Ligninolytic Fungi from the Indian Subcontinent and Their Contribution to Enzyme Biotechnology

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Abstract

Lignin is the most abundant polyphenolic aromatic biopolymer on Earth, which is extremely recalcitrant toward biodegradation, owing to its heterogeneous structure and biochemical composition. Extensive research efforts have been made to understand the polymeric structure of lignin in a better way and develop a simple, cost-competitive, and eco-friendly method for its degradation. Over the past few years, wood-rotting fungi, especially white-rot fungi have emerged as a crucial group of microorganism capable of mineralizing lignin biopolymers more efficiently. Such fungi have evolved to produce a unique set of extracellular oxidative enzymes in different combinations. Further, they also produce enzymes in multiple isoforms and isozymes that catalyze ligninolysis using radical mediated oxidative reactions. The major ligninolytic enzymes include laccase, manganese peroxidase, lignin peroxidase, and versatile peroxidase. The ligninolytic activities of these enzymes can be enhanced by various natural and/or chemical redox mediators as well as some other auxiliary enzymes (aryl-alcohol oxidase, glyoxal oxidase, quinone reductases, aryl-alcohol dehydrogenases, and feruloyl esterase) to facilitate lignin degradation process. These enzymes have attracted attention of several researchers due to their broad substrate specificity, which make them readily available for numerous biotechnological and industrial applications including paper and pulp industry, food-feed and beverage industry, biofuel industry, bioremediation of hazardous pollutants, and degradation of toxic textile dye effluents. In this chapter, we appraise different ligninolytic fungi from Indian subcontinent and the research findings by native microbiologists and

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biotechnologists on the fungal enzymatic systems. Finally, the biotechnological and industrial applications of ligninolytic fungi and their enzyme arsenals are also discussed.

Keywords

Lignin · Ligninolytic fungi · Ligninolytic enzymes · Laccase · Lignin peroxidase · Manganese peroxidase · Lignin degradation

6.1 Introduction

The term "lignin" was derived from the Latin root "lignum," which means wood (Wong et al. 2020). It represents the second-most abundant renewable biopolymer on this planet and one of the major components of plant cell wall, besides cellulose and hemicellulose (Wang et al. 2019; Tao et al. 2020). The lignin polymer comprises of random aromatic molecules with estimated global presence around 300×10^9 tons (Becker and Wittmann 2019). It has been estimated that around 20×10^9 tons of lignin are produced annually by natural lignification processes (Li and Takkellapati 2018; Tribot et al. 2019). Lignin is an essential backbone of plant cell wall comprising up to 15–40% of plant biomass (Zhu et al. 2020). The biological function of lignin is to provide structural integrity in plant cell wall and resistance against pathogens by preventing enzymatic hydrolysis of the structural polysaccharides (cellulose and hemicellulose) (Mutuku et al. 2019; Vaahtera et al. 2019). Structure-wise, lignin is an irregular three-dimensional heterogeneous biopolymer of highly cross-linked aromatic alcoholic precursors (monolignols), which includes coniferyl alcohol, *p*-coumaryl alcohol, and sinapyl alcohol (Sharma et al. 2007; Ponnusamy et al. 2019; Liao et al. 2020). The oxidative coupling of the monolignols results in the formation of lignin subunits, viz., *p*-hydroxyphenyl subunit (H), guaiacyl subunit (G), and syringyl subunit (S), respectively (Vanholme et al. 2019). Although these subunits share the common feature of having basic phenylpropanoid structure, they vary in the number of methoxy groups in their aromatic rings (Sun et al. 2018; Lu et al. 2020). The H subunit is characterized by non-substituted phenoxide moiety, while G and S units contain monomethoxy phenoxide and dimethoxy phenoxide, respectively (Rinaldi et al. 2016; Gillet et al. 2017). Moreover, the ratio of these phenolic subunits varies among interspecies, as well as within the tissues of the same plant (Campbell and Sederoff 1996; Barros et al. 2015). Generally, softwood lignin is predominantly composed of G subunits (up to 90%), whereas lignin in Gramineae or Poaceae family roughly contains equal quantities of G, S, and H subunits (Lourenço and Pereira 2017). It has been shown that lignin from hardwood constitutes equimolar mixture of G and S unit, along with a small amount of H unit (Gellerstedt and Henriksson 2008; Sharma et al. 2020b). Numerous structural studies have shown that the highly cross-linked lignin structure is predominantly stabilized by various biological strong ether or ester linkages including β-aryl ether (β-*O*-4), β-β, β-5, 5–5, 5-*O*-4, and β-1 couplings (Giummarella

et al. 2019). Among these, β-*O*-4 bonds are the most frequent linkages formed during lignifications and may account for 50% and 80% in softwood and hardwood, respectively (Anderson et al. 2019; Zhu et al. 2019).

Not surprisingly, lignin is the most rebellious and recalcitrant structure among the lignocellulosic tissues; it resists biochemical degradation and valorization (Renders et al. 2017). The high structural complexity of lignin demands multiple biochemical reactions to achieve its efficient degradation that may occur simultaneously (Chio et al. 2019). These biochemical reactions include phenol oxidation, demethylations, hydroxylation of benzylic methylene groups, fission of inter-monomeric linkages, oxidation of benzyl alcohols to the corresponding aldehydes or ketones, side-chain modifications, and cleavage of the aromatic ring (Sun et al. 2018), followed by the breakdown of complex aliphatic metabolites (Mobley et al. 2018). Generally, one of the most efficient ways of lignin valorization is the use of chemical and/or biological treatment (Cao et al. 2018). However, in comparison to biological treatment, the chemical tricks of lignin valorization demands high energy input and chemical agents, thereby significantly increasing the capital cost and causing environmental damage (Chen and Wan 2017). In this scenario, there is an increasing research interest in biological treatments employing natural lignin degraders, including both ligninolytic microorganisms and their enzymatic system, to break down the lignin polymers (Janusz et al. 2017). Under favorable conditions, the lignin biodegradation process is accomplished in two concomitant stages: (1) depolymerization of intact lignin polymer and (2) mineralization of the heterogeneous aromatics unit (Ruiz-Dueñas and Martínez 2009). A wide range of literature supports the efficient degradation of native lignin by fungal cultures, whereas some reports have shown the lignin degradation with bacterial cultures but with less efficiency (Bugg et al. 2011; de Gonzalo et al. 2016; Xu et al. 2018). Lignin is a macromolecule having high molecular weight (more than 100 kDa), which is hard to be assimilated and depolymerized inside the microbial cell; thus, the biological degradation is only possible by the action of extracellular ligninolytic enzymes (Tolbert et al. 2014). Generally, ligninolytic enzymes are divided into two major groups, namely, lignin-degrading accessory enzymes and lignin-modifying enzymes (Hatakka 1994; Wong 2009). The unique ability of these oxidative enzymes to use various phenolic and non-phenolic components of lignin as a substrate in the enzymatic reactions is also exploited in several biotechnological applications (Eriksson 2000; Sharma and Kuhad 2008). A considerable volume of literature is present on various biotechnological and commercial applications of ligninolytic fungi and their enzymatic systems including fuel (Saini et al. 2020b), agriculture, cosmetic and pharmaceuticals (Mohit et al. 2020), food and feed (Sharma et al. 2012), brewery and wine (Ghosh and Ghosh 2019), textiles and laundry (Manoharachary et al. 2005; Singh et al. 2014a, b), and pulp and paper (Dwivedi et al. 2009) as well as in research and development (Fig. 6.1). However, a cumulative study emphasizing detailed mechanisms and various applications of ligninolytic fungi and their ligninolytic machinery in Indian perspective is still scanty (Kuhad et al. 2007; Kuhar et al. 2007). Therefore, this book chapter aims to shed light on the diversity of ligninolytic fungi in the Indian subcontinent and the occurrence of several lignin degrading

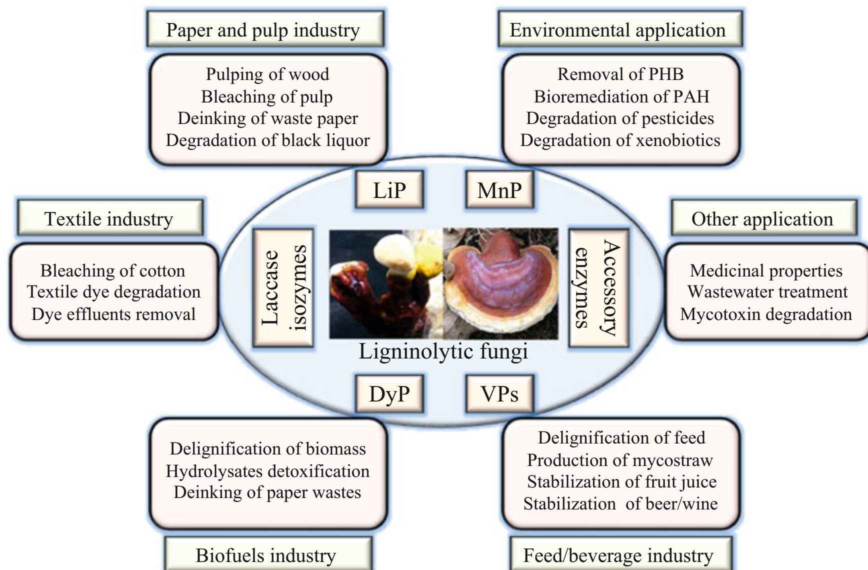

Fig. 6.1 An overview of biotechnological and industrial applications of ligninolytic fungi and their enzymatic system

enzymes. Further, the biotechnological applications of various ligninolytic enzymes are also discussed.

6.2 Lignin-Degrading Fungi

Lignin is the main component of the middle lamella and widely distributed among the secondary walls of the vascular plants (Barros et al. 2015). The mode of polymerization makes it optically inactive, amorphous, and insoluble in water, which is hard for microbes to penetrate and degrade it (Chen et al. 2012). However, in due course of evolution, several microorganisms including bacteria, actinobacteria, and fungi have evolved and adapted to oxidize and utilize lignin as a complex carbon source for their survival and cellular metabolism (de Souza 2013). Due to the unique lignin-degrading property, ligninolytic microorganisms are collected and identified, and a few have been intensively studied by several researchers in India (Sharma et al. 2005; Kuhar et al. 2007; Kumar et al. 2015a, b, 2019; Rudakiya and Gupte 2019). The exact mechanism by which lignin is degraded by microorganisms is still not yet unequivocally understood, but significant recent advances have been made to gain insight into their genomes incorporating modern-omics techniques (Sharma 2016; Shankar et al. 2019; Jain et al. 2019). The ability of microbes to disintegrate lignin polymers efficiently is thought to be attributed to their mycelial growth, which allows the organism to transport scarce

nutrients (Joutey et al. 2013). Over 100 species of the bacteria have been identified possessing the ability of lignin degradation but generally cause limited fraction and much slower degradation in comparison to ligninolytic fungi (Sharma and Kuhad 2009; Datta et al. 2017).

More than a million species of fungi are known to possess the lignin-degrading ability, majorly belonging to the phylum Basidiomycota and Ascomycota (Sigoillot et al. 2012). Further, they are grouped into brown-rot, soft-rot, and white-rot fungi according to the characteristics of the wood residues and degraded lignin (Kapoor et al. 2005; Kuhad et al. 2007). Soft-rot fungi generally cause incomplete and slow degradation of lignin and preferentially attack the hardwoods than softwoods (Hatakka and Hammel 2011). They belong to the largest division of the fungi, Ascomycota, and account for over 60% of all the fungi on Earth, but a few have been identified with lignin-degrading efficiency (Kang et al. 2019). It has been shown that some species of soft-rot fungi can dissolve the secondary cell wall of angiospermic wood and reduce the acid-insoluble Klason lignin content, eventually leading to the formation of microscopic pits and discoloration of wood (Shary et al. 2007). Previous studies revealed that soft-rot fungi can also catalyze the oxidative cleavage of Cα-Cβ and β-*O*-aryl linkages during lignin degradation (Kumar and Chandra 2020). A very few soft-rot fungi with lignin-degrading ability have been isolated from Indian continent, viz., *Lecythophora hoffmannii* (Bugos et al. 1988), *Chaetomium globosum* (Popescu et al. 2011), *Petrillidium boydii* (Kuhad et al. 2007), *Daldinia concentrica* (Nnagadesi and Arya 2015), and *Phialophora mutabilis* (Daniel and Nilsson 1988). On the other hand, brown-rot fungi selectively attack the conifers and cause limited lignin degradation, employing the action of nonspecific oxidants such as hydroxyl radicals (Arantes et al. 2012). Some species of brown-rot fungi are able to demethylate the aromatic and nonaromatic lignin moieties, consequently leading to ring splitting and chemical alteration in lignin structure (Venkatesagowda and Dekker 2020). Among the representatives of brown-rot lignin degraders of Indian origin, *Lentinus lepideus*, *Gloeophyllum trabeum*, *Fomitopsis pinicola*, *Pholiota adiposa*, *Poria placenta*, and *Tyromyces palustris* have been extensively studies (Goñi et al. 1993; Okeke et al. 1994; Wang et al. 2006). Unlike soft- and brown-rot fungi, white-rot fungi are the most intensively studied and are also the most efficient lignin-degrading fungi (Hatakka 1994; Kuhad et al. 2007; Kuhar et al. 2007). They predominately degrade lignin from deciduous trees, and also degrade some coniferous wood trees (Hastrup et al. 2012). The characteristic feature of white-rot fungi is the bleached appearance due to the large-scale degradation of lignin from the decomposed substrate (Eriksson et al. 1990; Kuhad et al. 2007). Further, they can be identified by their mode of lignin degradation and are grouped under two categories, namely, selective and nonselective delignifiers (Dashtban et al. 2010). The selective delignifiers predominantly degrade the lignin polymer and barely affect the structural carbohydrates of the wood material (Leonowicz et al. 1999), whereas the nonselective delignifiers synchronously degrade all the structural components of the attacked woody biomass (Janusz et al. 2017). More than 1000 species of lignin-degrading white-rot fungi have been recorded in the past few decades; further, the number is increasing due to

their various biotechnological and commercial applications (Maciel et al. 2010; Yadav and Yadav 2015). Numerous white-rot fungi have been isolated from different regions of India, for example, *Coriolus versicolor*, *Ceriporiopsis subvermispora*, *Coriolopsis caperata*, *Cyathus bulleri*, *Cyathus stercoreus*, *Daedalea flavida*, *Ganoderma austral*, *G. lucidum*, *Neurospora crassa* (discrete strains), *Pleurotus eryngii*, *Pleurotus florida*, *Pleurotus ostreatus*, *Phlebia brevispora*, *Phlebia radiata*, *Phlebia subserialis*, *Pycnoporus sanguineus*, *Pycnoporus cinnabarinus*, *Schizophyllum commune*, *Trametes ljubarskyi*, *Trametes hirsuta*, and *T. versicolor* (Sharma et al. 2005; Deswal et al. 2014; Sahu and Pramanik 2015; Kumar et al. 2015a, b, 2019; Meehnian and Jana 2016; Saha et al. 2016, 2017; Mustafa et al. 2016; Pamidipati and Ahmed 2017). Among these potent lignin degraders, *C. versicolor*, *T. versicolor*, *Phlebia radiata*, *Pleurotus* spp., and *Phanerochaete chrysosporium* have been extensively exploited for industrial applications worldwide and are presented as model organisms for studying lignin degradation and commercial applications, which are discussed in this book chapter. However, lignin degradation employing fungal cultures occurs at a slower pace, thus requiring a long incubation time (Schoenherr et al. 2017). Questions have been raised over industrial applications of fungal strains due to increased capital costs, owing to a very long degradation time (Madadi and Abbas 2017). To foil such challenges, crude or purified ligninolytic enzymes have been introduced as a versatile lignin degradation system in a relatively short incubation time (Mäkelä et al. 2017; Krumova et al. 2018; Kumar and Chandra 2020).

6.3 Lignin-Degrading Enzymes

Ligninolytic enzymes possess a critical role in the modification and degradation of lignin biopolymers (Kumar and Chandra 2020). Structural rigidity along with complex chemical composition of lignin mandates the ligninolytic microorganisms to produce an array of extracellular oxidative enzymes for efficient degradation (Kameshwar and Qin 2016; Ayeronfe et al. 2018). Broadly, these extracellular oxidative machineries, which include laccase (EC 1.10.3.2), lignin peroxidases (LiPs) [EC 1.11.1.14], manganese peroxidases (MnPs) [EC 1.11.1.13], and versatile peroxidases (VPs) [EC 1.11.1.16], play a direct role in the lignin modification and degradation (Krumova et al. 2018; Bilal and Iqbal 2020). Recently, a novel lignin-degrading peroxidase, namely, dye-decolorizing peroxidase (DyP) [EC 1.11.1.19], has been reported from several fungal cultures (Duan et al. 2018; Rajhans et al. 2020). In addition, several other ancillary enzymes have also been identified, such as glyoxal oxidases (EC 1.2.3.15) (Daou and Faulds 2017), feruloyl esterase (EC 3.1.1.73) (Andlar et al. 2018), alcohol oxidases (EC 1.1.3.13) (Carro et al. 2016), aryl-alcohol dehydrogenase (EC 1.1.1.90), and quinone reductase (EC 1.6.5.5), which enhance peroxidase activities and facilitate lignin degradation (Abdel-Hamid et al. 2013). Till date, numerous microbial communities including bacteria (de Gonzalo et al. 2016), fungi, and actinobacteria (Priya et al. 2018) have been reported for ligninolytic enzyme production (Kamimura et al. 2019). Among

these, white-rot fungi, having the ability to produce several different classes of oxidative enzymes, are always preferred for commercial scale production and applications (Mäkelä et al. 2017; Debnath and Saha 2020).

6.3.1 Laccases: The Leading Industrial Biocatalyst

Fungal laccases are glycosylated multicopper polyphenol oxidases that catalyze the degradation of lignin polymer through the reduction of oxygen molecule into water and concomitant oxidation of the aromatic and nonaromatic units (Tk et al. 1968; Thurston 1994; Sharma and Kuhad 2008). They are also known as benzenediol or blue multicopper oxidases or oxygen oxidoreductases or *p*-diphenol oxidases, which are superior to those of oxidoreductase class (Solomon et al. 1996). Yoshida was the pioneer in reporting laccase from the latex of Japanese lacquer tree *Rhus vernicifera* in 1883 (Yoshida 1883). Later, the presence of laccase was recorded in fungi by Laborde in 1897 (Maciel et al. 2010). Since then, laccase activity has been reported in higher plants, insects, few bacteria, and numerous fungal strains (Sharma et al. 2007; Sharma and Kuhad 2008, 2009; Senthivelan et al. 2016). Laccases are predominantly distributed in the wood-rotting basidiomycetes including *Cyathus stercoreus*, *Cerrena maxima*, *Daedalea flavida*, *Daedalea quercina*, *Pleurotus ostreatus*, *Pleurotus djamor*, *Lentinus squarrosulus*, *Lentinus tigrinus*, *Lentinula edodes*, *Pycnoporus cinnabarinus*, *Phlebia brevispora*, *Trametes villosa*, *T. versicolor*, *T. ochracea*, *Ganoderma lucidum*, *Trametes hirsuta*, *T. gallica*, *T. maxima*, and *T. ljubarskyi* (Arora and Rampal 2002, Sharma et al. 2005, Prasad et al. 2005, Patel et al. 2009, Dhakar and Pandey 2013, Kumar et al. 2015a, b, Singha and Panda 2015, Yadav 2018, Suman et al. 2018). However, some brown-rot fungi, such as *Postia placenta* (Yelle et al. 2011), *Fomitopsis* sp. (Nidadavolu et al. 2013), and *Coniophora puteana* (Shekher et al. 2011), and a few soft-rot fungi, including *Aspergillus nidulans* (Sahay et al. 2020), *Melanocarpus albomyces* (Pundir et al. 2016), *Neurospora crassa* (Chaurasia et al. 2013), *Trichoderma* spp. (Sadhasivam et al. 2010; Divya et al. 2014), *Fusarium* sp. (Chhaya and Gupte 2010), and *Penicillium chrysogenum* (Nayanashree and Thippeswamy 2015; Senthivelan et al. 2019), were also reported as potent laccase producer. The majority of laccases identified in wood-rotting fungi are extracellular glycoproteins; some reports have also reported intracellular laccase in different fungal cultures (Rigling and Alfen 1993; Nagai et al. 2003). Mostly, fungi secrete several isoforms of laccase having average molecular mass in the range between 38 and 150 kDa (Kumar et al. 2017b). These isoenzymes emerge from the same or different genes, and their number predominantly depends upon the source of enzyme (mycelia or fruiting body), species, and growth conditions (Kumar et al. 2017b, 2019; Jain et al. 2019).

Fungal laccases are inducible metalloproteins and monomeric glycoproteins with 10–20% carbohydrate content (Copete et al. 2015). The high level of glycosylation stabilizes the laccase structure and shelters them against thermal degradation (Arregui et al. 2019). Molecular characterization of laccase isozymes has uncovered that primary structure of enzyme constitutes 450–550 amino acid residues spaced in

three successive domains, with a β-sheet topology (Dedeyan et al. 2000). The first domain holds initial 150 amino acids; the second domain covers residues between 150 and 300, and the third domain extends between 300 and 500 amino acids (Agrawal et al. 2018a). Generally, the presence of two strong disulfide bridges confined between domains I and II sustain the enzyme structure (Schindl et al. 2019). Interestingly, earlier reports have also suggested the presence of the third disulfide bridge between domains II and III (Sharma et al. 2016).

The catalytic site in all the laccase isozymes is highly conserved and requires four copper (Cu) atoms arranged in two metallic active sites, which reduce the oxygen into water molecule (Kumar and Chandra 2020). Among these, one Cu molecule figures the substrates to be oxidized, owing to its redox potential, and the rest transfer the electrons to O_2 (Claus 2004). The four Cu molecules of laccases are distributed in three redox sites, i.e., T1Cu, T2Cu, and T3Cu, which differ in their spectroscopic and electronic paramagnetic properties (Chauhan et al. 2017). T1Cu (a type-I copper) has the highest redox potential and is bound to one cysteine and two histidine residues (Jones and Solomon 2015). T1Cu has a characteristic absorbance around 600 nm, responsible for the greenish-blue color of purified laccase (Gunne et al. 2014). Due to the absence of T1Cu, enzyme lacks its blue color and is therefore deemed as “yellow” or “white” laccase (Mot et al. 2020). T2Cu also coordinated with two histidine residues and is involved in the electron transfer (Gunne et al. 2014). On the other hand, T3Cu core are diamagnetic with strong absorption peak near 330 nm and participates in the fixation and reduction of dioxygen (Sitarz et al. 2016). Additionally, T2Cu/T3Cu redox sites may also engage in the enzyme inhibition by interacting with anions such as fluoride or cyanide (Thurston 1994).

Fungal laccases are broadly grouped into three classes depending upon the redox potential of the T1Cu: low (0.4–0.5 V), medium (0.5–0.6 V), and high (0.7–0.8 V) (Zimbardi et al. 2016). Owing to their low redox potential, laccases generally oxidize lignin model compounds having free phenolic groups such as mono-, di-, and polyphenols, arylamines, aminophenols, diamines and aromatic amines, and anilines (Sharma et al. 2016; Upadhyay et al. 2016). The oxidation reactions catalyzed by laccases involve the loss of a single electron and formation of free phenoxy radicals which can act as low molecular weight organic mediators for the enzymes (Shraddha et al. 2011). These intermediate mediators remain unstable; therefore, they leave the enzyme site and perform laccase-mediated oxidation or depolymerizing reactions (Munk et al. 2018). However, non-phenolic compounds cannot be directly oxidized by laccases due to their larger size or due to their relatively high redox potential (Bourbonnais and Paice 1990). Nevertheless, in the presence of suitable chemical mediators, laccases can also oxidize high redox potential non-phenolic model substrates (Bourbonnais et al. 1995; Morozova et al. 2007). The addition of artificial mediators (ABTS and HoBT) (Baiocco et al. 2003; Christopher et al. 2014) and lignin-derived natural mediators (acetosyringone and methyl syringate) (Johannes and Majcherczyk 2000) is a common practice employed in several biotechnological and industrial applications, including biomass delignification and detoxification for biofuel production, bioremediation of polluted soils, processing of food and beverages, degradation of xenobiotics and heavy metals, treatment of effluents

enriched with lignin derivatives, and degradation of hazardous textile dyes (Fig. 6.1) (Rodríguez Couto and Toca Herrera 2006; Morozova et al. 2007).

6.3.2 Lignin Peroxidases: General Properties and Mechanism

Lignin peroxidases were originally discovered in the mid-1980s, from the nitrogen- and carbon-limited medium of basidiomycetous fungus *P. chrysosporium* (Glenn et al. 1983). After the discovery of LiPs from *P. chrysosporium*, several other LiP-producing fungal cultures of Indian origin have been reported, for example, *Ganoderma lucidum*, *T. versicolor*, *Schizophyllum commune*, *Bjerkandera* sp., *Lentinus squarrosulus*, *Pycnoporus sanguineus*, *Phlebia floridensis*, *Phanerochaete sordida*, *Phlebia tremellosa*, and *Phlebia radiata* (Arora and Gill 2005; Bajwa and Arora 2009; Sharma et al. 2011; Selvam et al. 2012; Tripathi et al. 2012; Kaur et al. 2016; Shaheen et al. 2017). They are produced in several isoforms with a molecular mass ranging from 30 to 46 kDa (Vares et al. 1995). LiPs are heme-containing glycoproteins that genuinely catalyze the oxidation of lignin, therefore generally deemed as true ligninases with a high redox potential (Wang et al. 2018). In addition to their high redox potential, LiPs generally have very low pH optima near pH 3.0–4.5, which makes them superior to other classical peroxidases (Kersten et al. 1990). They are recognized as a family of extracellular monomeric glycosylated (up to 20–30%) enzymes having one ferric protoheme per molecule (Falade et al. 2016). The chemical structure of LiP constitutes 343 amino acids along with 370 water molecules, 4 carbohydrates, and 2 calcium ions (Choinowski et al. 1999). On the other hand, the globular structure of LiP is helicoidal in nature and composed of eight major and eight minor α-helices and two antiparallel beta-sheets organized into two domains at both sides of the heminic group (Hammel et al. 1994). This arrangement not only inlaid the protein but also forms an active center cavity to access the solvents via two small channels (Edwards et al. 1993; Bhaskar et al. 2006). The resulting heminic cavity constitutes 40 residues that bound the protein via hydrogen linkages (Poulos 2014). Moreover, the heminic group is interrelated with a water molecule and His amino acid that magnifies the redox potential of LiPs (Piontek et al. 2001). Some studies have also revealed that the presence of a tryptophan (Trp171) residue on the enzyme's surface also pumps the redox potential (Kamitsuji et al. 2005; Sáez-Jiménez et al. 2016).

Lignin peroxidases catalyze the monoelectronic and hydrogen peroxide (H_2O_2)-dependent oxidation depolymerization of lignin compounds through a multistep reaction (Falade et al. 2016). However, questions have been raised about the sensitivity of extracellular LiPs in the presence of H_2O_2, which can partially inactivate the activity of enzyme (Böckle et al. 1999). The addition of veratryl alcohol (VA) to the reaction mixture is a common practice employed to improve the enzyme production and stability (Alam et al. 2009; Falade et al. 2016). Some researchers have conceptualized that VA not only shield the enzyme from the action of H_2O_2, but also engage as a redox mediator between the enzyme and substrates which are

unable to get inside the heme iron center (Koduri and Tien 1995; Huang et al. 2003; Christian et al. 2005; Romero et al. 2019).

High redox potential enables LiPs to oxidize a wide variety of phenolic and non-phenolic lignin compounds (MacDonald et al. 2016). LiPs catalyze the oxidation of phenolic compounds more rapidly over non-phenolic units by removing one electron and creating intermediate free radicals such as phenoxy radicals and veratryl alcohol (Romero et al. 2019). Unlike classical peroxidases which can only act on strongly activated aromatic substrates, LiPs can also oxidize the moderately activated aromatic rings without involving the participation of redox mediators (Plácido and Capareda 2015). LiPs are highly active on a variety of phenolic (guaiacol, methoxybenzenes, vanillyl alcohol, syringic acid, and catechol) and non-phenolic lignin compounds (diarylpropane, VA, and β-*O*-4 lignin dimers) (Chan et al. 2020; Kumar and Chandra 2020). The oxidation of β-*O*-4 lignin dimer involves the generation of radical cations followed by a variety of pathways, including side-chain cleavage, demethylation, and phenol dimerization (Lange et al. 2013). LiPs catalyze several oxidation processes of lignin polymers, such as Cα-Cβ cleavage of the propyl side chains, phenol oxidation, oxidation of benzyl alcohols into aldehydes or ketones, hydroxylation of benzylic methylene groups, and ring cleavage of non-phenolic (aromatic) model compounds of lignin (Reddy et al. 2003; Mobley et al. 2018). LiPs also have great biotechnological potential and industrial applications (Fig. 6.1) due to their high redox potentials and low substrate specificity (Falade et al. 2016; Janusz et al. 2017; Chowdhary et al. 2020).

6.3.3 Manganese Peroxidases: Characteristics and Functions

Manganese peroxidases are extracellular heme-containing glycoproteins, secreted in several isoforms in wood-degrading basidiomycete fungi, including white-rot fungi (Dashtban et al. 2010). They are also termed as hydrogen-peroxide oxidoreductases, representing the most common type of lignin-modifying peroxidases and deemed as class II peroxidase (Morgenstern et al. 2008). Just after the discovery of LiP, MnP was also reported from the batch culture of *P. chrysosporium* in 1984 (Rivela et al. 2000). The production of MnP has been recorded from many other fungal cultures including *Panus tigrinus*, *Trametes versicolor*, *Lenzites betulinus*, *G. lucidum*, *Phanerochaete flavido-alba*, *Phanerochaete chrysosporium*, *Agaricus bisporus*, *Pycnoporus sanguineus*, *Bjerkandera* sp., *Schizophyllum commune*, *Nematoloma frowardii*, and *Phlebia* sp. (Gill and Arora 2003; Nazareth and Sampy 2003; Dhawan et al. 2005; Shanmugam et al. 2005; Padma and Sudha 2013; Pandey et al. 2018; Rao et al. 2019).The molecular mass of the most purified MnPs is around 45 kDa, whereas the mass of crude enzymes ranges between 38 and 62.5 kDa (Janusz et al. 2017). The globular structure of MnP comprises two domains with ten major helixes, a minor helix around the heme ion center (Bhaskar et al. 2006). Additionally, the active site of MnP is unique among peroxidases and comprises two Ca^{2+} ions, histidine and arginine residues, and five disulfide bridges (Kumar and

Chandra 2020). The chemical structure of MnP constitutes around 350 amino acid residues, of these 43% are identical with LiP sequence (Plácido and Capareda 2015).

MnPs are unique among heme peroxidases that catalyze peroxide-dependent oxidation of Mn^{2+} (primary reducing substrate) to Mn^{3+}, which is then released in the aqueous solution and remains quite unstable (Wong 2009). The stability of Mn^{3+} is instigated by chelation with simple organic acids such as malonate and oxalate, thus producing diffusible oxidizing chelate-oxalate (Grąz and Jarosz-Wilkołazka 2011). Indeed, many fungal cultures have been reported to secrete such organic acids along with MnP to stimulate the enzyme activity and Mn^{3+} stability (Martin 2002). The resulting Mn^{3+} chelator complex acts as a low molecular weight redox mediator, which can diffuse into the substrate and oxidize a wide range of phenolic substrates including amines, phenolic lignin substructures, phenols, phenolic lignin model compounds, and reactive dyes (Reddy et al. 2003). The oxidation of phenolic compounds is initiated by one-electron transfer to generate an intermediate phenoxy radical, which further helps in the dissolution of the compounds (Padma and Sudha 2013; Wang et al. 2018).

The oxidation capability of Mn^{3+} chelator complex is only restricted to phenolic lignin compounds (Datta et al. 2017). Unlike LiP, MnPs are not adequate for oxidizing the more fractious non-phenolic substrates (Higuchi 2004). However, it has been repeatedly theorized that MnP can impart the non-phenolic lignin structures, incorporating small mediators such as thiyl or lipid radicals (Qin et al. 2017). Therefore, the oxidation of non-phenolic substrates demands the generation of reactive radical species along with a second mediator (Higuchi 2004). Simple organic acids such as oxalate and malonate are the most commonly known second mediators to facilitate the production of reactive radical species including superoxide, carbon-centered radicals, lipid peroxyl, and formate radicals (Watanabe et al. 2001). The resulting reactive species are used by MnP as source of peroxides to facilitate the decomposition of non-phenolic lignin compounds in the absence of H_2O_2 (Pollegioni et al. 2015). Earlier studies have shown that, the strong MnP-lipid complex can also catalyze the dissolution of Cα-Cβ and β-aryl ether bonds of a non-phenolic lignin model (Urzúa et al. 1998; Ohashi et al. 2011).

6.3.4 Versatile Peroxidase: A Superior Lignin Degrader

Versatile peroxidases (VPs) are superior among the heme-containing ligninolytic fungal peroxidases, which were first discovered in wood-rotting fungus *Pleurotus eryngii* in 1996 (Sigoillot et al. 2012). Earlier, they were recognized as manganese peroxidase, having oxidative properties for aromatic compounds (Ruiz-Dueñas et al. 2009). Later, they were certified as a new peroxidase type belonging to oxidoreductase family (Ravichandran and Sridhar 2016), having a molecular mass between 40 and 45 kDa in several isoforms (Salame et al. 2012). Versatile peroxidases are majorly distributed among *Pleurotus* and *Bjerkandera* spp., such as *P. eryngii*, *P. pulmonarius*, *P. ostreatus*, *B. adusta*, and *B. fumosa* (Verma and Madamwar 2002; Tripathi et al. 2012; Pozdnyakova et al. 2018). Several other basidiomycetes,

including *Marasmiellus palmivorus*, *Physisporinus vitreus*, *Lentinus squarrosulus*, *Dichomitus squalens*, *T. versicolor*, and *Ganoderma* spp., have been also identified as potent producers of VPs (Kuhad et al. 2007; Aarthi et al. 2018; Ravichandran et al. 2019; Saikia et al. 2020).

Versatile peroxidases are attractive wild-type ligninolytic enzymes having characteristic bifunctional oxidative capability and a broad spectrum substrate preference (Camarero et al. 1999). The genomic studies have revealed that VPs share the catalytic properties of both MnP and LiP and are capable of oxidizing Mn^{2+} to Mn^{3+}, as well as degradation of high redox potential non-phenolic lignin substrates like MnP and LiP, respectively (Martínez 2002; Pérez-Boada et al. 2005). Unlike LiP and MnP, VPs are also competent in catalyzing the oxidation of complex lignin structures such as hydroquinone and substituted phenol units without any mediator (Ruiz-Dueñas et al. 2009). These hybrid peroxidases are also able to oxidize high redox dye such as dye Reactive Black 5 in the presence of VA (Pérez-Boada et al. 2005). Previous studies suggested that hybrid molecular structure of VPs, which provide multiple substrate binding sites along with their different pH optima (3.0 and 5.0), favors the degradation of these wide spectrum substrates (Ravichandran and Sridhar 2016; Knop et al. 2016; Gonzalez-Perez et al. 2016). These unique capabilities of versatile peroxidases have attracted lots of research attention and make them a potent "green catalyst" for numerous industrial applications (Fig. 6.1).

6.3.5 Dye-Decolorizing Peroxidases

Dye-decolorizing peroxidases (DyPs) constitute a newly reported superfamily of heme-containing peroxidases that do not show any phylogenetical homology with former fungal peroxidases including LiPs, MnPs, and VPs (Colpa et al. 2014). DyPs are bifunctional catalysts; besides their oxidative activity, they also possess additional hydrolytic activity (Singh and Eltis 2015). They were first identified in 1999 from fungus *Bjerkandera adusta* (formerly known as *Geotrichum candidum*) and named after their ability to catalyze the transformation of a wide range of industrial dye such as RB5, which are poorly converted by other peroxidases (Fernández-Fueyo et al. 2015; Amara et al. 2018). DyPs have a molecular mass of 40–65 kDa and are glycosylated up to 9–31% (Colpa et al. 2014). The molecular structure of DyP contains two domains, α-helices and antiparallel β-sheets, and a heme cofactor positioned in between the cavity of the two domains (Habib et al. 2019).

DyPs are important biocatalysts, which have attracted a great research interest due to their potential applications in lignin degradation (Abdel-Hamid et al. 2013). Compared with classical fungal peroxidases, DyPs work under much lower pH conditions and have wide substrate specificity (Duan et al. 2018). They can oxidize all typical substrates of other heme peroxidases including ABTS, anthraquinones, adlerol, and carotenoids (Shrestha et al. 2017). Several studies have shown that DyPs catalyze the oxidation of phenolic compounds, such as 2,6-dimethoxyphenol and guaiacol (Kim and Shoda 1999; Ogola et al. 2009; Duan et al. 2018). On the other

hand, some reports have emphasized the catalytic ability of DyPs to oxidize the non-phenolic lignin model compounds including β-*O*-4 dimeric lignin, VA, and Mn^{2+} (Liers et al. 2013). The ligninolytic activity of DyPs has been identified in very few fungal cultures, such as *Termitomyces albuminosus*, *Irpex lacteus*, and *Auricularia auricula-judae* (Salvachúa et al. 2013; Linde et al. 2014; Amara et al. 2018).

6.3.6 Accessory Enzymes for Lignin Degradation

In addition to these key ligninases, fungal ligninolytic machineries also include other extracellular enzymes which may act as auxiliary enzymes in the lignin degradation process (Andlar et al. 2018). These include hydrogen peroxide generating extracellular oxidases, which produce H_2O_2 mandatory for other peroxidases to catalyze the oxidative degradation of lignin-derived compounds (Falade et al. 2016; Datta et al. 2017). Examples include the aryl-alcohol oxidase secreted by various fungal cultures, including *Pleurotus eryngii*, *Pleurotus sajor-caju*, *Pleurotus ostreatus*, *Bjerkandera adusta*, and *Geotrichum candidum* (Ghosh et al. 1998, Singh et al. 2010a, b, Tripathi et al. 2011, Kumar and Rapheal 2011), and glyoxal oxidase found in few fungal cultures such as *P. chrysosporium*, *Pycnoporus cinnabarinus*, and *Myceliophthora thermophila* (Sharma et al. 2013b; Ansari et al. 2016). Moreover, fungi also secrete dehydrogenases such as aryl-alcohol dehydrogenases and quinone reductases, which are also involved in the degradation of lignin-derived compounds (Mathieu et al. 2016). Interestingly, some studies have shown that cellobiose dehydrogenase, which is a key member of cellulolytic system, also portrays an effective role in lignin degradation in the presence of H_2O_2 and chelated Fe ions (Temp and Eggert 1999; Harreither et al. 2009). However, the low production titer of these enzymes and inefficient fermentation condition is still a major obstacle that hampers the commercial scale production and application of these auxiliary enzymes (Gutiérrez et al. 2000; Kadowaki et al. 2018; Liu and Wilkins 2020). Nevertheless, with the advancement of modern-omics techniques besides the isolation of novel microbial strains capable of producing significant enzyme doses, the applicability of these enzymes may emerge in the near future.

6.4 Biotechnological and Industrial Applications of Ligninolytic Fungi and Enzymes

6.4.1 Biofuel Industry: Delignification and Detoxification

The conversion of lignocellulosic biomass to energy-enriched biofuels and value-added products is mainly achieved by three steps: (1) delignification of lignocellulose to release cellulose and hemicellulose fibers, (2) depolymerization of structural carbohydrates to produce fermentable sugars, and (3) fermentation of liberated sugars (Kumar et al. 2017a; Chandel et al. 2018). Biological treatments using

ligninolytic fungi and their enzymes have appeared as a new alternative to replace the physicochemical tricks (Sindhu et al. 2016; Ummalyma et al. 2019). In recent years, these biological agents have been extensively exploited for delignification and detoxification of lignocellulosic biomass prior to fermentation (Gupta et al. 2009; Kapoor et al. 2015; Bagewadi et al. 2017; Chandel et al. 2019).

Delignification of lignocellulosic biomass using ligninolytic fungi/enzymes can be categorized under four different methods: (a) fungal delignification, (b) enzymatic delignification, (c) enzyme-mediator system, and (d) integrated biological treatment (Wan and Li 2012, Singh et al. 2014a, b; Moreno et al. 2015). Fungal delignification is generally achieved by directly growing the microorganisms on the targeted biomass under a submerged or a solid-state condition (Chandel et al. 2015). However, the fungal pretreatment may result in loss of fermentable sugars and require a long treatment time (up to 20–50 days) to achieve high delignification percentages (Saha et al. 2017; Kainthola et al. 2019). The effectiveness of fungal pretreatment has been improved by employing an active fungal consortium and integration of fungal treatment with certain physical/chemical methods (Salvachúa et al. 2011; Shirkavand et al. 2016; Meehnian et al. 2017). Additionally, the use of ligninolytic enzymes with or without redox mediators has been accepted as an effective and simpler method to achieve high delignification percentage, consequently addressing the key limitations of fungal treatment (Table 6.1) (Gupta et al. 2009; Moilanen et al. 2014; Plácido and Capareda 2015; Saini et al. 2020b). For enzymatic delignification, laccase isozymes with or without redox mediators are always preferred, followed by MnP and LiP. The mixtures of ligninolytic enzymes have also been employed for some delignification treatments that have shown improved lignin removal efficiency in a short time (Heap et al. 2014; Kudanga and Le Roes-Hill 2014; Giacobbe et al. 2018).

In addition to delignification, enzymatic detoxification of biomass represents one of the few promising biotechnological applications of ligninolytic enzymes in the biofuel industry (Table 6.1) (Kapoor et al. 2015; Suman et al. 2018). The traditional physical and chemical pretreatment processes produce toxic compounds such as phenolic derivatives, furan, furfural, and weak acids (Gupta et al. 2009; Silveira et al. 2018; Saini et al. 2020a). Since these compounds strongly inhibit the cellulolytic enzymes and fermentation process, they need to detoxify in order to enhance enzyme and yeast performance (Tejirian and Xu 2011; Qin et al. 2016). Biological detoxification using ligninolytic fungi/enzymes have been shown to reduce the concentration of inhibitory compounds (Fang et al. 2015; Moreno et al. 2015). The toxic phenolic derivatives are predominantly detoxified by key ligninases (Rameshaiah and Jagadish Reddy 2015). Previous studies have shown that aryl-alcohol oxidases are capable of detoxifying furan derivatives such as 5-hydroxymethylfurfural and polyunsaturated alcohols (Carro et al. 2015; Feldman et al. 2015). Besides positive impacts such as high detoxification and delignification percentage, eco-friendly, and low sugar losses, fungal and enzymatic treatments have certain drawbacks such as high costs, low commercial availability, and long process duration (Ramarajan and Manohar 2017; Wagner et al. 2018). Nevertheless, delignification and detoxification capabilities of ligninolytic fungi/enzymes can be improved by using genomic and

Table 6.1 Recent applications of ligninolytic fungi and their enzymes in biofuel sector carried out by Indian mycologists

Culture	Substrate and process	Experimental condition	Results	References
Pleurotus florida, *Coriolopsis caperata*, and *Ganoderma* sp.	Sugarcane bagasse; delignification	Delignified at 30 °C for 15 days under SSF condition at 25% (w/v) moisture content	Reduced 7.91%, 5.48%, and 5.58% lignin, respectively	Deswal et al. (2014)
Coriolus versicolor	Sorghum bagasse; delignification	Treated at 27.5 °C in a mesh tray bioreactor with 75% relative humidity under SSF condition	Reduced 46.09% lignin after 20 days of treatment	Mishra and Jana (2019)
Daedalea flavida	Cotton stalk; delignification	Delignified at 28 °C with 75% moisture content under SSF condition	Degrade 27.83% lignin after 40 days of incubation	Meehnian and Jana (2016)
Lentinus squarrosulus	Kans grass; delignification	Treated at 35 °C with 15% (w/v) consistency and 3125 IU/g laccase	Removed 81.67% lignin after 6 h	Rajak and Banerjee (2016)
Trametes versicolor	Rice straw and poplar waste; detoxification	Detoxified the pretreated biomass at 28 °C with 1.2 U/ ml laccase for 12 h	Reduced 76% and 94% phenolic inhibitors, respectively	Kapoor et al. (2015)
Trametes maxima	Sugarcane bagasse; detoxification	Detoxification was done with 0.1 U/ml laccase at 32 °C	Removed 66% of phenolics derivatives after 1.5 h	Suman et al. (2018)
Lentinus squarrosulus	Finger millet and paddy straw; delignification	Treated with 25 IU/g of enzyme at 60 °C for 24 h	Reduced 17 and 11% lignin from straws, respectively	Ravichandran et al. (2019)
Pleurotus ostreatus	Wheat straw and banana stem; delignification	Delignified at 30 °C with substrate to moisture ratio of 1:4 (w/v) under SSF condition	Degraded 40 and 29% lignin content after 32 days of incubation	Thakur et al. (2013)
Pleurotus ostreatus, *P. chrysosporium*, and *Ganoderma lucidum*	Rice straw; delignification	Delignification was done 30 °C with 70% relative humidity for 35 days	Reduced 21.85%, 38.74%, and 17.81% lignin content	Kainthola et al. (2019)
Coriolus versicolor	Sweet sorghum bagasse; delignification	Treatment was done at 27.5 °C with 70% (w/v) humidity	Reduced 24.8% lignin content after 20 days	Mishra and Jana (2019)

protein engineering approaches and appropriate interaction between different enzymes to evolve a dominant lignin degradation system for biofuel industry.

6.4.2 Food, Feed, and Beverage Industry

The direct use of lignocellulosic biomass as ruminant animal feed exhibits one of the oldest and most recent applications (Sharma et al. 2012). The abundance of poorly digestive lignin polymer hampers the use of such biomass by rumen microbes, thereby demanding lignin removal prior to feed application (Sheikh et al. 2018). Enzymatic delignification of lignocellulosic biomass has received considerable attention due to their efficiency in improving animal feed performance (Sridhar et al. 2015; Ravichandran et al. 2019). A number of extracellular enzymes including various cellulolytic, hemicellulolytic, and ligninolytic are extensively exploited for animal feed industry (Sharma et al. 2005; Thammaiah et al. 2016). Among these, ligninases have received much research interest due to their ability to enhance the digestibility, to improve the nutritional value, and to reduce the excretion of nitrogen and phosphorous (Table 6.2) (Kumar et al. 2015a, b; Chowdhary et al. 2019). Direct solid-state fermentation of biomass by selective and nonselective lignin-degrading white-rot fungi is also a very attractive alternative (Kuhad et al. 2013). Various Indian origin white-rot fungi, such as *B. adusta*, *P. chrysosporium*, *T. versicolor*, *Fomes fomentarius*, *Cyathus* sp., *Phlebia rufa*, *Coriolus hirsutus*, *Irpex lacteus*, *G. lucidum*, *G. applanatum*, *Dichomitus squalens*, *Pleurotus flabellatus*, *P. ostreatus*, *P. tuber-regium*, and *Lentinus subnudus*, have been studied for solid-state bioconversion of lignocellulosic biomass to enhance animal feed properties (Table 6.2) (Sharma et al. 2012, 2013a; Shrivastava et al. 2014; Raghuwanshi et al. 2014; Nayan et al. 2020). Solid-state fermentation of lignin-rich wheat straw with selective lignin degraders into high-energy cattle feed usually termed as "mycostraw" is a common practice to increase crude protein content and energy constituents for ruminant feed (Shrivastava et al. 2011, 2012; Nayan et al. 2018).

The utility of various ligninases has been reported in the processing of certain foods, feed, and beverages (Brijwani et al. 2010). Ligninases have been observed to eliminate phenolics saccharides from the fruit juices and fermented alcoholic beverages, which eventually reduce browning, haze formation, and turbidity (Minussi et al. 2002; Mäkelä et al. 2017). Ligninases not only stabilize the fruit juice and fermented alcohol beverages but also improve the color appearance, flavor, aroma, and taste of such beverages (Gassara-Chatti et al. 2013; Lettera et al. 2016; Ghosh and Ghosh 2019). Some previous studies have shown that LiPs and MnPs have the potential to generate natural aromatic flavors in various food products (dos Santos Barbosa et al. 2008, Kumar and Chandra 2020). Moreover, some white-rot fungi can be used to convert agricultural lignocellulosic wastes directly to human food, like edible fruit bodies of *Lentinus*, *Pleurotus sajor-caju*, *Agaricus bisporus*, *Cantharellus*, and *Volvariella* (Goyal et al. 2006; Ahlawat and Tewari 2007; Kumari et al. 2011; Thiribhuvanamala et al. 2012; Kumla et al. 2020).

Table 6.2 Ligninolytic fungi/enzymes application in food/feed/beverage industries explored in India

Culture	Feed/food/beverage	Research finding	References
Ganoderma sp. and *Crinipellis* sp.	Wheat straw	Fungal treatment increased the feed digestibility by degrading ether extract, neutral detergent fiber (NDF), and acid detergent fiber content (ADF)	Sharma et al. (2012)
Schizophyllum commune	Paddy straw, finger millet straw, wheat straws, etc.	Laccase treatment significantly reduced the indigestible NDF, ADF, and acid detergent lignin (ADL), consequently enhancing the in vitro dry matter digestibility (IVDMD)	Kumar et al. (2015a, b)
Ceriporiopsis subvermispora	Wheat straw	Fungal treatment preferred NDF, ADF, and ADL components and increased the carbohydrates-to-lignin ration (C/L ratio)	Nayan et al. (2017)
Coriolus versicolor and *Ganoderma lucidum*	Ragi straw	Ligninolytic enzymes significantly increased the protein content and dry matter digestibility (5%) and reduced the composition of lignin derived compounds	Sridhar et al. (2015)
Lentinus squarrosulus	Paddy straw, finger millet straw, little millet straw, etc.	Enzymes treatment reduced the NDF (2.6–4.2%) and ADL (2.9–5.2%) content and significantly increased the IVDMD (14–32%)	Ravichandran et al. (2019)
Ganoderma sp.	Wheat straw	Fungal treatment reduced the indigestible lignin constituents and increased the C/L ration (1.28–fold) with high IVDMD (32.2%)	Raghuwanshi et al. (2014)
Ganoderma lucidum	Pomegranate, lemon, and apple juice	Enzyme treatment significant reduced the toxic phenolics compounds (79–85%) and improved clarity, stability, and quality of the fruit juice	Manavalan et al. (2015)
Aspergillus flavus	Apple juice	Enzyme treatment brings a reduction in phenolic, flavonoid, and turbidity, which indicates the suitability of the juice	Ghosh and Ghosh (2019)

6.4.3 Paper and Pulp Industry: Biopulping, Biobleaching, and Deinking

Separation of lignin from the cellulosic fibers is a necessary step required during pulp and paper production from the woody substrates (Eugenio et al. 2019). Various woody materials including bamboo, eucalyptus, and leftover agricultural biomass have been exploited for paper manufacturing depending upon the type and quality of the paper (Trotter 1990; Eriksson 1998; Bajpai 2018a). Pulping and bleaching of

these woody substrates are the two important steps required for paper production (Bajpai 2018b). During pulping, the native substrates are subjected to different mechanical and chemical methods to reduce the fibrous state (Hubbe et al. 2007). Conventional and the present-day chemical methods involve consumption of enormous amounts of chlorine, sulfite, or oxygen-based chemical oxidants, which impose serious drawbacks to the natural environment (Leponiemi 2008; Liu et al. 2018). Besides environmental adverse effects, the chemical tricks are also cost-intensive processes, generating low pulp yield between 40% and 50% (Ince et al. 2011). To overcome these obstacles, microbial or enzymatic systems capable of delignifying woody material can be used (Bajpai 2018b). In this scenario, white-rot fungi and their oxidative enzymes are potentially useful agents because they not only diminish the energy and cost consumption but also improve the strength properties and are environmentally friendly due to reduced effluent toxicity (Singh et al. 2010a, b, Singh and Singh 2014, Janusz et al. 2017). The biopulping of woody material using white-rot fungi was first considered by Lawson and Still (1957) at West Virginia Pulp and Paper Company Research Laboratory (Akhtar et al. 1997). Since then, many white-rot fungi have been studied, and some of them were found to be efficient biobleachers, viz., *Bjerkandera* spp., *P. chrysosporium*, *Botrytis cinerea*, *Polyporus ciliates*, *Phlebia radiata*, *Lentinus tigrinus*, *Stereum hirsutum*, *Stropharia coronilla*, and *T. versicolor* (Table 6.3) (Kuhad et al. 2007; Kuhar et al. 2007; Saleem et al. 2018; Nathan et al. 2018; Chaurasia and Bhardwaj 2019; Sharma et al. 2019) in pulping processes and pilot mill trials. Previous studies have shown that ligninases such as laccase and LiP portray an important role in biopulping, but direct evidences for LiP are not available (Vrsanska et al. 2016; Damián-Robles et al. 2017). It has been theorized that biopulping using fungi and ligninolytic enzymes could save 30%–45% of the energy consumed in comparison to mechanical and chemical processes (Falah et al. 2011; Giles et al. 2015; Chukwuma et al. 2020).

Pulping is followed by bleaching of kraft pulp, which demands huge amount of chlorine and chlorine-derived chemicals, consequently leading to environmental disturbance (Kaur et al. 2019). To overcome these drawbacks, enzymatic processes have been envisaged to provide environmentally intact technology, and the use of laccase and laccase-mediator system remains the choice of technology to achieve the goals (Table 6.3) (Onysko 1993; Fillat and Roncero 2009; Singh et al. 2015, 2019). Previous studies have shown that laccase-mediator system such as violuric acid, ABTS, and HBT can enhance ISO brightness and reduce the kappa number and yellowness effect of the kraft pulp (Pala et al. 2004; Lee et al. 2011; Chutani and Sharma 2015; Tsatsis et al. 2017). Additionally, heme peroxidases such as MnP and LiP are also seen to be competent in decolorizing the kraft pulp mill effluents (Saraswathi and Saseetharan 2010; Chandra et al. 2018; Gaur et al. 2018). Although over 70% of the world's annual pulp is produced by chemical and mechanical processes, a large financial investment has been made to improve the biobleaching and biopulping processes using ligninolytic fungi and enzymes, which are likely to be accepted in the near future.

Beside biopulping and biobleaching, decolorization of paper and pulp mill effluents, and deinking of paper waste using ligninolytic enzymes to enhance the

Table 6.3 Ligninolytic fungi/enzymes from Indian subcontinent and their applications in paper and pulp industry

Fungal culture	Application	Research finding	References
Ganoderma sp., *Trametes* sp., and *Poria* sp.	Biobleaching of hard wood Kraft pulp	All fungal cultures significantly reduced the kappa number (5–12%) and increased the brightness of the pulp (30–45%)	Selvam and Arungandhi (2013)
Stereum ostrea and *Trametes versicolor*	Biobleaching of Kraft pulp	Kappa number was reduced to 17% after fungal treatment; addition of Mn^{2+} drastically enhanced the pulp brightness	Seshikala (2014)
Ganoderma lucidum MDU-7	Deinking of paper waste	Laccase-mediator system significantly reduced the ink particles (61%) and detoxified the paper hydrolysates	Saini et al. (2020b)
Nigrospora sp. and *Trametes* sp.	Decolorization of Kraft black liquor	Mixed fungal culture resulted in maximum decolorization (73%) and COD removal (71%)	Rajwar and Rai (2015)
Pleurotus ostreatus	Biobleaching of mixed wood pulp	Addition of xylanases to the culture extract of *P. ostreatus* significantly improved the pulp properties	Dwivedi et al. (2009)
Trichoderma harzianum	Biobleaching and bioremediation of paper industry effluent	*T. harzianum* was evaluated for ligninolytic activity; crude enzyme extract was found effective in biobleaching and bioremediation	Sadhasivam et al. (2010)
P. chrysosporium and *Pleurotus* sp.	Detoxification of paper industrial effluents	Both fungal strains were found to reduce the toxic chemicals mutagens and COD of the paper industrial effluents	Kulshreshtha et al. (2012)
Peniophora sp.	Deinking of paper waste	Laccase treatment improved the strength and brightness of recycled pulp, 1.7-fold and 6%, respectively	Shankar et al. (2018)
Fusarium equiseti	Biobleaching of waste newspaper	Enzymatic bleaching with laccase reduced the kappa number and increased the brightness (15%)	Nathan et al. (2018)
Daedalea flavida, *Polyporus hirsutus*, and *Phellinus* sp.	Bioremediation of pulp and paper mill effluents	Fungal cultures were shown to decolorize the waste effluents (62–66%) and reduce the COD (38–42%)	Selvam et al. (2011)

reusability of waste papers represent one of the few promising biotechnological applications of ligninolytic fungi (Kuhad et al. 2010; Chutani and Sharma 2015; Saini et al. 2020b; Chandranupap and Chandranupap 2020). Traditionally, deinking was performed under high temperature conditions, employing various chemical surfactants, which makes the process expensive and causes high environmental

damage (Pala et al. 2004; Virk et al. 2013; Chutani and Sharma 2016; Biswas et al. 2019). Therefore, to tackle these challenges, enzymatic methods are envisaged and proven to be economically feasible (Saxena and Chauhan 2017, Shankar et al. 2018, Valls et al. 2019, Sharma et al. 2020a). Among all, laccase-mediator system has been reported to be efficient in ink degradation and has been successfully scaled up to large-scale applications (Table 6.3).

6.4.4 Transformation and Degradation of Textile Dye Effluents

Different type of dyes and pigments are extensively used in the textile industries; the unadhered dye effluents from these industries are directly discharged to natural water bodies without any treatment (Chequer et al. 2013). The coarse textile effluents majorly constitute a large number of heavy metals such as Co, Cu, Cd, Mg, Fe, Cr, Ni, Hg, and Mn, which are highly pernicious and carcinogenic in nature (Carmen and Daniela 2012; Lellis et al. 2019). These unhealthy impurities have adverse impacts on the water quality in terms of biological oxygen demand, total organic carbon, chemical oxygen demand, pH, and color of the water resources (Tchounwou et al. 2012; Ali et al. 2019). Based on the chemical structure, the textile dyes are classified as anthraquinone, indigo, triarylmethane, phthalocyanine, and azo dyes; among these, azo dyes are deemed harmful due to their excessive utilization and high water solubility (Benkhaya et al. 2017, 2020; Ahlawat et al. 2019).

Traditionally, several attempts have been made to treat these hazardous effluents using various physicochemical processes, viz., filtration, precipitation, adsorption, coagulation, photolysis, and oxidation with H_2O_2 or ozone (Lee et al. 2006; Chutani and Sharma 2015; Hayat et al. 2015; Saini et al. 2020b). Unfortunately, the applications of these physicochemical methods are confined mainly due to excessive need of additional environmental hazardous chemical additives, incomplete and unsafe disposal of generated sludge, and high operating costs (Singh and Arora 2011; Pereira and Alves 2012; Jamee and Siddique 2019). In this context, biological methods have been shown as novel alternatives with low-cost and environmentally benign processes capable of degrading complete organic pollutants without involving the addition of other chemicals (Patel et al. 2013; Rajhans et al. 2020).

The biological degradation of hazardous textile dyes has been reported using various microorganisms including fungi, bacteria, and actinomycetes, employing single or complex microbial consortia (Singh et al. 2010a, b; Gao et al. 2018, Jamee and Siddique 2019, Varjani et al. 2020). Some of the modern molecular modelling and docking experiments have also been reported for the dye degradation potential of laccases from bacterial and fungal sources (Singh et al. 2014a, b; Ahlawat et al. 2019, Vani et al. 2020). Among these, white-rot fungi have been shown as better dye degraders over prokaryotes due non-specific nature of their extracellular ligninolytic enzymes capable of degrading a wide range of dyes (Table 6.4) (Gahlout et al. 2013; Patel et al. 2013; Srivastava et al. 2014). The degradation of textile dyes using a white-rot fungus, *P. chrysosporium*, was first reported by Glenn and Gold in 1983 (Glenn et al. 1983). Subsequently, numerous white-rot fungi, including *Bjerkandera*

Table 6.4 Applications of ligninolytic fungi/enzyme in bioremediation of organopollutants and hazardous dye effluents

Fungal culture	Pollutants	Result and findings	References
Ganoderma lucidum	PAH (phenanthrene and pyrene)	High degradation of phenanthrene (99.65%) and pyrene (99.58%) was achieved after 30 days of treatment at 27 °C	Agrawal et al. (2018b)
Pleurotus ostreatus	PAH (benzo (a) pyrene)	Addition of non-ionic surfactant (T-80) to the fungal treatment enhanced the degradation of PAH (1.18-fold)	Bhattacharya et al. (2014)
Trametes versicolor	Azo dyes and dye industry effluents	Batch mode fungal treatment removed 34.60% orange G, 98.27% Congo red, and 78.05% Amido black 10B, and 98.43% dye effluents	Selvam et al. (2012)
Ganoderma cupreum	Azo dyes (reactive violet 1)	Degradation was increased by adding nitrogen and carbon source to the decolorization medium	Gahlout et al. (2013)
Coriolopsis byrsina	PAH (pyrene)	High degradation of pyrene in vivo (96.1%) and in vitro (51.85%) condition was achieved, and final nontoxic compound were identified	Agrawal and Shahi (2017)
Phanerochaete chrysosporium	Reactive textile dye (yellow MERL and red ME4BL)	*P. chrysosporium* was found to produce laccase and MnP VP to catalyze the degradation of reactive textile dyes	Koyani et al. (2013)
P. flabellatus, *P. ostreatus*, and *P. citrinopileatus*	Azo dye (direct red)	Decolorization of dye was increased by adding 0.1% T-80, and laccase, MnP, and LiP were shown to catalyze the dye degradation	Srivastava et al. (2014)
Myceliophthora vellerea	Textile dye (reactive blue 220)	Fungal treatment using immobilized packed-bed reactor achieved 80% dye degradation and 50% decolorization up to the seventh cycle	Patel et al. (2013)
Trametes hirsuta	PAH (benzo (a) pyrene and phenanthrene)	Addition of rhamnolipid enhanced the fungal degradation efficiency (1.8-fold) and achieved high degradation of phenanthrene (91.26%) and benzo (a) pyrene (87.72%)	Rathankumar et al. (2020a)
P. ostreatus, *P. flabellatus*, *P. florida*, and *P. sajor-caju*	Azo dye (direct blue 14)	Up to 90% of dye degradation was achieved after 6–12 days of incubation, and all fungus culture were shown to produce laccase and MnP involved in dye decolorization	Singh et al. (2013)

(continued)

Table 6.4 (continued)

Fungal culture	Pollutants	Result and findings	References
Geotrichum candidum	Azo dye (methyl orange, Congo red, and trypan blue)	Significant degradation of azo was reported; methyl orange (94%), Congo red (85%), and trypan blue (70%). DyP, LiP, and laccase were identified to catalyze the degradation	Rajhans et al. (2020)
Ganoderma lucidum	Pesticide (lindane)	Pesticide degradation was found higher (75.5%) under SmF condition in comparison to SSF condition (37.5%)	Kaur et al. (2016)

adusta, *Coriolus versicolor*, *Lentinus edodes*, *Lentinus polychrous*, *Lentinus polychrous*, *Lenzites elegans*, *Laccaria fraternal*, *Hirschioporus larincinus*, *Funalia trogii*, *Fomes lividus*, *Inonotus hispidus*, *Pleurotus ostreatus*, *Pleurotus eryngii*, *Phlebia radiate*, *Phlebia tremellosa*, *Pycnoporus cinnabarinus*, *Sclerotium roysii*, *T. versicolor*, *Trametes modesta*, *Trametes hirsute*, and *Thelephora* sp., have been shown to decolorize various dyestuffs (Table 6.4) (Selvam et al. 2003; Singh and Pakshirajan 2010; Gulzar et al. 2020; Saha and Mukhopadhyay 2020; Singh et al. 2020; Munagapati et al. 2020; Vats and Mishra 2020; Zofair et al. 2020). Additionally, soft-rot fungi such as *Aspergillus flavus*, *Aspergillus terreus*, *Geotrichum candidum*, *Trichoderma harzianum*, *Mucor* spp., and *Penicillium* spp. have been identified to degrade several textile dyes including acid red, bromophenol blue, and Congo red (Ramya et al. 2007; Sadhasivam et al. 2010; Ranjusha et al. 2010; Kumar et al. 2012; Saroj et al. 2014; Rajhans et al. 2020; Singh and Dwivedi 2020). Dye degradation using white-rot fungi was largely attributed to LiP and MnP enzymes (Jayasinghe et al. 2008). In recent years, laccase and novel DyP enzymes have also gained a great research interest in relation to dye degradation (Lai et al. 2017; Yang et al. 2019; Iark et al. 2019). The utilization of laccase in combination with mediators and other auxiliary enzymes has been proved to be a valid alternative eco-friendly method with less capital-cost investment (Table 6.4).

6.4.5 Bioremediation of Hazardous Pollutants

Throughout the past century, human activities have released many hazardous organopollutants into the natural environment responsible for air, soil, and water pollution (Rodríguez Couto and Toca Herrera 2006; Álvarez-Rogel et al. 2007; Li et al. 2017). Some of these, including recalcitrant xenobiotic chemicals, pesticides, trinitrotoluene, synthetic dyes, polycyclic aromatic hydrocarbons, organochlorines, polychlorinated biphenyls, benzene, ethylbenzene, toluene, xylene, and munition wastes, remain persistent in the environment, which are known to be cytotoxic, carcinogenic, and mutagenic (McGuinness and Dowling 2009, Juwarkar et al. 2010, Varsha and Chenna 2011). Scientists are working toward decreasing these toxic

pollutants. The currently employed techniques are, however, either costly or time-consuming and may accumulate other hazardous by-products. In this sense, the use of white-rot fungi that produce ligninases is reported to be the most promising in detoxification and degradation of toxic pollutants (Torres et al. 2003; Viswanath et al. 2014; Deshmukh et al. 2016). Due to low substrate specificity of their oxidative enzymes and structural similarities between lignin and organopollutants, fungi are able to perform the breakdown of various recalcitrant effluents (Pointing 2001; Pozdnyakova 2012; Upadhyay et al. 2016). The degradation of organopollutants using white-rot fungi was first achieved by *P. chrysosporium* (Bumpus et al. 1985). Since then, numerous white-rot fungi, such as *Bjerkandera* sp., *Clavariopsis aquatic*, *Cyathus bulleri*, *G. lucidum*, *Pleurotus* sp., *Polyporellus brumalis*, *Phanerochaete sordida Schizophyllum commune*, *P. cinnabarinus*, *Pleurotus pulmonarius*, *T. versicolor*, *Trametes trogii*, *Trametes hirsutus*, *Coriolopsis* sp., and *Phlebia* sp., have been reported as potent degraders of various organopollutants (Table 6.4) (Skariyachan et al. 2016, Bhattacharya et al. 2017, Vaseem et al. 2017, Patil and Yadav 2018, Kumar et al. 2018, Navada and Kulal 2019, Chakraborty et al. 2019, Rathankumar et al. 2020b, Taha et al. 2020, Dhiman et al. 2020). Additionally, ligninolytic enzymes including laccases, LiP, MnP, and VPs from these fungi have also been successfully applied in the treatment of a wide range of toxic effluents (Bhattacharya et al. 2009; Rao et al. 2010; Rathankumar et al. 2020a). Enzyme-mediated degradation of organopollutants involves the polymerization of the pollutants themselves or copolymerization with other nontoxic substrates to facilitate their removal by means of filtration, sedimentation, or adsorption (Shen et al. 2011; Falade et al. 2016; Pathak and Navneet 2017). However, the majority of degradation studies have been conducted on artificially contaminated soils or on synthetic medium spiked with organic pollutants (Table 6.4). Therefore, it is important to investigate both fungal and enzyme performance under non-sterile conditions to transfer the laboratory technology to the actual large-scale contaminated field sites.

6.5 Concluding Remarks

In the foregoing discussion, we have emphasized on the current state of knowledge on lignin-degrading microorganisms, especially white-rot fungi. White-rot fungi have drawn enormous research interest due to their ability to produce vast amounts of extracellular oxidative ligninolytic enzymes. They are also selective lignin degraders and are responsible for efficient deconstruction of woody or lignocellulosic substrates. Since the discovery of ligninolytic fungi, extensive research efforts have been made on the isolation of novel ligninolytic microorganisms, characterization of novel ligninolytic enzymes, and cloning of genes encoding enzymes from the existing microbes. Currently, exploration of fungal proteome and secretome is an effective tool to identify novel enzymes. It can also be used to study the succession, interaction, and complementation between different ligninases involved in lignin degradation pathways. Lignin degradation is thought to proceed via multistep reactions involving an array of main oxidative ligninolytic enzymes in the first

step and several other accessory enzymes to help and achieve the degradation in later stages. However, the low specificity of ligninolytic enzymes engaged in the degradation pathways of lignin makes it difficult to understand the whole processes. Additionally, most of the lignin degradation pathway studies are carried out using lignin model compounds; still, comprehensive study using native form of lignin encountered by fungi/enzyme creating a natural environment in vitro is necessary. Therefore, future research should be aimed at determining the role and cooperation of enzyme consortia in lignin degradation, exploring the function of redox mediators and auxiliary enzymes in the catalytic mechanism of the ligninases, and reconstituting in vitro the actual environment for fungal/enzyme ligninolytic systems for lignin degradation.

The practical use of ligninolytic fungi and their enzymes for biotechnological and industrial applications holds a great potential. The advantages and disadvantages of ligninolytic fungi/enzymes should be evaluated before attempting industrial scale operations. Though biotechnological significance of these fungi/enzymes have increased drastically, there are still some aspects to be investigated, particularly process optimization and cost reduction. Both can be achieved by isolating native fungal stains and enzymes that are best suited for wide substrate spectrum and required narrow reaction conditions. Here genetic engineering such as protein engineering and gene editing technologies can have an important role to play. Searching for novel and native fungal strains and taking advantage of the enormous microbial diversity of the Indian subcontinent can enhance the choice for the customized industrial applications.

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