can be applied to certain processes that enhance or modify the colour appearance of food or beverage for the elimination of undesirable phenolics, responsible for the browning, haze formation and turbidity in clear fruit juice, beer and wine (Rodríguez and Toca, 2006). Laccase is also employed to ascorbic acid determination, sugar beet pectin gelation, baking and in the treatment of olive mill wastewater (Ghindilis, 2000; Minussi et al. 2002; Rodríguez and Toca, 2006; Selinheimo et al. 2006; Minussi et al. 2007). And lignin peroxidase (LiP) and manganese peroxidase (MnP) have potential to produce natural aromatic flavours (Lesage-Meessen et al. 1996; Lomascolo et al. 1999; Zorn et al. 2003; Barbosa et al. 2008).

Pulp and paper industry

Laccases are able to depolymerize lignin and delignify wood pulps, kraft pulp fibers and chlorine-free in the biopolpation process (Bourbonnais et al. 1997; Lund and Ragauskas, 2001; Chandra and Ragauskas, 2002; Camarero et al. 2004; Rodríguez and Toca, 2006; Vikineswary et al. 2006). One of the most studied applications in the industry is the laccases-mediator bleaching of kraft pulp and the efficiency of which has been proven in mill-scale trials (Strebotnik and Hammel, 2000). This ability could be used in the future to attach chemically versatile compounds in the fiber surfaces and let recycled pulp for new use (Rodríguez and Toca, 2006; Mocchiutti et al. 2005; Saparrat et al. 2008; Widsten and Kandelbauer, 2008). Lignin peroxidases (LiP) compared with laccase, are the biocatalysts of choice for bleaching (Bajpai, 2004; Sigoillot et al. 2005). LiP and MnP were reported to be effective in decolourizing kraft pulp mill effluents (Ferrer et al. 1991; Michel et al. 1991; Moreira et al. 2003). In laboratory scale the consumption of refining energy in mechanical pulping was reduced with MnP pretreatment with a slight improvement in pulp properties (Kurek et al. 2001; Wasenberg et al. 2003; Maijala et al. 2007).

Textile industry

Laccases-mediator system finds potential application in enzymatic modification of dye bleaching in the textile and dyes industries (Abadulla et al. 2000; Kunamneni et al. 2008). Most currently existing processes to treat dye wastewater are ineffective and not economical (Mc Kay, 1979; Cooper, 1993; Riu et al. 1998; Rodríguez and Toca, 2006). Therefore, the development of processes based on laccases seems an atractive solution due their potential in degrading dyes of diverse chemical structure (Abadulla et al. 2000; Blanquez et al. 2004; Hou et al. 2004; Rodríguez and Toca, 2006) including synthetic dyes currently employed in the industry (Wong and Yu, 1999; Rodríguez et al. 2005; Rodríguez and Toca, 2006; Kunamneni et al. 2008). Lignin peroxidases (LiP) were evaluated by decolorizing different synthetic dyes too (Cripps et al. 1990; Pointing, 2001; Robles-Hernández et al. 2008; Gomes et al. 2009). And MnP can biodegrade dyes, as well as decolorize various types of synthetic dyes in aqueous cultures and packed-bed bioreactors (Kasinath et al. 2003; Shin, 2004; Champagne and Ramsay, 2005).

Table 3. Enzymes applications in different sectors.

Food Industry		
Laccase	Phenolic remotion from the food and beverage Ascorbic acid determination Sugar beet pectin gelation	Ghindilis, 2000; Minussi et al. 2002; Rodríguez and Toca, 2006; Selinheimo et al. 2006; Minussi et al. 2007
Lignin peroxidase	Source of natural aromatics Production of vanillin	Lesage-Meessen et al. 1996; Lomascolo et al. 1999; Barbosa et al. 2008
Manganese peroxidase	Production of natural aromatic flavours	Lomascolo et al. 1999; Zorn et al. 2003; Barbosa et al. 2008
Pulp and paper industry		
Laccase	Depolymerization of lignin Delignify wood pulps Bleaching of kraft pulps	Bourbonnais et al. 1997; Strebotnik and Hammel, 2000; Lund and Ragauskas, 2001; Chandra and Ragauskas, 2002; Camarero et al. 2004; Rodríguez and Toca, 2006; Vikineswary et al. 2006; Widsten and Kandelbauer, 2008
Lignin peroxidase	Decolouriment of kraft pulp Mill effluents	Ferrer et al. 1991; Bajpai, 2004; Sigoillot et al. 2005
Manganese peroxidase	Kraft pulp bleaching	Michel et al. 1991; Kurek et al. 2001; Moreira et al. 2003; Wasenberg et al. 2003; Maijala et al. 2007
Textile industry		
Laccase Lignin peroxidase Manganese peroxidase	Textile dye degradation and bleaching	Mc Kay, 1979; Cripps et al. 1990; Cooper, 1993; Riu et al. 1998; Wong and Yu, 1999; Abadulla et al. 2000; Pointing, 2001; Kasinath et al. 2003; Blanquez et al. 2004; Hou et al. 2004; Shin, 2004; Champagne and Ramsay, 2005; Rodríguez et al. 2005; Rodríguez and Toca, 2006; Kunamneni et al. 2008; Robles-Hernández et al. 2008; Gomes et al. 2009
Bioremediation		
Laccase	Biodegradation of xenobiotics Polycyclic aromatic hydrocarbons(PAHs)degradation	Pointing, 2001; Bamforth and Singleton, 2005; Rodríguez and Toca, 2006; Anastasi et al. 2009
Lignin peroxidase	Degradation of azo, heterocyclic, reactive and polymeric dyes Mineralizationof environmental contaminants Xenobiotic and pesticides degradation	Bumpus and Aust, 1987; Abraham et al. 2002; Ohtsubo et al. 2004; Robles-Hernández et al. 2008; Gomes et al. 2009; Wen et al. 2009
Manganese peroxidase	PAH’s degradation Synthetic dyes Bleach from paper producing plants DDT, PCB, TNT	Köller et al. 2000; Robles-Hernández et al. 2008
Organic synthesis, Medical, Pharmaceutical, Cosmetics and Nanotechnology Applications		
Laccase	Polymers production Coupling of phenols and steroids Medical agents Carbon-nitrogen bonds construction Complex natural products synthesis Personal higienic products Biosensors and bioreporters	Milstein et al. 1989; Bauer et al. 1999; Xu, 1999; Durán and Esposito, 2000; Ghindilis, 2000; Baminger et al. 2001; D’Souza, 2001; Fabbrini et al. 2001; Kuznetsov et al. 2001; D’Acunzo et al. 2002; Mayer and Staples, 2002; Mikolasch et al. 2002; Stahl et al. 2002; Akta and Tanyolac, 2003; Baiocco et al. 2003; Barilli et al. 2004; Heller, 2004; Nicotra et al. 2004; Xu, 2005; Rodríguez and Toca, 2006; Kunamneni et al. 2008; Mikolasch and Schauer, 2009; Ponzoni et al. 2007

Lignin peroxidase	Functional compounds synthesis Cosmetics and dermatological for skin Bioelectro-catalytic activity at atomic resolution	Christenson et al. 2004; Higuchi, 2004; Belinky et al. 2005; Barbosa et al. 2008
Manganese peroxidase	Acrylamide polymerization Polymer styrene degradation Direct electron transfer (DET)	Soto et al. 1991; Iwahara et al. 2000; Ferapontova et al. 2005; Lee et al. 2006

Bioremediation

Laccases are involved in green biodegradation due its catalytic properties. The xenobiotic compound is a major source of contamination in soil and laccase degrade it (Rodríguez and Toca, 2006). Moreover, polycyclic aromatic hydrocarbons (PAHs), which arise from natural oil deposits and utilisation of fossil fuels, are also degraded by laccases (Pointing, 2001; Anastasi et al. 2009). Many PAHs have been found in exhibit cytotoxic, mutagenic and carcinogenic properties that represents serious risk to human health (Bamforth and Singleton, 2005). Lignin peroxidases (LiP) present a non specific biocatalyst mechanism. MnP showed that mineralization of many environmental contaminants are used for bioremediation process. Due to their ability to degrade azo, heterocyclic, reactive and polymeric dyes, it degrades 1.1.1-trichloro-2.2-bis-(4-chlorophenyl) ethane (DDT), 2.4.6-trinitrotoluene (TNT) and polycyclic aromatic hydrocarbons (PAH's) too (Köller et al. 2000; Abraham et al. 2002; Ohtsubo et al. 2004; Robles-Hernández et al. 2008; Gomes et al. 2009; Wen et al. 2009). LiP from *P. chrysosporium* was one of the first enzymes of basidiomycete capable for PAH degradation (Bumpus and Aust, 1987).

Organic, medical, pharmaceutical, cosmetic and nanotechnology applications

Recently, increasing interest has been focused on the application of laccase as a new biocatalyst in organic synthesis (Milstein et al. 1989; Mayer and Staples, 2002) (Table 3). Enzymatic polymerization using laccase has drawn considerable attention since laccase or laccase-mediator system (LMS) are capable of generating straightforwardly polymers that are impossible to produce through conventional chemical synthesis (Akta and Tanyolac, 2003). Laccases have been employed for several applications in organic synthesis as the oxidation of functional groups, the coupling of phenols and steroids, medical agents (anesthetics, anti-inflammatory, antibiotics and sedatives), the construction of carbon-nitrogen bonds and in synthesis of complex natural products and industries of cosmetics (Baminger et al. 2001; Fabbrini et al. 2001; D'Acunzo et al. 2002; Mikolasch et al. 2002; Baiocco et al. 2003; Barilli et al. 2004; Nicotra et al. 2004; Xu, 2005; Rodríguez and Toca, 2006; Ponzoni et al. 2007; Mikolasch and Schauer, 2009).

A new enzymatic method based on laccase was developed to distinguish simultaneously morphine and codeine in drug samples injected into a flow detection system (Bauer et al. 1999). Laccases also can be applied as biosensors or bioreporters (Bauer et al. 1999; Xu, 1999; Durán and Esposito, 2000; Ghindilis, 2000; D'Souza, 2001; Kuznetsov et al. 2001; Kunamneni et al. 2008; Szamocki, et al. 2009). Laccases still could be immobilized on the cathode of biofuel cells that could provide for small transmitter systems (Ghindilis, 2000) and laccase-based miniature biological fuel cell is of particular interest for many medical applications calling for a power source implanted in a human body (Rodríguez and Toca, 2006; Heller, 2004).

Lignin peroxidase (LiP) exhibit highest bioelectro-catalytic activity at atomic resolution and this makes available for commercial development of biosensors for polymeric phenol or lignin (Christenson et al. 2004) (Table 3). In the future LiP may be of great interest in synthetic chemistry, where they have been proposed to be applicable for production of cosmetic and dermatological preparations for skin (Belinky et al. 2005).

Manganese peroxidase (MnP) produced by the basidiomycete *Bjerkandera adusta* was used for acrylamide polymerization (Iwahara et al. 2000). MnP from *Phanerochaete chrysosporium* can degrade styrene that is an important industrial polymer used as a raw material for wrapping and transporting goods, it has polluted water, air and soil (Soto et al. 1991; Lee et al. 2006). MnP is also a redox enzyme with efficient direct electron transfer (DET) properties with electrodes. It is enabled to use for many applications such the development of biosensors based on DET, effective biofuel cells, and selective bioorganic synthesis (Ferapontova et al. 2005) (Table 3).

CONCLUDING REMARKS

Ligninolytic enzymes are involved in the degradation of the complex and recalcitrant polymer lignin. This group of enzymes is highly versatile in nature and they find application in a wide variety of industries. The biotechnological significance of these enzymes has led to a drastic increase in the demand for these enzymes in the recent time. Ligninolytic enzymes are promising to replace the conventional chemical processes of several industries. Thus, there is a broad field of investigation that is almost entirely open to new findings and it is quite reasonable to propose that many new applications will be found in the near future.

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