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Structural Insights, Biocatalytic Characteristics, and Application Prospects of Lignin Peroxidase for Sustainable Biotechnology - A Critical Review of Recent Progress and Future Directions

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Abstract

Lignin is a complex polymer made up of phenylpropane units coupled by a variety of ether and carbon linkages, giving them an inert and recalcitrant nature. Despite serving as the most abundant source of aromatic high-value products, lignin till date has remained underexploited due to its complexity. Lignin modifying enzymes (LMEs) have gained widespread recognition in enzymatic degradation within the broader context of environmental sustainability and pollution management. Lignin peroxidase (LiP), an enzyme produced by white-rot fungi, has garnered attention for its ability to degrade complex organic pollutants, including lignin-derived compounds and various synthetic dyes as well as the urgent need for effective biocatalysts in waste treatment processes is also addressed. LiP offers a great deal of promise for use in a number of industrial areas, including food, cosmetics, second-generation biofuels, bio-pulping, and bio bleaching. Dual functions of LiP as a crucial biocatalyst include lignin depolymerization and enzyme immobilization. Furthermore, we have discussed innovative strategies for the immobilization of LiP on magnetic nanoparticles found in lignocellulosic biomass. This not only enhances the efficiency of lignin valorization processes but also promotes sustainable practices in biorefineries, paving the way for the development of eco-friendly industrial applications. As closing remarks, the overall advantages of lignin peroxidases as well as several important potential uses have been described.

Keywords: Lignin peroxidase, Lignin modifying enzymes, Depolymerization, Environmental pollutants, Bio fuel

Introduction

Lignin is a complex polymer made up of phenylpropane units interconnected by a variety of ether and carbon bonds [1]. Lignin is made of phenolic units (p-hydroxyphenyl, guaiacyl and syringyl), which contributes to its stiffness and resistance to degradation (**Figure 1**) [2]. Oxidative enzymes, such as lignin peroxidase (LiP), manganese peroxidase (MnP) and laccase (LAC), emitted by a filamentous organism from the class basidiomycetes, are the primary chemicals having the choice to degrade the unmanageable plant cell-wall constituent called lignin. Phenyl propanoid units are connected by various non-hydrolysable C-C and C-O bonds in this somewhat different and many-sided biopolymer [3]. The deterioration of lignin in nature is primarily caused by white-decay basidiomycetes, a highly specific group of microorganisms that secrete a consortium of oxidative impetuses, resulting in a finished surface and a whitish variety of spoiled wood. White-decay basidiomycetes deteriorate lignin by means of the cooperative action of classII heme-containing peroxidases and laccases, the main ligninolytic compounds, as well as a variety of helper catalysts. The oxidation of substrates is catalyzed by lignin peroxidase, manganese peroxidase, and adaptable peroxidase, which use hydrogen peroxide (H_2O_2) as an oxidant [4].

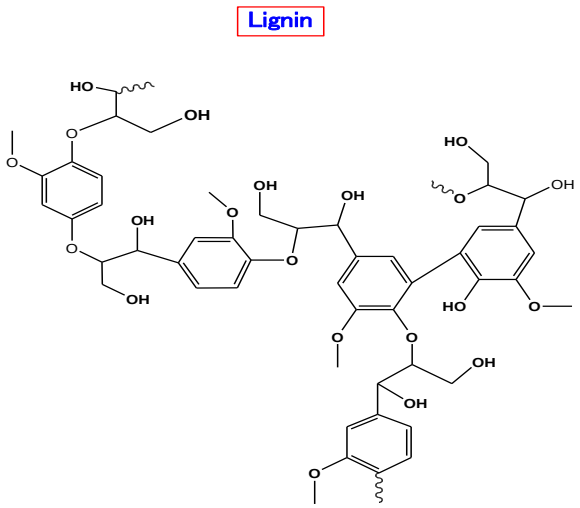

Figure 1 Two-dimensional structure of lignin polymer molecule [5].

Ligninolytic compounds have likely applications in endless fields, including the synthetic, fuel, food, agribusiness, paper, material and restorative ventures. Ligninolytic organisms, especially white-rot fungus, which are members of the basidiomycetes class, produce a variety of oxidative enzymes, including laccases, manganese peroxidases, and lignin peroxidases, which help break down lignin [4]. This oxidative degradation results in the formation of various valuable derivatives, including p-coumaryl alcohol, coniferyl alcohol, and sinapyl alcohol, which are monolignols that serve as building blocks for lignin synthesis (**Figure 2**) [5]. Their capacities to take out xenobiotic substances and produce polymeric things make them astoundingly effective for bioremediation purposes [6]. Ecological biotechnology is the utilization of all pieces of biotechnology to deal with normal issues [7]. Consequently, the turn of events, biosecurity application, and guideline of organic frameworks for the remediation of polluted conditions like land, water, and air that lead to clean advancements and reasonable improvement are instances of natural purposes of biotechnology [8]. This survey gives a brief show on the enzymatic difference in lignin to significant items, with unprecedented thought in regards to the job of parasitic lignin peroxidases. Business utilizations of lignin peroxidases are analyzed, including biofuels, bio pulping and bio-remediation, food and corrective enterprises, and bioremediation. The headway, hardships and state of the art philosophies to create and deliver this chemical fiscally for modern and biotechnological applications will be highlighted

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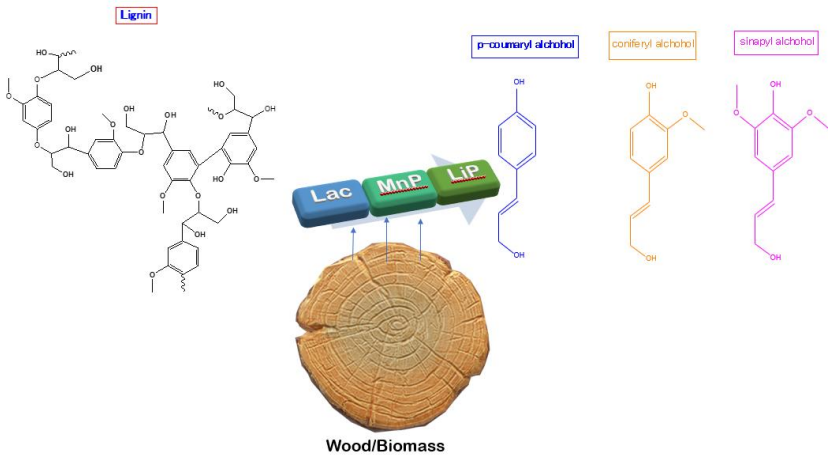


Figure 2 Lignin degradation.

Methods and discussion

This review encompasses crucial aspects of LiP, including the sources and classification of lignin. These classifications illustrate the complexity of lignin with different phenolic structures linked via C-C and C-O bonds, which affect its reactivity and potential as a feedstock for multiple applications. This review highlights the key applications and advantages of lignin peroxidase (LiP) across diverse fields. The study reveals the remarkable efficiency of LiP in degrading recalcitrant compounds, which are often resistant to traditional treatment methods. LiP's role in the biofuel sector plays a vital role due to its ability to catalyze the degradation of lignin within lignocellulosic biomass, which significantly enhances the production of fermentable sugars for bioethanol synthesisas seen in the treatment of corn stover, ultimately leading to higher glucose yields. This enzymatic action increases the glucose yields from biomasses as well as aids in the fermentation process by fostering yeast activity, converting sugars into bioethanol and CO_2. The pharmaceutical industry benefits from LiP through its ability to facilitates the biotransformation of drugs which can thereby enhance drugs efficiency. For example, the degradation of pharmaceutical pollutants, including drugs such as diclofenac, underlines its potential for environmental cleanup efforts in wastewater treatment. Furthermore, in the food industry, LiP's ability to degrade phenolic compounds enhances food safety and food quality as it helps flavors through the production of natural compounds like vanillin and o-quinones. This functionality aligns with consumer demand for clean and high-quality food and beverages.

Lignin

Lignin is a complex aromatic polymer which is primarily found in cell wall of plant, which provides structural support and rigidity. After cellulose it is the second most found biopolymer on earth [9-11]. **Table 1** shows lignin content in various lignocellulosic materials, respectively.

Sources of lignin

Lignocellulosic biomass

These are plant-based material which are composed of cellulose, hemicellulose, and lignin. Lignin shares dominant composition in lignocellulosic biomass.

Table 1 Highlights the lignin content in lignocellulosic materials.

Lignocellulosic materials	Lignin (%)	References
Hardwood	18 - 25	[12]
Softwood	25 - 35	[12]
Corn cobs	15	[12]
Wheat straw	15	[13]
Rice husk	18	[12]
Grasses	10 - 30	[12]
Sugarcane Bagasse	20	[12]
Sweet sorghum	21	[13]
Cotton seed hair	0	[13]
Paper	0 - 15	[12]
Newspaper	18 - 30	[13]
Waste Chemical pulp	5 - 10	[13]
Primary waste	24 - 29	[13]

Lignocellulosic materials	Lignin (%)	References
Cattle manure	3 - 5.7	[13]
Bamboo	20 - 30	[14]
Hemp	15 - 25	[15]

Pulp and paper industry

Industrial lignin is majorly produced by the byproduct of pulp and paper industry. Approximately 50 - 70 million tons is produced. This includes kraft lignin (KL) which is produced during the kraft pulping process. Kraft lignin breaks lignocellulosic biomass by using sodium hydroxide and sodium sulfide. Nearly about 50- 90 million tons of KL is produced per year, with only about 2 % being utilized for value-added products [16]. Sulfite lignin is also produced through the sulfite pulping process, here in this method wood is treated by various sulfite salts. This pulping process generates around 7 million tons of lignin per year [17].

Soda lignin is generated as a by-product from flax and the soda via anthraquinone process. This product is used in South American and Asian developing countries as a fiber source for the production of paper and other hardwood pulp for packaging papers and board's application. The soda pulp mill shave very low production capacity due to annual feed stock variability. The reduction of chemical oxygen demand (COD) has been observed about 50 % as lignin removed from the effluent and increase the economic rational of the mill. India and France were the 2 countries pioneering in establishing soda lignin recovery services [17]. However, there is room for much advancement in these facilities that need to be equipped in the coming years.

Bio-ethanol production

Third-generation bioethanol production from lignocellulosic materials also reflects significant contributions in sourcing lignin. For every kg of ethanol produced, nearly about 0.5 kg of lignin is generated, which leads to extraction of about 200,000 tons of lignin per year [11]. Other industrial sources like wood processing industries also contribute to lignin production, making it a valuable resource for various industrial applications [17]. The primary focus of ethanol production is sugar extraction, with little attention paid to the structural and chemical examination of the by-product lignin. For both economic and environmental reasons, lignocellulosic biomass is a better option for producing ethanol than sugar. It is anticipated that transportation fuel in the future will need to come from lignocellulosic biomass. As a result, it is anticipated that lignin and bioethanol production would rise during the coming years.

Classification of peroxidase enzymes

Class I enzyme

Class I enzymes are basically enzymes that catalyzes oxidation-reduction reaction, particularly in context of lignin degradation. These enzymes are characterized by their ability to facilitate the transfer of electrons from a substrate to an electron acceptor, where hydrogen peroxide (H_2O_2) act as a co-substrate in their catalytic reactions [16]. Its catalytic mechanism often involves the reduction of H_2O_2 to water. Furthermore, these enzymes oxidize a wide range of substrates, including both phenolic and non-phenolic compounds. This broad specificity is essential for their role in lignin degradation [18,19]. Class I enzymes include several key oxidoreductases like lignin peroxidase (LiP), produced by white-rot fungi such as *Phanerochaete chrysosporium*, which catalyzes by cleaving C-C and C-O bonds [20], manganese peroxidase (MnP), also from white-rot fungi, which utilizes manganese ions for the oxidation of phenolic compounds and also to facilitate lignin degradation and laccase, primarily found in various fungi and bacteria, catalyzes using molecular oxygen as an electron acceptor. Additionally, cytochrome P450 enzymes, found in various organisms, are also involved in the oxidation of various organic substrates including steroids, fatty acids, and xenobiotics [21].

Class II peroxidases

Class II peroxidases, also known as lignin-modifying enzymes (LMEs), are a group of heme-

containing enzymes that play a crucial role in the degradation of lignin and other phenolic catalytic mechanisms and substrate specificities vary among class II peroxidases. These enzymes need heme groups in order to carry out their catalytic activity. These enzymes can carry out oxidative reactions because the iron in the heme group contributes to the activation of hydrogen peroxide [22]. These enzymes often work by generating reactive intermediates, including compound I, which can oxidize a range of substrates, including phenolic compounds and lignin [23]. Hydrogen peroxide is usually needed for the reaction as an electron acceptor compounds [24]. It is a lot of perceived that class II peroxidases can oxidize substrates that are either phenolic or non. Since it licenses tangled lignin plans to be isolated even more really, this versatility is major for both natural cycles and biotechnological uses.

Class III peroxidases

Class III peroxidases are widely present in plant kingdom and account for almost 70 % of the total plant-derived peroxidases. Different sources belonging to this group of peroxidases have been the subject of several studies in the context of environmental bioremediation, such as, horseradish peroxidase (HRP), soybean peroxidase (SBP) and ginger peroxidase (GP) [30-32]. Class III peroxidases have very similar structure to that class II peroxidases, plant secreted peroxidases are also involved in the hydroxylation of an important number of various chemical structures which differ from the peroxidative cycle [33]. Once H_2O_2 react with the heme of peroxidase in native state, an intermediate comprising an oxo-ferryl Fe (IV) center and a cationic radical porphyrin is generated, called compound I. The next step in the catalytic cycle is the formation of compound II and free radical from a reducing substrate. Compound II is then returned to the resting state of the enzyme by the reduction of a second molecule of the substrate [34,35]. Reaction of excess hydrogen peroxide with resting state enzyme gives compound III which is a catalytically inactive intermediate.

Table 2 Classification of peroxidase enzymes along with their sources.

Family	Enzyme	Source	Reference
Class I	Ascorbate peroxidase (APX)	*Brachypodium dystachion*	[25]
	Catalase-peroxidase (CP)	*Bacillus* SF	[26]
Class II	Lignin peroxidase (LiP)	*Pichia methanolica* *Ganoderma lucidum* IBL-05	[27-30]
	Manganeseperoxidase (MnP)	*Trametes* sp. 48424	[31]
	Versatile peroxidase (VP)	*Cerrena unicolor* BBP6 *Lentinus squarrosulus*	
Class III	Ginger peroxidase (GP)	Ginger	[32]
	Soybean peroxidase (SBP)	Soybean hulls	[33]
	Horseradish peroxidase (HRP)	Horseradish	[34,36]

Lignin peroxidase

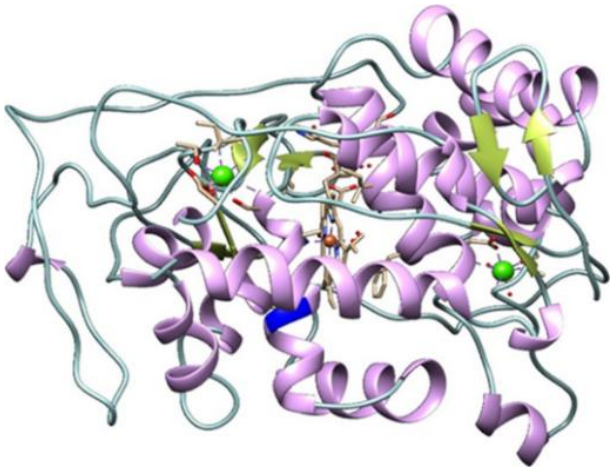


Figure 3 Crystallographic diagram of the *P. chrysosporium* LiPH8 protein, the catalytic Trp171 is colored blue, the calcium particles are green, and the heme group containing the ferric particle is brown. The α-helices and β-sheets are derived from and depicted as green bolts and light purple curls, respectively [37].

The primary and the most focused manufacturers of ligninolytic enzymes such as LiP, also known as diarylpropane peroxidase or ligninase I, are white-rot basidiomycetes [38]. LiP is supplied as a secondary enzyme in producers such as *P. chrysosporium* in response to nitrogen and carbon exhaustion, and it may be hindered by elevated nitrogen concentrations [22,39]. Different LiP-encoding genes are present in *P. chrysosporium* strains, which release the enzyme as different isozymes (H1, H2, H6, H7, H8 and H10), with H8 having the best description [40,41]. Approximately 343 amino acid residues make up this extracellular globular glycoprotein, which has a molecular weight of 38 - 42 kDa [42]. Unique characteristics of lignin peroxidases include, depending on the isozyme, a putative pI of 3.3 - 4.7 and a low optimum pH of 3.0 - 4.5 [43]. Class II peroxidases share a high level of structural homology, including a preserved heme group, calcium-binding sites and disulfide bonds [44]. LiP shares structural similarities with horseradish peroxidase (HRP), including 8 major and minor α-helices [37] and typically few β-sheets in the C-terminal region (**Figure 3**). Lignin peroxidase contains 2 calcium-binding sites that are thought to be essential for maintaining the enzyme's active site, 4 disulfide bonds that maintain the overall protein structure, and pre-summed cysteine residues that shape it [44]. To protect it from proteolytic destruction, the enzyme is N- and O-glycosylated [45]. The heme residue in LiP is inserted between the protein's internal proximal and distal locations. The heme residue for some substrates cannot collaborate or be oxidized because lignin peroxidases have a smaller heme access cavity than old-style peroxidases like HRP and the parasite coprinus cinerea peroxidase (CiP), which has a low redox potential. Veratryl alcohol (VA; 3,4-dimethoxybenzyl alcohol), a distinctive phenolic substrate of LiP, is released with LiP in native producers. It functions as a small diffusible redox bridge to change inaccessible substrate [46]. This tool utilizes the abnormal collaboration between a fragrant substrate, such lignin, and the protein dynamic site [47]. Regardless of middle individuals, lignin peroxidases are the fair ligninolytic molecules that catalyze the oxidation of the sweet-smelling phenolic and non-phenolic units of lignin. Trp171, which is connected to the heme bunch, is credited with completing this long-range electron transfer (**Figure 3**). Although the final option employs Trp164, the Trp171 residue located at the protein's outer layer is a remarkable feature of both LiP and VP [48,49]. MnP lacks the Trp171 enzyme, making it unsuitable for oxidizing high-redox chemicals. Furthermore, the penta-worked iron porphyrin ring at the special location that produces a single electron rather than exactly another heme-containing peroxidase is credited with the limit of LiP's ability to oxidize high-redox potential combinations [44].

Sources of lignin peroxidase

Since the discovery of white-rot fungi, lignin peroxidase (LiP) and its sources have been known to play. The study of lignin-decomposing fungus and bacteria has enhanced our understanding of lignin degradation which is a crucial process in both natural ecosystems and industrial applications. The first lignin-degrading fungus notably identified was *Phanerochaete chrysosporium*, which was isolated in the early 1980s. As a part of the class Basidiomycetes, *Phanerochaete chrysosporium* was found to produce a wide range of ligninolytic such as lignin peroxidase (LiP), manganese peroxidase (MnP), and laccase,which all together facilitate the breakdown of lignin through oxidative mechanism. The identification of LiP in *Phanerochaete chrysosporium* is marked as a turning point in the study of lignin degradation. The study showed that LiP catalyzes the oxidation of lignin and lignin containing model compounds in the presence of hydrogen peroxide (H_2O_2), which effectively cleaves the C-C and C-O bonds in lignin. This enzymatic ability to oxidize a wide variety of phenolic and non-phenolic substrates also results in the breakdown of lignin into smaller aromatic compounds and phenolic units, making these fungi a focal point for biotechnological applications, particularly in bioremediation and the pulp and paper industry. Over the years, the role of bacteria and fungi, such as *Trametes versicolor*, *Pseudomonas putida* and *Ganoderma lucidum*, has gained recognition because they produce LiP and other ligninolytic enzymes as shown in **Tables 3** and **4**. This recognition has helped expanding the understanding of the microbial sources of LiP and their ecological roles in lignin degradation, addressing environmental challenges and advancing biotechnological solutions.

Table 3 List of lignin peroxidase (LiP) producing fungal genera and species.

Sl. No.	Lignin Peroxidase (LiP) producing Fungal species	Substrate	Reference
1	*Aspergillus niger*	Rice straw	[50,51]
2	*Alternaria* sp.	Rotten wood sample	[52]
3	*Alternaria gaisen TERIDB6*	Wheat straw	[53]
4	*Alternaria* sp.	Effluent sample	[54]
5	*Agaricomycetes* sp.	Effluent sample	[54]
6	*Candida tropicalis*	Wheat straw	[55,56]
7	*Ceriporiopsis subvermispora*	Cedarwood	[57]
8	*Cylindrobasidium evolvens*	Effluent sample	[54]
9	*Daedaleopsis septentrionalis*	Effluent sample	[54]
10	*Ganoderma lucidum*	Pineapple leaves	[58]
11	*Irpex lacteus*	Banana waste	[55,56]
12	*Loweporus lividus MTCC-1178*	Institute of Microbial Technology (Chandigarh, India)	[59]
13	*Lentinula edode LE16*	Sugarcane bagasse	[60]
14	*Lenzites betulinus*	Wheat straw	[55,56]
15	*Phanerochaete chrysosporium*	Wheat straw and cornstalk	[55,56]
16	*Pleurotus eryngii*	Wheat straw	[55,56]
17	*Phlebia radiate*	Wheat straw	[55,56]
18	*Pleurotus ostreatus*	Wheat straw	[55,56]

Sl. No.	Lignin Peroxidase (LiP) producing Fungal species	Substrate	Reference
19	*P. sajor-caju*	Banana waste	[61]
20	*Schizophyllum commune IBL 06*	Banana waste	[62]
21	*Trametes versicolor*	Rice straw	[63]
22	*Trametes versicolor G20*	Bamboo culms	[64]
23	*Trichoderma reesei*	Rice straw	[49,50]
24	*Trichoderma viride*	Wheat straw	[55,65]

Table 4 List of lignin peroxidase (LiP) producing bacterial genera and species.

Sl. No.	Lignin Peroxidase (LiP) producing bacterial species	Substrate	Reference
1	*Bacillus amyloliquefaciens*	Tobacco straw and lignin	[66]
2	*Bacillus licheniformis*	Azure B	[67]
3	*Bacillus megaterium*	Straw grass	[68]
4	*Bacillus* sp.	Pulp and paper mill industry	[69]
5	*Bacillus subtilis*	Lignin compounds, azo dyes	[70]
6	*Brevibacillus agri*	Lignin	[70]
7	*Corynebactrium jeikeium*	Paper mill pulp effluent	[71]
8	*Enterobacter lignolyticus*	Lignin, non-phenolic lignin compounds	[72]
9	*Klebsiella pneumoniae*	Lignin, organic substrate	[73]
10	*Ochrobactrum tritici*	Kraft lignin	[74]
11	*Paenibacillus glucanolyticus*	Kraft lignin	[75]
12	*Pseudomonas aeruginosa*	Lake watercontaining Decomposingplant material	[76]
13	*Pseudomonas putida*	Kraft lignin	[74]
14	*Serratia liquefaciens*	Kraft lignin	[77]
15	*Sphingomonas paucimobilis*	Paper mill pulp effluent	[71]
16	*Streptomyces viridosporus*	Corn stover	[78]
17	*Thermobifida fusca*	Lignin model compounds	[79]

Chemical catalytic mechanism of lignin modifying enzymes (LMEs)

Lignin-degrading enzymes such as, laccases and peroxidases, are utilized *in vitro* enzymatic conversion that presents several advantages over direct microbial conversion, such as improved substrate-enzyme interactions, decreased cultivation times, and enhanced ATP/NAD(P)H balance [80]. Additionally, different yeast species, including *Saccharomyces cerevisiae*, *Yarrowia lipolytica*, *Pichia pastoris*, *Pichia methalonica*, *Kluyveromyces lactis*, *Kluyveromyces maxianus*, and *Cryptococcus* sp. have proven effective in producing laccases and peroxidases using exogenous genes from a range of sources, including *Ascomycota* and Basidiomycota fungi, plants, oomycetes, and bacteria [81]. **Figure 4** illustrates the catalytic pathways of lignin-degrading enzymes for converting lignin-derived compounds into valuable products. It

highlights the breakdown of lignin into aromatic monomers while showcasing how lignin undergoes oxidation and reduction reactions to yield biofuels, biochemicals, and other products, emphasizing the potential of biotechnological approaches in sustainable lignin valorization and the advancement of a circular bioeconomy.

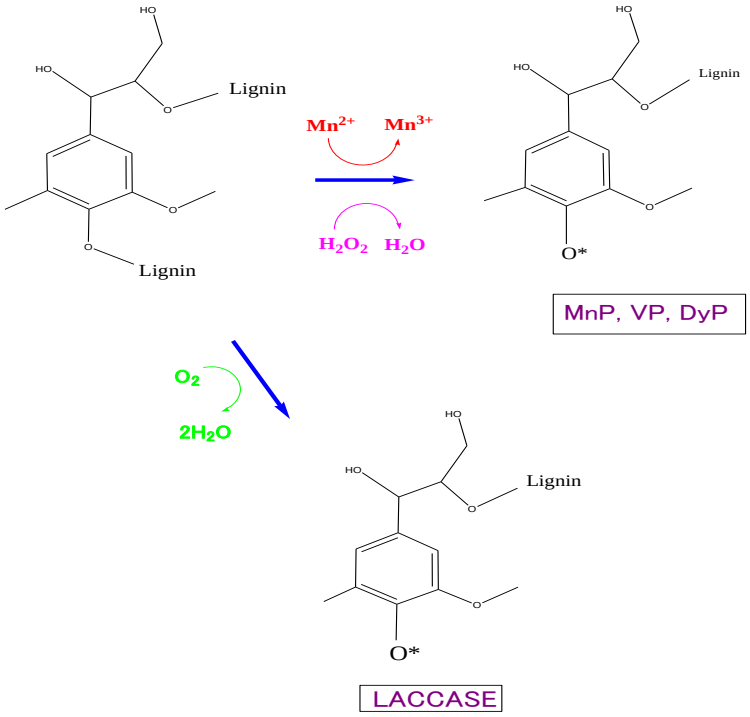


Figure 4 Lignin modifying enzymes (LMEs) include peroxidases (LiP, MnP, VP and DyP), which use a hydrogen peroxide-dependent catalytic mechanism, while laccase (LAC) relies on molecular oxygen (O_2).

Lignin peroxidase (LiP, EC 1.11.1.14) is a highly active enzyme that contains heme (Fe) and is characterized by a high redox potential of 1.4 V. It can effectively act on a wide range of lignin and lignin-derived compounds, including both phenolic and non-phenolic substrates. The crystal structures of LiP have been extensively documented, particularly for fungal sequences, with several entries available in the Protein Data Bank (PDB), such as 1LGA, 1LLP, 1QPA, 1B80, 1B85, 6ISS, and 3Q3U. In contrast, there is a scarcity of bacterial crystal [79,82,83]. For example, the crystal structure of LiP from *Trametopsis cervina* (PDB: 3Q3U) consists of 338 amino acids in a single chain and has an approximate molecular weight of 35 kDa [84]. The secondary structure elements (SSE) of LiP 3Q3U include 35.80 % alpha helices, 7.69 % extended strands, 4.14 % beta turns, and 52.37 % random coils [85]. Similar enzymes, such as DNA ligase D (LigD) from *Sphingobium* sp. SYK-6 (PDB: 4Y9D), also target lignin through β-aryl ether cleavage, comprising 305 amino acids and having a molecular weight of about 32.3 kD [86,87].

One electron's oxidation produces radical cations, which in turn cause side chain cleavage, demethylation, intramolecular incorporation, and molecular rearrangements of the substrate. This is the oxidation mechanism of LiP. Although bacterial-derived LiP has proven effective in breaking down kraft lignin (KL), these enzymes' protein crystal structures are noticeably absent from databases. In general, bacteria are less efficient than white-rot fungus (WRF) at degrading lignin, breaking down xenobiotics, and discoloring dyes. The potential of synthetic or recombinant LiP and dye-decolorizing peroxidase (DyP) variants has also been brought to light by recent investigations. These variants demonstrate greatly improved catalytic capabilities in difficult settings [88-90].

Figure 5 Illustrates the enzyme's catalytic mechanism. Initially, LiP binds to the lignin substrate, positioning the β-O-4 linkage at its active site. The

enzyme then activates hydrogen peroxide (H_2O_2) to form a highly reactive oxo-ferryl species, which facilitates a 1-electron transfer to theβ-O-4 bond, generating a radical cation intermediate. This unstable intermediate undergoes cleavage of the β-O-4 linkage, which results in formation of smaller oxidized degradation products. This reaction is critical for lignin's breakdown, enhancing the accessibility of cellulose and hemicellulose for further processing in biotechnological applications such as biorefinery and bioremediation.

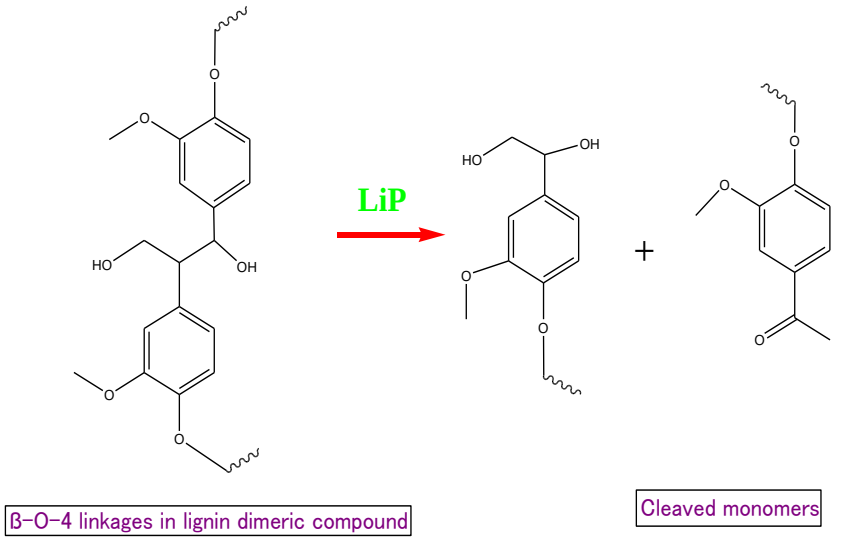


Figure 5 Schematic representation of lignin dimer compounds (β-O-4), catalytic cleavage and cleaved lignin monomer units.

Catalytic mechanism of lignin peroxidase

The catalytic mechanism of lignin peroxidase (LiP) consists of several key steps that facilitate the oxidative breakdown of lignin and its derivatives shown in **Figure 6**.

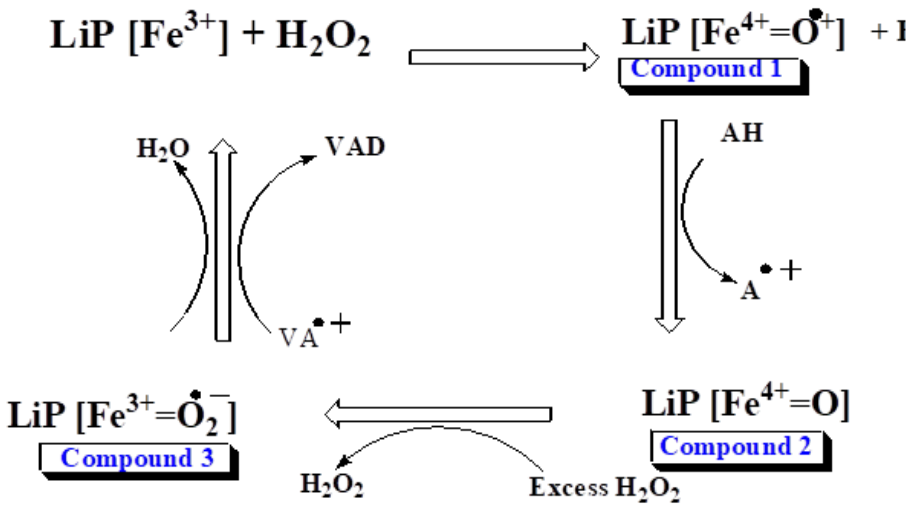


Figure 6 Catalytic mechanism of lignin peroxidase.

The catalytic mechanism of lignin peroxidase (LiP) consists of several key steps that facilitate the oxidative breakdown of lignin and its derivatives. Here's a streamlined overview of the process:

Substrate binding: The mechanism starts when lignin or substrates related to lignin bind to the LiP active site. The structure of the enzyme is specifically made to work well with these substrates. **Hydrogen peroxide activation**: LiP needs hydrogen peroxide as a co-substrate since it has a heme group in its structure. Heme group contains iron atom that can switch between oxidation states (Fe^{2+} and Fe^{3+}). This heme group is pivotal for the enzyme's catalytic function, as it facilitates the transfer of electrons necessary for oxidation reactions. When H_2O_2 binds to the heme iron, it activates the heme and leads to the formation of reactive intermediates, including radical species that can effectively engage in oxidation reactions. For H_2O_2 to be activated, the iron atom in the heme group is essential. H_2O_2 is decreased during restricting to make Compound I, an oxoferryl iron moderate cation broadly engaging.

$$Fe^{3+}\text{ (hemegroup)} + H_2O_2 \rightarrow Fe^{4+}\text{ (ferrylform)} + H_2O + e^- \quad (1)$$

Making of compound I

H_2O_2 decline changes over the heme from its ferric (Fe^{3+}) state to a very responsive ferryl (Fe^{4+}) structure. This center (Compound I) can oxidize many substrates, including both phenolic and non-phenolic compounds [35].

$$Fe^{3+}\text{ (heme group)} + H_2O_2 \rightarrow Fe^{4+}\text{ (Compound I)} + H_2O \quad (2)$$

One-electron oxidation

A 1-electron transfer mechanism is used to oxidize the substrate. In this process, the substrate produces radical cations that aid in the breakage of many bonds in the lignin structure, such as C-C and C-O-C (ether) bonds.

$$R\text{-}OH + Fe^{4+}\text{ (Compound I)} \rightarrow R\cdot + Fe^{3+}\text{ (heme)} + H_2O \quad (3)$$

where R-OH represents a phenolic substrate.

Reactions that follow

The radical cation may experience further reactions after the first oxidation, including 1) Cleavage of side chains: In lignin, oxidation may cause the side chains that are connected to the aromatic rings to split. 2) Demethylation: The elimination of methyl groups from the substrate is known as demethylation. 3) Molecular rearrangements: The oxidation process may cause structural rearrangements in the substrate. 4) Enzyme recuperation: After the oxidation connection, the synthetic ought to return to its dynamic condition. Conventionally, this really expects that for LiP to partake in extra synergist cycles, Compound I ought to be returned to its ferrous state.

$$Fe^{4+}\text{ (Compound I)} + e^- \rightarrow Fe^{3+}\text{ (heme group)} \quad (4)$$

5) Product release: At last, the compound's oxidized things are freed from the powerful site, allowing it to tie new substrate particles and carry on the catalytic activity. LiP is a crucial compound for lignin biodegradation and bioremediation applications because of its ability to separate complex lignin structures, as displayed by this procedure.

Catalytic activity on wide spectrum of chemicals found in the environment

The LiP catalytic cycle is comprised of 3 stages: Compound-I synthesis of oxo-ferryl intermediate (Fe^{4+}), compound-II reduction, and H_2O_2 oxidation of ferric enzyme in a stationary state (**Figure 6**) [48,20]. A lignin model molecule called arylglycerol-aryl ethers of β-O-4 type linkage can be oxidized by synthetic LiP.Benzylic methylene, aldehydes or ketones, phenol oxidation, and 1 electron oxidation are among its oxidative properties. Also, it can oxidize a variety of phenolic compounds, for instance, vanillyl alcohol, acetosyringone, guaiacol, syringic acid, and catechol. Viable wastewater and color treatment has been reported utilizing adsorbents from various sources. Oxidoreductases meaningfully affect the climate and produce no harm during the moderation cycle.

Substrates categorized as non-phenolic and phenolic

As well as aromatic mixtures like guaiacol, vanillic acid, and syringic acid, ligninolytic enzymes can oxidize lignin model dimers and non-phenolic atoms such veratryl alcohol. When it comes to degradation chemicals, β-O-4 lignin with β-aryl ether or β-0-4 lignin connections is the most significant type. Although phenolic units are present in lignin, phenolic

compounds can also be produced via enzyme-catalyzed breakdown.

Oxidation of phenolic substrates

LiP facilitates this oxidation through a 1-electron transfer mechanism, utilizing hydrogen peroxide (H_2O_2) as a co-substrate. For example, when guaiacol (2-methoxyphenol) undergoes oxidation, LiP produces a guaiacol radical, which can react further to yield various products.This radical can go through ring breakage to produce more small phenolic compounds like catechol (1,2-dihydroxybenzene) or even carboxylic acids like acetic acid. It can likewise dimerize with 1 more radical to shape a dimeric particle. One more huge course is the formation of quinones, for example, 2,6-dimethoxybenzoquinone, which are steady substances that can partake in different cycles and help in the overall breakdown of lignin [91,92]. Notwithstanding guaiacol, LiP may likewise oxidize an extensive variety of other phenolic compounds, including catechol and vanillic corrosive (4-hydroxy-3-methoxybenzoic corrosive). Vanillic acid can be oxidized to yield vanillin (4-hydroxy-3-methoxybenzaldehyde) and other oxidation items, while catechol can be changed over completely to o-quinone, which can polymerize into bigger structures.

The flexibility of enzyme in oxidizing an extensive variety of phenolic substrates can be credited to its capacity to make radical intermediates, which can partake in different chemical reactions such side-chain cleavage and demethylation. This expansive substrate selectivity shows that LiP isn't just equipped for debasing lignin, yet additionally a solid match for bioremediation projects that eliminate manufactured dyes and phenolic compounds from the environment [93,94,95].

Figure 7 descripts the oxidation of o-Chlorophenol by lignin peroxidase (LiP) involves several key steps, starting with the formation of a phenoxy radical when o-Chlorophenol interacts with LiP in the presence of hydrogen peroxide (H_2O_2). This process generates a high-valent iron-oxo species that oxidizes the phenolic hydroxyl group. The resulting o-Chlorophenoxy radical can then undergo various reactions, including dimerization to form the first reaction product (2-chloro-6-(2-dichlorophenoxy)-phenol). The reaction proceeds further and a second product appears: 2-chloro-6-(2-dichlorophenoxy)-1,4-benzoquinone.

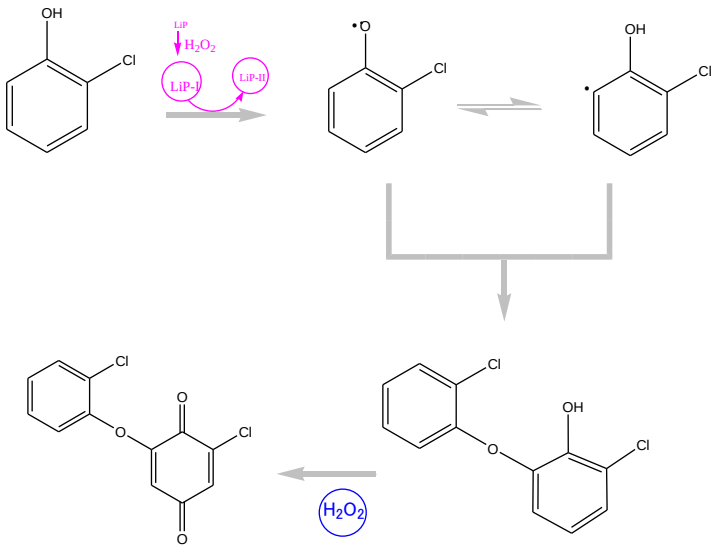


Figure 7 LiP-catalyzed oxidation of phenolic lignin model compound.

Non-phenolic substrate oxidation

LiP oxidizes an extensive variety of non-phenolic compounds, including veratryl achohol (VA) and non-phenolic diaryl-propane structures. Veratryl alcohol is oxidized by LiP, to give an instance, veratraldehyde is produced by the radical cation cycle of α-β(carbon)

interface cleavage. LiP can oxidize β-O-4 arylglycerol-aryl ethers, which are fundamental non-phenolic lignin substrate answerable for lignin structures. These mixtures ought to oxidize to create various oxidized products, for example, acids and aldehydes, which are valuable for isolating complex lignin structures [96,92].

Electron-donating groups can stabilize radical intermediates therefore they help oxidize non-phenolic substrates by the enzyme. LiP aims the non-phenolic group of compounds that have structural affinities towards lignin, as proved by its ability to oxidize dimethyl phenylenediamine. Studies regarding LiP has also revealed that LiP Is its ability to oxidize dimethyl phenylenediamine. Studies regarding LiP has also revealed that LiP is effective in oxidizing other non-phenolic compounds produced during the degradation of lignin, such as guaiacol and syringaldehyde. Because of its wide range of selectivity towards the substrate, LiP serves the potential to be used in bioremediation processes to break down chemicals and produced dyes, among other environmental contaminants. Because LiP is so versatile, it can be used as a viable tool for tackling environmental concerns [92,97].

The first step involves the formation of a high redox potential oxo-ferryl intermediate as result of the reaction of the heme cofactor with H_2O_2. In a second step 2 consecutive 1e-reductions are carried out (**Figure 8**): (i) a 1e-reduction of LiP by a reducing substrate yields to compound II (LiP-II) and a substrate radical cation, and (ii) a 1e-reduction that returns the enzyme to the ferric oxidation state, completing the catalytic cycle. The radical cation of the substrate produced in this cycle undergoes rearrangements and non-enzymatic degradations (**Figure 8**), which in turn leads to a set of reactions that results in lignin depolymerization.

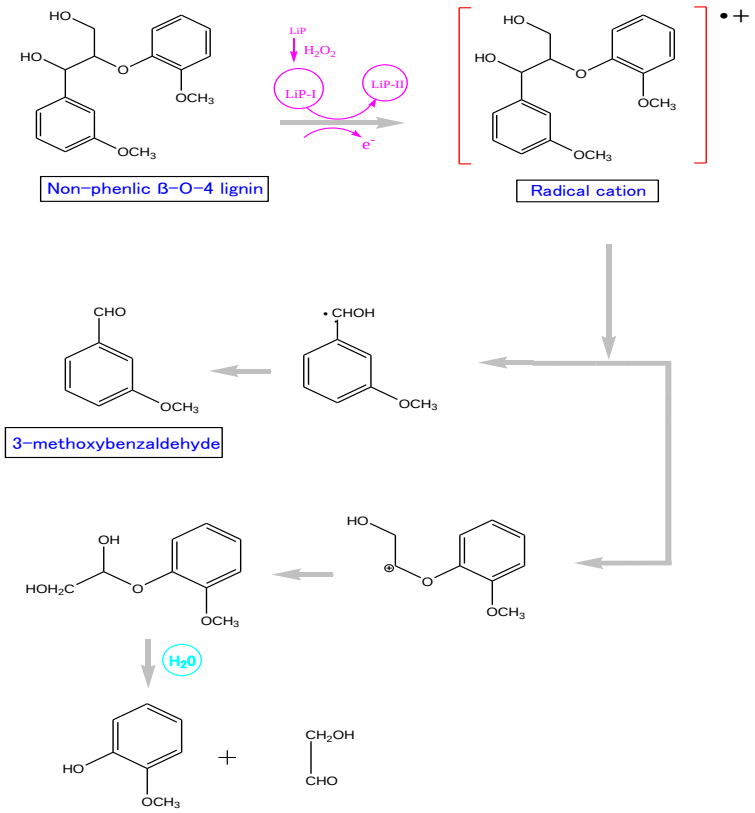


Figure 8 LiP-catalyzed oxidation of non-phenolicβ-O-4 linkage lignin model compound and formation of cleaved products.

Oxidation of veratryl alchohol

Veratryl alcohol is a substrate of the LiP enzyme which is required for the degradation of lignin by the white-rot fungus lignin. Veratryl aldehyde is produced when LiP oxidizes veratryl alcohol. As a result of deprotonation inα-carbon, another veratryl alcohol

molecule undergoes aldehyde production in the course of the process. Additional reactions that occur under aerobic conditions include the breakdown of aromatic rings and quinone. Deprotonation at the α-carbon converts the unstable and transient intermediate known as the veratryl radical cation into a radical intermediate. Veratryl aldehyde can subsequently be created by reacting this intermediate with water. In **Figure 9**, the catalytic mechanism is displayed.

Enzymatic bioconversion plays a crucial role in the biotransformation of lignin-derived compounds, hence making a substantial contribution to the carbon cycle and facilitating bioremediation. Deep research has elucidated the precise mechanics of these reactions, highlighting LiP's role in promoting electron transport and reactive intermediate generation. Furthermore, an in-depth comprehension of these pathways is necessary for the development of enzyme-based solutions to address environmental issues, particularly the degradation of persistent organic pollutants.

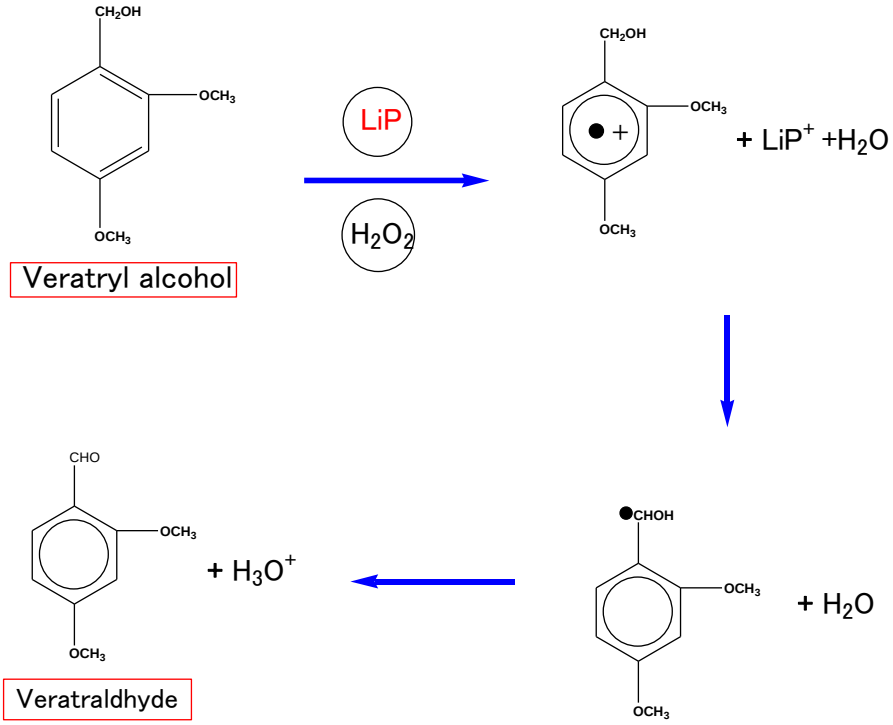


Figure 9 Veratryl alcohol radical cation degradation via α-carbon deprotonation.

Eliminating emerging contaminants through LiP mediation

These days, environmental contaminants (ECs) associated with personal hygiene, biomedicine, cosmetics, and pharmaceuticals are major issues [98]. Wastewater from textile, paper, tannery, pharmaceutical, and household waste is a significant source of environmental pollution [99]. Currently, chemical methods include oxidizers (like chlorine or ozone), acids, alkalis, and other chemicals that facilitate the breakdown of pollutants in wastewater, whereas physical methods involve techniques like adsorption and filtration to remove contaminants without chemical alteration. Despite their cost-effectiveness, these methods often inadequately address complex and persistent emerging contaminants, necessitating more advanced treatment alternatives [99]. Enzymatic-mediated techniques are considered the most efficient and environmentally friendly approaches for biodegradation of various environmental contaminants [100-103]. Multiple ECs are often discharged into water bodies without proper treatment, causing potential health risks and impacting aquatic ecosystems. This section focuses on effective biocatalysts (oxidoreductase) like LiPs used to biodegrade and transform hazardous pollutants [104].

Enzymes with high chemo- and stereoselectivity are recognized as highly effective green biocatalysts for mitigating environmental [99].

Figure 10 illustrates how lignin peroxidase (LiP) effectively catalyzes the oxidation of various emerging contaminants, including phenolic compounds and synthetic dyes, demonstrating its potential application as a biocatalyst in the bioremediation of contaminated environments by breaking down these complex organic pollutants into less harmful substances. LiPs have low substrate specificity, non-specific redox potential, and can oxidize large aromatic phenolic and non-phenolic compounds.

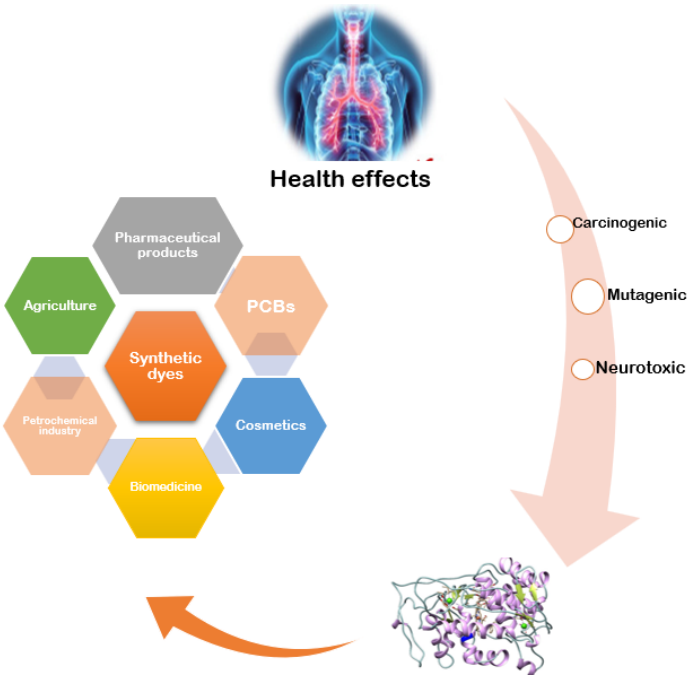


Figure 10 Highlights various contaminants that can be treated by LiP.

LiP mediated dyes decolorization

Different methods for removing dyes from wastewater, including physical, chemical, catalyst, and adsorbent methods, have disadvantages, including environmental impact. Physical chemical processes, adsorption/oxidation, and photocatalytic techniques are often impractical and fail to remove recalcitrant azo dyes. Metal oxides and nano-catalysts have been developed to enhance photocatalytic efficiency for hazardous dye compound treatment. Synthetic dyes from industries like textiles, paper, and leather are challenging to degrade due to their complex molecular aromatic structures. Micro-organism-based treatments are relatively inexpensive and environmentally friendly. White-rot fungi have shown significant strength and efficacy in eliminating dyes using ligninolytic enzymes synthesis. *Phanerochaete chrysosporium* has been found to be more effective in degradation of azo dyes and has significantly increased enzyme activity and stability [105]. Likewise list of dyes from different sources that were degraded by LiP listed in **Table 5**.

Table 5 List of dyes from different sources that were degraded by LiP.

Sl. No.	Dyes	Source	References
1	Acid Orange II	*P. chrysosporium*	[105]
2	Acid blue-158	*Bjerkandera adusta strain*CX9	[106]
3	Anthraquinone alizarin blue	*Trichoderma harzianum*	[107]
4	Black B	*Trichoderma harzianum*	[107]
5	Cibacet brilliant blue	*Trametes pubescens*	[108]
6	Congo red dye	*Bacillus cohnni strain*	[109]
7	Direct red-5B	*Trametes pubescens strain*	[108]
8	Disperse-dye	*Emmia latemarginata,Mucor circinelloides*	[110]
9	Indigo carmine	*Phanerochaete chrysosporium*	[105]
10	Indigo dye	*Emmia latemarginata,Mucor circinelloides*	[110]
11	Pyrogallol Red	*Phanerochaete chrysosporium*	[105]

Catalytic depolymerization of lignin

Lignin depolymerization is often considered challenging because of its structural complexity and strong bonding. Old traditional methods often require critical conditions which leads to low yield of desired products and the formation of unwanted byproducts. Catalytic depolymerization of lignin involves different catalysts to facilitate its breakdown. Catalytic depolymerization includes catalyst like acidic, basic and metal catalyst, these can facilitate the breakdown of lignin into smaller phenolic compounds and also promotes the cleavage of ether. Various types of linkages in lignin and their reactions are crucial as it directly corresponds to development of efficient methods to convert lignin into useful products, that supports waste valorization and sustainable development.

After various different attempts to address catalytic depolymerization of lignin. There are 6 possible main methods that could be useful for catalytic lignin depolymerization: 1) oxidative depolymerization, 2) reductive depolymerization, 3) acid-catalyzed depolymerization, 4) oxidized lignin depolymerization and 5) lignin biochemical transformation. The most eminent method is oxidative depolymerization, this method involves oxidizing agents such as hydrogen peroxide(H_2O_2), oxygen, or ozone to cleave the C-C and C-O bonds of lignin which results in formation of smaller molecular weight aromatic compounds, organic acids like vanillic acid and also primarily aromatic aldehydes like vanillin and syringaldehyde. These byproducts are of high commercial value and adaptability therefore are very suitable in industries including food, fragrance, and chemicals. Another significant approach which involves hydrogen gas or metal catalysts as reducing agents to facilitate the addition of hydrogen to lignin is reductive depolymerization. This method effectively yields valuable products which can be further processed into fuels or solvents like phenolic alcohols. Furthermore, hydrogenolysis, hydrolysis, and pyrolysis are collectively known as hydrothermal treatment is a method for the depolymerization of lignin, this method usually ranges between 100 and 600 °C in the presence of water to promote the breakdown of lignin [111-113]. This process alters with the solubility and reactivity of lignin, leading to the production of valuable phenolic compounds and organic acids.

Enzymatic catalysis is another method which employs specific enzymes such as lignin peroxidase

(LiP) and laccases. This method is advantageous because it can employ in room temperature and pressure, with less use of energy. The enzymes use oxygen or hydrogen peroxide as co-factors, which results in the formation of valuable phenolic compounds that can selectively cleave complex lignin bonds, facilitating its transformation into lower molecular weight compounds that can be utilized in various applications, including biofuels and biochemical.

In the catalytic depolymerization of lignin, LiP is the key enzyme that works effectively in oxidative depolymerization LiP catalyzes to cleave various different linkages within the lignin structure, especially the C-C and C-O bonds, which leads to breaking down of intricate lignin polymer into smaller, more manageable aromatic compounds. LiP can effectively oxidize β-O-4 ether linkages of lignin structure, which builds up as a substantial portion of lignin's inter-unit interactions. In the presence of hydrogen peroxide (H_2O_2), LiP oxidizes leading to the formation of reactive radicals that facilitate the breakdown of lignin into low molecular weight phenolic compounds, like vanillin, p-coumarate, benzoate, catechol and guaiacol. These products are very valuable as it serves as building blocks for various industrial applications, encompassing the production of biofuels and bioplastics. Additionally, LiP can also participate in biochemical transformation processes, where it contributes to the microbial degradation of lignin. Certain fungi like *P. chrysosporium* utilize LiP to degrade lignin in their natural environments, leading to breakdown in the β-1 lignin model compound involving single electron transfer between aromatic rings. Resulting in detoxification of lignin-derived aromatic compounds by catalyzed oxidative cleavage of this enzyme. Enzymatic catalysis of LiP on lignin can result in the cleavage of complex linkages, such as the β-5 and Cα-Cβ bonds, which can further improve the accessibility of lignin for microbial metabolism. This bioconversion helps in recycling of lignin in ecosystems as well as also creates opportunity for biotechnological applications where lignin can be transformed into valuable products through microbial fermentation processes.

Known identified lignin degraded compounds their respective molecular structure is systematically summarized in **Table 7**. Molecular weight is vital for predicting chemical behavior, guiding subsequent applications, and optimizing processes for industrial or research purposes, as different molecular weights are associated with varying properties and potential applications, such as precursors for valuable chemicals or biofuels. Overall, molecular weight serves as an essential characteristic that enhances the characterization and utility of lignin-derived compounds

Table 6 Highlights of various linkage type and their reaction type for depolymerization.

SL. No	Linkage type	Structure	Reaction type	Products	References
1	β-O-4	Ether	Cleavage	Guaiacol, Vanillin and Oligomers	[114]
2	Cα-Cβ	C-C bond	Oxidative cleavage	Syringaldehyde and Acetophenone	[115]
3	β-5	C-C bond	Cleavage	Cresol and Phenol	[116]
4	C-C	C-C bond	Advanced cleavage	Toluene and Xylenes	[117]

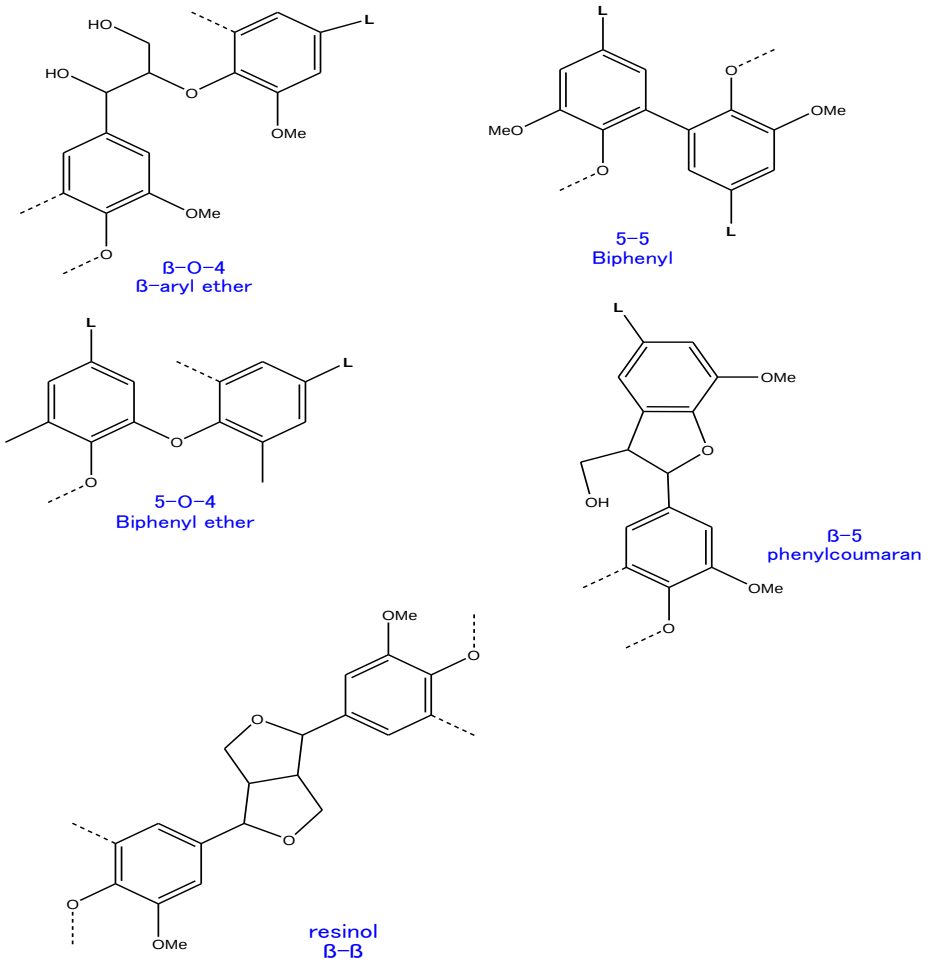
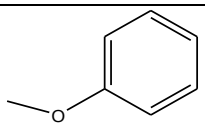
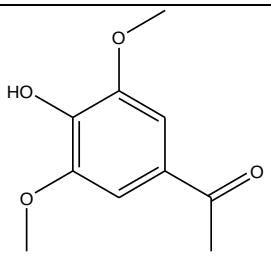
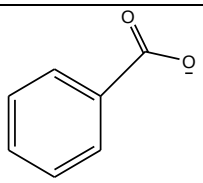
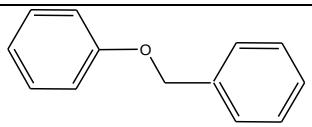
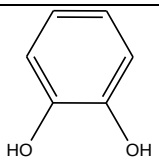
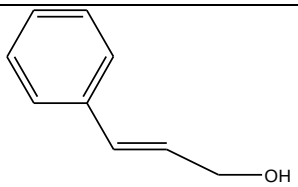
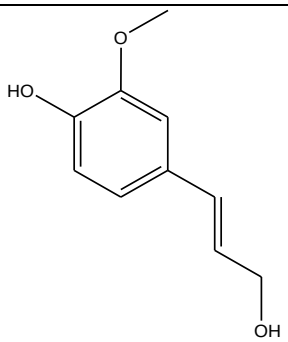
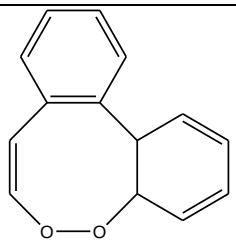
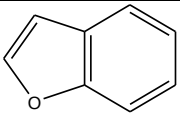
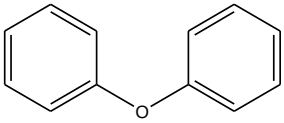
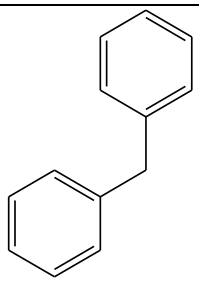
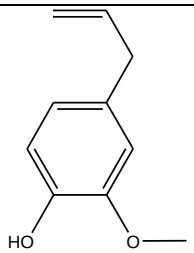
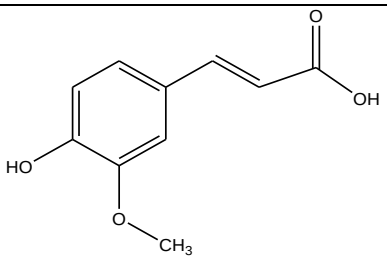
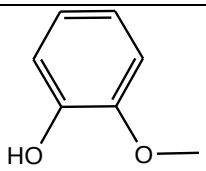
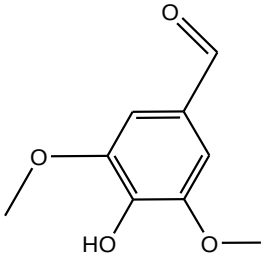
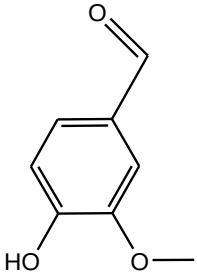


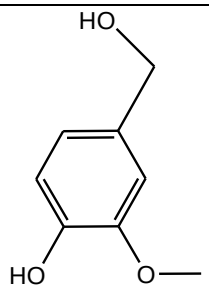
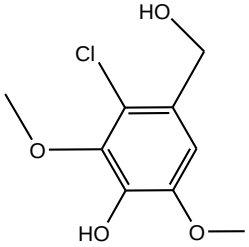
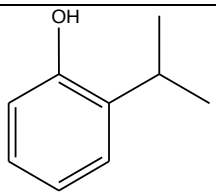
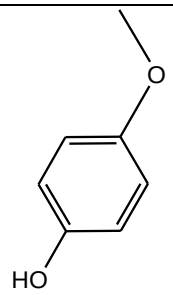
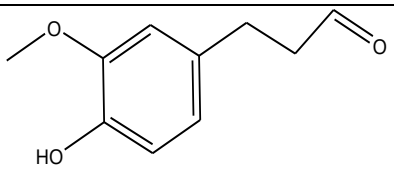
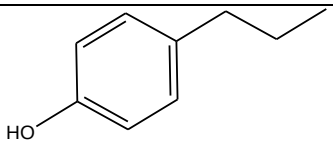
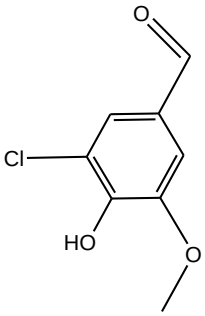
Figure 11 Highlights of different types of lignin linkages.

Table 7 The chemical and molecular formulas of lignin's catalytic depolymerized product into monomers and oligomers are mentioned.

SL. No.	Lignin derived compound	Type	Structure	Molecular weight (g/mol)	Reference
1	Anisole	Monomer		108.14	[118]
2	Acetosyringone	Monomer		196.19	[119]

SL. No.	Lignin derived compound	Type	Structure	Molecular weight (g/mol)	Reference
3	Benzoate	Monomer		144.11	[120]
4	Benzyl phenyl ether	Dimer		184.23	[121]
5	Catechol	Monomer		110.11	[122]
6	Cinnamyl alcohol	Monomer		134.17	[121]
7	Coniferyl alcohol	Monomer		180.20	[121]
8	Dibenzodioxocin	Dimer		210.228	[122]
9	Dihydrobenzofuran	Monomer		120.15	[122]
10	Diphenyl ether	Dimer		170.21	[121]

SL. No.	Lignin derived compound	Type	Structure	Molecular weight (g/mol)	Reference
11	Diphenylmethane	Dimer		168.23	[123]
12	Eugenol	Monomer		164.20	[123]
13	Ferulate	Monomer		193.18	[123]
14	Guaiacol	Monomer		124.14	[124]
15	Syringyl alcohol	Monomer		184.19	[125,126]
16	Vanillin	Monomer		152.15	[123]

SL. No.	Lignin derived compound	Type	Structure	Molecular weight (g/mol)	Reference
17	Vanillyl alcohol	Monomer		154.16	[126]
18	2-Chlorosyringaldehyde	Monomer		216.62	[126,127]
19	2-Isopropylphenol	Monomer		136.19	[122]
20	4-Methoxyphenol	Monomer		124.14	[129]
21	4-Propylguaiacol	Dimer		166.22	[123]
22	4-Propylphenol	Monomer		136.19	[129,130]
23	5-Chlorovanillin	Monomer		186.59	[128]

Potential industrial, environment and biotechnological applications of LiP

LiP serves in diverse applications especially in industrial processes like biofuel production and pulp processing, as well as its environmental role in wastewater treatment and bioremediation. It also showcases its biotechnological potential in enhancing food quality and pharmaceutical efficacy as shown in **Figure 12**.

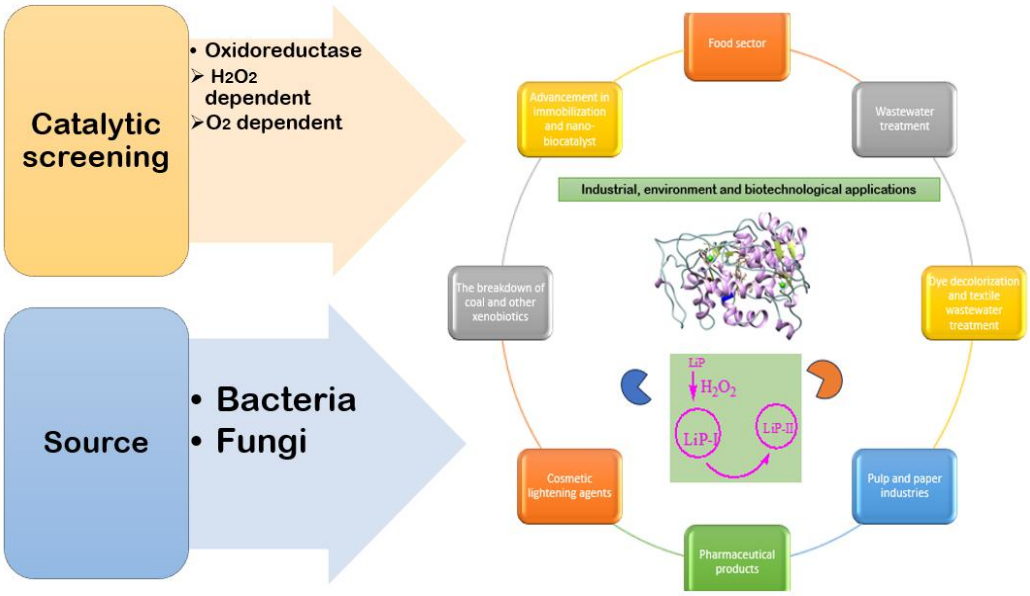


Figure 12 Demonstrating the potential Industrial, environment and biotechnological applications of LiP.

Pulp and paper industries: Remediation, and bio-bleaching

The pulp and paper industry are a critical sector within the global economy, primarily focused on the production of pulp, which serves as the fundamental raw material for paper and related products. The industry employs 2 predominant methods for pulp production: mechanical and chemical pulping. Mechanical pulping involves the physical grinding of wood logs to separate cellulose fibers, while chemical pulping utilizes various chemical agents to dissolve lignin and liberate cellulose, resulting in a higher quality pulp. Apart from specialized pulps made for particular uses like tissue paper, packaging, and premium printing papers, this industry also makes a variety of pulps, both bleached and unbleached. Environmental issues caused by the pulp and paper industry are reforestation, excessive water consumption, and pollution from chemical manufacturing. sustainable and environmentally friendly methods are becoming more and more important. With the proper utilization of bioremediation and lignin-modifying enzymes, particularly lignin from wood, the adverse environmental impacts of industrial wastes are getting significantly minimized. The sustainable and eco-friendly alternative methods for breaking down lignin in wood is offered by a bio pulping via ligninolytic microorganisms, such as lignin peroxidase. *Phanerochaete* strains have been shown to be capable of bio pulping hardwood kraft pulp effectively, with a positive correlation between increased LiP activity and improved pulp brightness and quality [131,132].

In the recent studies the combination of LiP with *Aspergillus* species xylanase have been found to be showing a significant advancement in the removal of lignin and hemicellulose, which leads to high pulp yields while minimizing chemical consumption. This bio pulping process also promotes the production of valuable by-products, including vanillin, for the food and cosmetic sectors [133,134]. All things taken into account, the advancements in bio pulping position it as a competitive alternative for conventional techniques, satisfying customer demand for more ecologically friendly industrial processes. The pulp and paper industry plays a crucial role in the global economy

since it manages sustainability and environmental concerns as well as by supplying valuable resources.

Dye decolorization and textile wastewater treatment

LiP has successfully achieved decolorization rates ranging from 80 to over 90 % for a variety of synthetic dyes, specifically those derived from *Phanerochaete chrysosporium*, including reactive and azo dyes. Dye breakdown has been improved and overall decolorization efficiency has increased when LiP is combined with other enzymes including laccase and manganese peroxidase (MnP). LiP not only decreases dye color but also detoxifies toxic chemicals in wastewater, increasing effluent quality. Studies in the field have effectively treated real textile effluent using LiP, indicating its promise as an industry-wide sustainable solution.

Wastewater treatment and the degradation of emerging pollutants

Eco-friendly treatments for wastewater from a variety of industries, such as food processing, tanneries, textiles, pulp and paper, and distilleries, include lignin-modifying enzymes (LMEs). LMEs, such as lignin peroxidase (LiP), manganese peroxidase (MnP), and laccase, employ oxidative mechanisms using H_2O_2 or O_2 to catalyze the degradation of lignin and other organic compounds in wastewater. These enzymes facilitate the cleavage of complex lignin structures by generating reactive radicals, leading to the oxidation of phenolic and non-phenolic aromatic compounds into smaller, less toxic byproducts like carboxylic acids and aldehydes. This enzymatic action significantly reduces chemical oxygen demand (COD), indicating improved water quality. By enabling effective pollutant breakdown without the need for harsh chemicals, LMEs present a more environmentally friendly and sustainable alternative to traditional wastewater treatments, minimizing secondary pollution and enhancing biodegradability. Non-steroidal anti-inflammatory drugs (NSAIDs) are categorized as emerging contaminants (ECs) concerns because of their toxic nature and possible hazards caused to both human, environmental health as well as its presence in water sources, raises concerning NSAID toxicity, which further adds to contributing to overall pollution and posing risks to aquatic life. In order to address these pollutants and improve the quality of the water, lignin-modifying enzymes (LMEs), which are listed in Table 8, are essential for wastewater treatment.

LMEs are highly effective in degrading rates for various NSAIDs, including naproxen (90 %) and ketoprofen (87 %) using the white-rot fungus *Pleurotus djamor*, as well celecoxib (92 %), diclofenac (96 %), and ibuprofen (95 %) by *Ganoderma applanatum* and *Laetiporus sulphureus* and also with a drug mixture (Celecoxib, Diclofenac and Ibuprofen) Overall degradation efficiency (99.5 %) [135,136]. In the recent studies the ligninolytic fungus *Rhizopus* sp. is utilized to degrade pharmaceutical compounds such as carbamazepine and diclofenac, while laccase-based applications have shown effective measures in removing NSAIDs, including Diclofenac and Naproxen [137,138].

Table 8 List of contaminants degraded via lignin modifying enzymes (LMEs).

SL. no	Substrate	LMEs	References
1	ABTS (2,2′-azinodi-3-ethyl-benzothiazoline-6-sulphuric acid)	Laccase	[91]
2	Acetaminophen	Laccase	[139]
3	Acid Red 299	Laccase	[140]
4	Bisphenol A	Laccase	[140]
5	Bismark Brown R	Laccase	[140]
6	Celecoxib	Laccase,Manganese peroxidase, LiP	[135]

SL. no	Substrate	LMEs	References
7	Diclofenac	Laccase,Manganese peroxidase, LiP	[135]
8	Direct Blue 1	Laccase	[140]
9	Estrone	Versatile peroxidase	[141]
10	Endocrine-disruptingchemicals (EDCs)	Laccase,Manganese peroxidase, LiP	[135]
11	Furosemide	Dye-decolorizing peroxidase	[142]
12	Paracetamol	Dye-decolorizing peroxidase	[142]
13	17β-estradiol	Versatile peroxidase	[141]
14	17α-ethinylestradiol	Versatile peroxidase	[141]
15	2-Mercaptobenzothiazole (MBT)	Dye-decolorizing peroxidase	[142]

High operational costs and technical limitations hinder large-scale implementation [143]. Pretreatment methods, such as flocculants, can significantly reduce chemical oxygen demand (COD) by about 75 % [144]. These reactors effectively remove color, COD, biochemical oxygen demand (BOD), and total dissolved solids (TDS) from wastewater [145]. Ultrafiltration can achieve high removal rates for contaminants, including (97 %) sulphate and (89 %) COD [146,147]. Lignin peroxidase, an enzyme from certain fungi, catalyzes the oxidative breakdown of lignin using hydrogen peroxide. Together, these methods can enhance lignin removal from wastewater, with ozonation potentially pre-treating effluents for better enzymatic degradation. This combination can lead to more efficient treatment and reduced environmental impact. Ozonation is effective for disinfecting wastewater and degrading pollutants. It can significantly lower COD, total organic carbon (TOC), and toxicity in effluents [148]. Using ozonation with photocatalysis effectively reduces TOC, COD, and color in bleached mill wastewater. High ozone doses can achieve 95 - 97 % color removal in as little as 15 min [148].

Lignin peroxidase is an essential enzyme specifically beneficial for wastewater treatment in industries that produce lignin-rich effluents. The enzyme efficiently breaks down lignin, a complex organic polymer, as well as other organic contaminants present in wastewater enhances biodegradability while also helping with detoxification and color removal. When combined with other treatment techniques lignin peroxidase can perhaps yield useful byproducts like biofuels. Utilizing lignin peroxidase minimizes the need for harsh chemical treatments, this environmentally method highlights the importance of lignin peroxidase in the search for long-term, practical wastewater treatment solution.

Advancement in immobilization and nano-biocatalyst

The schematic illustration of immobilization strategies for efficient bio catalysis depicts several methods used to attach enzymes, such as lignin peroxidase, to support materials, enhancing their stability and functionality has been demonstrated in **Figure 13**. Key strategies include physical adsorption, where enzymes are weakly bound to a support surface; covalent binding, which utilizes strong covalent bonds for stable attachment; cross-linking, forming stable enzyme aggregates through chemical links; microencapsulation, where enzymes are encapsulated in tiny protective capsules for improved stability; and membrane immobilization, which employs semi-permeable membranes to retain enzymes while allowing substrate access [149-150]. Each method presents unique advantages and limitations, tailored to specific application needs, thus optimizing enzymatic reactions in various industries such as bioremediation and biotechnology.

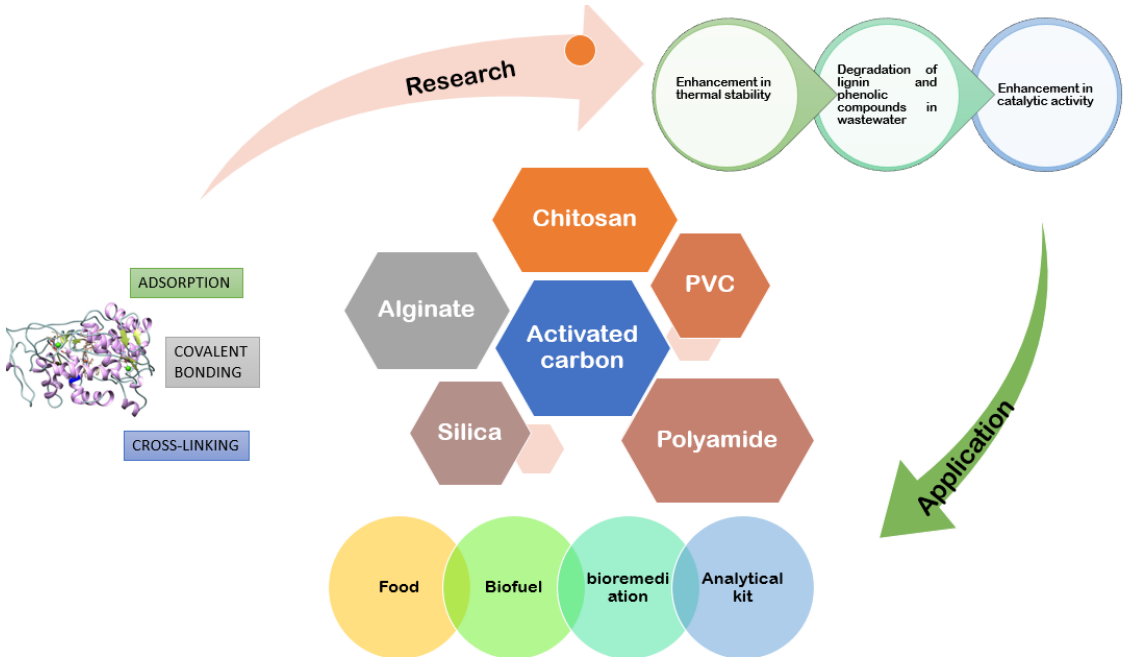


Figure 13 Demonstrates the uses of lignin peroxidase immobilization.

Numerous nanomaterials like graphene oxide, carbon nanotubes, and magnetic nanoparticles are reported as it supports for the immobilization of lignin peroxidase [151,152]. Nanomaterial possesses a large surface area, which makes it easier to insert more enzymes and increase catalytic efficiency. Immobilizing lignin peroxidase on magnetic nanoparticles improves the stability of the enzyme and facilitates simple separation and recycling. Immobilization enhances LiP's thermal and functional stability. Studies have revealed that immobilized enzymes are more resistant to denaturation at different range of pH and temperature, which is important for industrial application. Immobilized LiP's are more active than free enzymes, especially when inhibitory compounds are present in lignocellulosic biomass. Lignocellulosic biomass may sometime contain a variety of inhibitory chemicals like organic acids, sugars, and phenolic compounds that can minimize the activity of enzymes. Because of these inhibitors, immobilized lignin peroxidase is better able to sustain its activity as compared to free enzymes.

The most sustainable and eco-friendly synthesis of nanoparticles for enzyme immobilization, specifically for lignin peroxidase, is by using biogenic techniques. The process of creating nanoparticles by biogenic techniques involves the use of natural resources such bacteria, fungi, plants, and chitosan. For example, in lignocellulosic biomass, the production of silver nanoparticles (AgNPs) from plant extracts such as green tea can improve the stability and catalytic performance of immobilized lignin peroxidase against inhibitors [153]. Gold nanoparticles (AuNPs), produced by fungi like *Fusarium oxysporum*, increase the thermal stability and activity of lignin peroxidase, also facilitating the production of biofuel and bioremediation [154]. Iron oxide nanoparticles (Fe_3O_4), produced by bacteria such as *Bacillus subtilis*, make it simple to recover immobilized lignin peroxidase using magnetic fields, hence enabling recyclability and making it cost effective [155]. Lignin peroxidase is used to functionalize chitosan-derived nanoparticles, exhibiting increased stability and activity in lignin degradation and qualifying them for use in biorefineries [156]. In recent years, a lot of progress has been made but still more study is required to address the possible toxicity and scalability of the nanomaterials utilized in enzyme immobilization.

Bio fuel

Several applications can be served by Lignin peroxidase (LiP) in biofuel production, particularly for instance, in the conversion of lignocellulosic biomass into renewable energy. LiP is essential for the production of bioethanol and bioremediation. In bioethanol production, the degradation of lignin in corn

stover is enhanced by LiP, resulting in improved glucose yields during enzymatic hydrolysis. In bioremediation, LiP-producing fungi like *Phanerochaete chrysosporium* are used to degrade lignin in paper mill sludge, resulting in fermentation of the released sugars into bioethanol [157]. Fungal strains like *Trametes versicolor* and *Ganoderma lucidum* shows high lignin peroxidase (LiP) activity [158]. LiP can be harvested by the growth of theses fungi and can also use to boost the conversion of biomass into fermentable sugars involved in the process of generation of biofuels. This strategy indicates an environmentally beneficial way to use waste materials while production of sustainable biofuels.

For lignocellulosic biomass production used in the generation of biofuel, LiP and laccases working together is essential. With the use of both LiP and laccases, enzymatic activity eventually gets increased and also serves the potential to reduce the total expenses related to the manufacture and processing of enzymes.

Cosmetic lightening agents

Melanin is responsible for skin and hair color by converting tyrosine which is an amino acid. The oxidation of melanin is gaining the significant focus for developing new cosmetic lightening agents, as it helps reduce pigmentation and dark spot [20].

Due to the rise in concerns regarding the safety and effectiveness of hydroquinone (a conventional skin-lightening agent), researches have now started prompting the search for safer alternatives. Hydroquinone works by inhibiting the enzyme tyrosinase, which is for melanin synthesis, thereby reducing melanin production [159,160].

Ligninolytic enzymes, particularly lignin peroxidase, have shown a promising potential in oxidizing melanin directly, making them suitable for cosmetic applications [20]. Recent studies reveal that crude lignin peroxidase from *Phanerochaete chrysosporium* can successfully decolorize synthetic melanin, indicating its potential in skin-lightening products [161]. According to studies, LiP creams may have fewer adverse effects compared to traditional hydroquinone creams and can provide faster skin-lightening results. LiP cream was preferred over 2 % hydroquinone cream due to its better outcomes in improving skin roughness and texture [159]. **Figure 14** shows an in-depth explanation of the chemical processes along with the molecular mechanism involved in the melanin oxidation process by lignin peroxidase is given in the following.

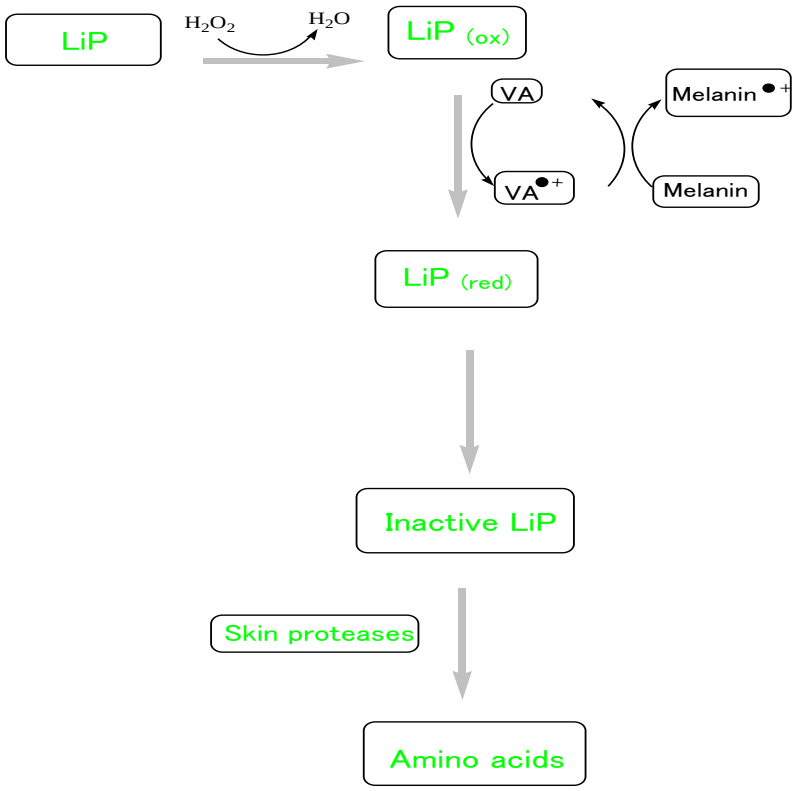


Figure 14 Reaction mechanism of LiP in melanin oxidation.

Ligninperoxidase activation

Here, the high-valent iron-oxo species (Fe^{4+}), also known as Compound I, is produced by oxidizing the ferric form of LiP (Fe^{3+}).

$$LiP\ (Fe^{3+}) + H_2O_2 \rightarrow LiP\ (Fe^{4+}) + H_2O \quad (5)$$

Melanin oxidation

Melanin and oxidized LiP interact. Melanin (also known as $Melanin^+$) is oxidized when LiP (in its oxidized form) gives the melanin polymer an electron. The ferric state (Fe^{3+}) is revered by the enzyme.

$$LiP\ (Fe^{4+}) + Melanin \rightarrow LiP\ (Fe^{3+}) + Melanin^+ \quad (6)$$

Reactive intermediate formation

Free radicals and other reactive intermediates can be produced when melanin oxidizes. For example, the oxidation of a phenolic unit in melanin can be represented as:

$$Melanin^+ \rightarrow Melanin\ radical + H^+ \quad (7)$$

Melanin decolorization

Melanin degradation might result in molecules that are less pigmented and smaller. The general response can be summed up as follows:

$$Melanin\ radical \rightarrow Smaller\ Products \quad (8)$$

These tiny products usually have a lighter tint or are colorless, which adds to the appearance of lighter skin.

LiP inactivation

Due to the change in the pH, the LiP enzyme may become inactive. The skin's very own proteases and glycosidases can then hydrolyze this inactive form into its more basic parts.

$$LiP\ (Fe^{3+}) \rightarrow Inactive\ LiP \quad (9)$$

Food sector

Lignin peroxidase also plays a crucial role in the food sector. Similarly LiP also serves in enhancement of waste management practices via bioremediating

food waste by effectively breaking down phenolic compounds that result in unpleasant odours. With the treatment of lignocellulosic materials, like corn stover with LiP can enhance their digestibility, making them more beneficial as animal feed [160].

Table 9 Various applications of lignin peroxidase in food sector.

SL. no.	Application	Properties	Reference
1	Baking	Increase strength, stability and texture.	[162-164]
2	Beer stabilization	Removal of polyphenols	[162,164]
3	Animal feed	Enhance their digestibility, making them more beneficial	[163,164]
4	Flavor	Source of natural aromatics, production of vanillin.	[163,164]
5	Fruit juice	Improves the clarity and flavor of the juice	[162,164]
6	Wine	Effectively reduces astringency and enhances the overall sensory profile of the wine	[162,164]

One of the significant applications is its ability to biodegrade phenolic compounds, which can enhance food quality, safety and generating flavour compounds, especially vanillin. LiP catalyses the oxidation of guaiacol to form vanillin through the following reaction.

$$C_7H_8O_2 + H_2O_2 \xrightarrow{LiP} C_8H_8O_3 + H_2O \quad (10)$$

$$\text{Catechol} + H_2O_2 \xrightarrow{LiP} \text{o-Quinone} + H_2O \quad (11)$$

Similarly, in the fruit juice processing, LiP degrades chlorogenic acid via an oxidative mechanism, this reaction leads to the breakdown of chlorogenic acid, improving the clarity and flavor of the juice. LiP helps break down phenolic compounds in fruit juices and wines, reducing undesirable flavors and astringency. This enhances the flavor and fragrance of the final products, satisfying the consumer demand for natural and clean-label options in the food and beverage industry [164]. In the field beverage industries, LiP catalyzes the oxidation of catechins through 2-electron transfer mechanism which effectively reduces astringency and enhances the overall sensory profile of the wine. Furthermore, in the field of baking industry, LiP catalyzes the oxidation of ferulic acid through a radical-mediated mechanism which results in enhancing dough machinability and improving the texture of baked goods [164]. LiP is classified as food-grade when produced using organisms like *Cyberlindnera jadinii*, which is recognized by regulatory agencies such as the FDA (Food and Drug Administration) for use in food and feed applications [165]. The recombinant strain ZHMX4, engineered to express the lip gene from *Phanerodontia chrysosporium*, demonstrates enhanced enzyme activity and genetic stability, making it a promising candidate for lignin degradation in industrial processes [161]. The purification of LiP involves multiple steps: harvesting biomass, disrupting cells, concentrating the enzyme through precipitation, and applying various chromatography techniques to achieve a high level of purity while retaining the enzyme's activity. These steps are crucial for ensuring the enzyme's suitability for safe use in food and agricultural industries.

Conclusions

In conclusion, lignin peroxidase represents a crucial biocatalyst with very notable potential for addressing a variety of environmental challenges, particularly in the of department of bioremediation and sustainable biofuel production. Its ability to degrade complex organic pollutants plays a key role in wastewater treatment and the detoxification of

industrial effluents. Future research directs, more exploration in the field of genetic engineering of fungal strains and in the integration of nanotechnology, which promises to enhance the efficiency and applicability of lignin peroxidase in various industrial processes. Furthermore, interdisciplinary collaboration will be essential in harnessing the full potential of LiP, as the demand for eco-friendly practices continues to rise, lignin peroxidase stands out as a promising tool for creating a cleaner and more sustainable future.

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