



Ligninolytic Microbes and Their Role in Effluent Management of Pulp and Paper Industry

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Abstract

Environmental hazards caused due to pollutants introduced into the environment by utilization of natural resources have been of great concern, with the industrialization at a faster pace. Pulp and paper industries utilizing wood as basic raw material comprise three important constituents: cellulose, lignin and hemicellulose. Lignin and hemicellulose contents are removed from cellulose fibres for production of high quality paper. Lignin is the most recalcitrant and non-hydrolysable component, and is difficult to degradation. Delignification/ decolourization of lignin during chemical bleaching leads to generation of highly toxic, mutagenic and carcinogenic pollutants such as chlorophenols, extractable organic halogens and organic halogens, polychlorinated biphenyls and polychlorinated dibenzodioxines affecting environmental communities. Hence, environmental-friendly approaches alternative to traditional bleaching have gained great attention. Microorganisms such as bacteria, actinomycetes and fungi possess unique strategy to overcome the limitation of lignin degradation. Fungi such as white-rot, brown-rot and soft-rot are potent lignin-degrading microorganisms, among them white-rot fungi are widely reported for extensive and rapid degradation due to the presence of complex system for production of extracellular enzymes such as lignin peroxidase, manganese peroxidase and versatile peroxidase. Brown-rot fungi, unlike white-rot fungi generally possess

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B. K. Kashyap et al. (eds.), *Waste to Energy: Prospects and Applications*, https://doi.org/10.1007/978-981-33-4347-4_13

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nonenzymatic oxidation reaction mechanism that produces hydroxyl radicals via Fenton chemistry. Soft-rot fungi such as *Fusarium*, *Aspergillus*, *Trichoderma*, *Penicillium*, *Alternaria* and *Xylaria* mainly degrade non-woody biomass by following the soft-rot decay process. Bacterial lignin degradation mechanisms are more specific than fungi and possess advantages over fungal degradation, like tolerance to wider range of temperature, pH, oxygen limitations, etc. and easy to genetically manipulate for over-production of lignin-degrading enzyme. Several strains of bacteria such as *Pseudomonas*, *Burkholderia*, *Bacillus*, *Ochrobactrum*, *Leucobacter*, *Rhodococcus*, etc. have reported for high level ligninolytic enzymes production. This chapter reviews the unique properties of microorganisms for potential application in biobleaching of pulp to reduce the burden of harmful by-products released in environment.

Keywords

Effluent · Pollutants · Waste management · Ligninolytic · Bacteria · Fungus

13.1 Introduction

Pulp and paper industry is the largest consumer of freshwater, generating a large amount of wastewater (effluent) causing a significant impact on the environment worldwide (Mehmood et al. 2019). Paper industry is one of the oldest and core industrial sectors in India, which comprises about 1.6% of total world paper and paperboard production (Kulshrestha 1972; Dey 2014; Singh 2017). Pulp and paper industries produce a significant amount of effluents containing various contaminants depending on the type of processes followed in the industrial plants. The generated effluents are highly toxic and potentially harmful and dangerous, which deserves assiduous disposal approach, and therefore should be treated in wastewater treatment plants for removal of pollutants before being released to the natural environment. In India more than 650 paper mills producing different types of paper products use a wide variety of cellulosic and non-cellulosic raw materials with annual water consumption of 905.8 million m³ at a rate ranging between 150 and 250 m³/ton of product and around 695.7 million m³ wastewater is being discharged annually by this sector (Kumar et al. 2017).

The raw material for Indian pulp and paper industry comes from three primary sources (Figs. 13.1 and 13.2) (Balakrishanan 1999; Beeindia 2015):

1. Forest wood: About 43% of raw material is sourced from bamboo and mixed hardwoods from forest felling, and eucalyptus wood from plantations (both organized plantations and farmers' fields/agroforestry plots).
2. Agricultural residues: About 28% of raw material for pulp and paper industries supplied from bagasse, rice, wheat straws and cotton stalks.
3. Waste paper: About 29% raw material for pulp and paper industries is recovered by recycling of domestic and imported waste paper.

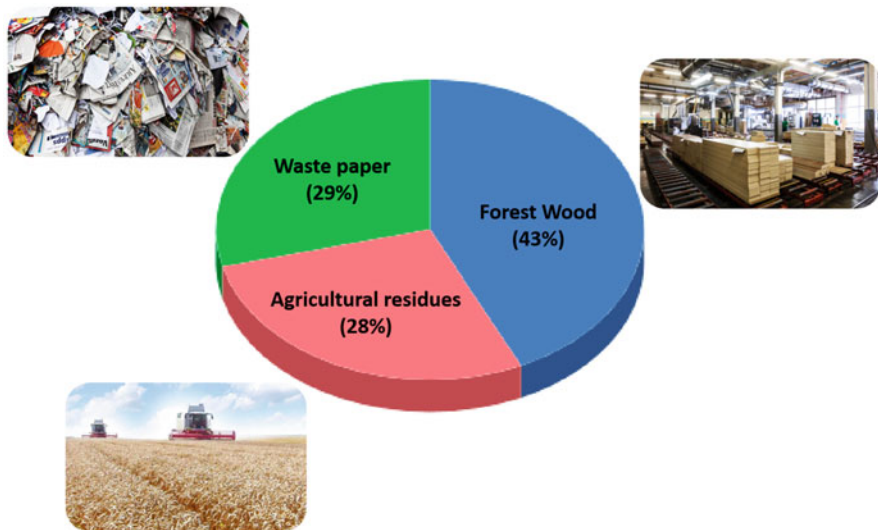


Fig. 13.1 Types of raw material used for pulp and paper industry

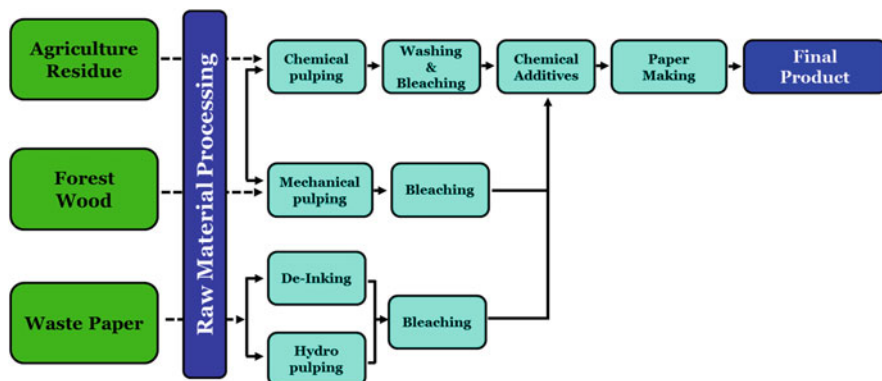


Fig. 13.2 Raw materials and their processing stages in the paper formation. *Source:* Satija (2018)

Among the raw materials, wood is the basic raw material used in paper production, which comprises of three essential constituents: cellulose, lignin and hemicellulose. The paper formed is a thin, nonwoven fabric produced by removing water from a slurry of plant fibres, and then compressing into a thin sheet. Conversion of wood to paper is accomplished by removing the lignin and hemicellulose contents from cellulose fibres. However, presence of too much lignin within the fibres, for instance for newsprint manufacturing by wood pulp is done by simply ripping the

fibres out of the wood, which will not bond well together resulting in the production of a very weak paper. Such paper also gets discoloured on standing, due to chemical changes caused in the lignin by light. Therefore pulp manufacturers prefer to dissolve and remove the lignin out of the wood by chemical solutions (Paliwal et al. 2015). Use of these chemicals in a process for removal of lignin leaves behind vast amounts of by-products such as chlorophenols, polychlorinated biphenyls, dibenzodioxins, etc. which are highly pollutant.

13.1.1 Lignin

Lignin is an aromatic biopolymer most abundantly found in the biosphere, contributing about 30% of total plant biomass (Zhu et al. 2017). It is the most crucial renewable resource of organic carbon on earth (Boerjan et al. 2003). It is a natural composite material providing the strength and rigidity in all the vascular plants (Brown 1985). Lignin is found in the cell wall of plants in association with cellulose and hemicellulose. It is the most recalcitrant component of the plant cell wall (Zhu et al. 2017) because inter-unit bonds in lignin are not hydrolysable and are challenging to degrade either chemically or biologically. Lignin surrounds cellulose in the plant cell wall forming a matrix, which is itself resistant to degradation. The strength and rigidity of stems in higher plants are the results of production and deposit of cellulose, hemicellulose and lignin in the plant cell walls (Fig. 13.3).

The primary precursors for p-hydroxyphenyl (H), guaiacyl (G) and syringyl (S) units of lignin are p-coumaryl alcohol, coniferyl alcohol and sinapyl alcohol, respectively (Fengel and Wegener 1989; Brunow 2001) (Fig. 13.4). Lignin is the polymer of these complex phenylpropanoid components cross-linked together through various covalent bonds (e.g. carbon-carbon, ester and ether linkages) (Brunow 2001).

By decreasing water permeation across the cell wall, lignin renders the plant resistant to biodegradation as well as to environmental stresses (Eriksson et al. 1990). Biochemically, lignin is an aromatic, amorphous, heterogeneous, three-dimensional, cross-linked polymer with low viscosity and insoluble in water. The molecular mass of lignin is high (600–1000 kDa), although not uniform, varying greatly within isolated samples (Kirk and Farrell 1987). The molecular mass of lignin is thus difficult to determine, and use of a conventional formula is not possible (Brunow 2001).

Lignin is generally removed from pulp by a chemical and mechanical process, and about 90–95% lignin dissolved in water and generated wastewater is known as black liquor. One of the commonly followed methods for removal of lignin from wood is known as the kraft process. In the kraft process, a solution containing sodium hydroxide and sodium sulphide is used for cooking, and the output of dark solutions of the degraded lignin is known as black liquor.

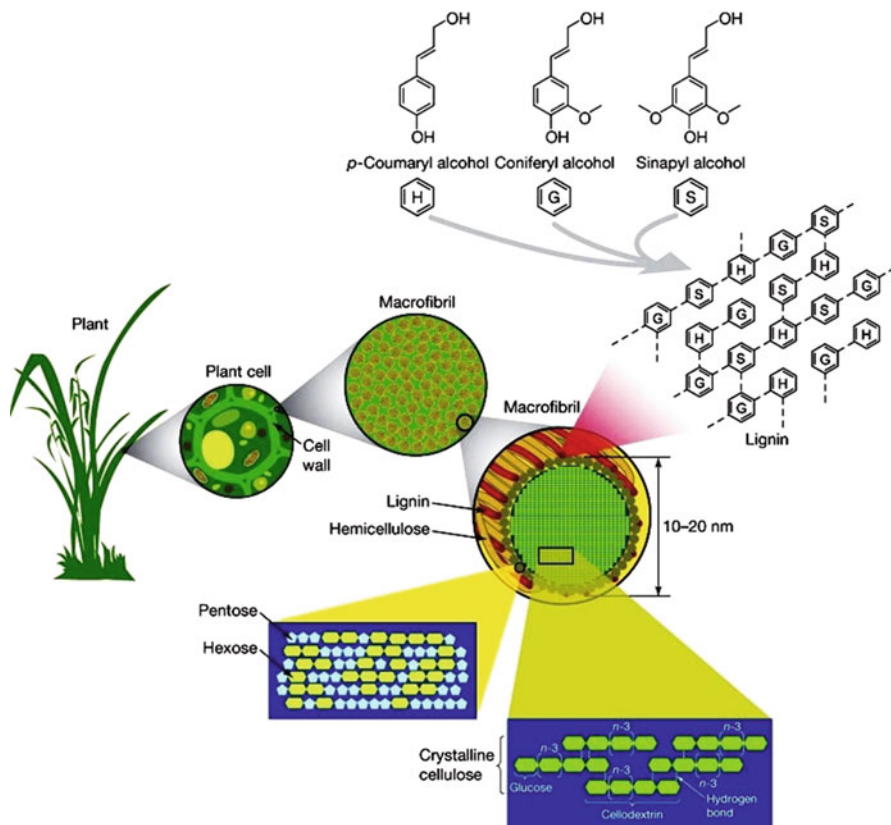


Fig. 13.3 Structure of lignocellulose biomass. *Source:* Rubin 2008

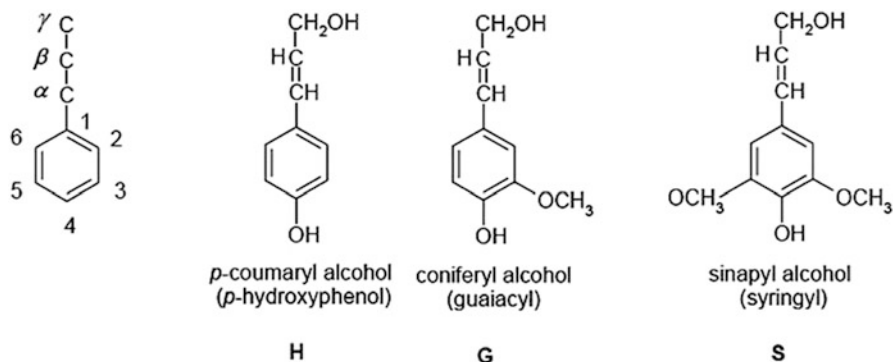


Fig. 13.4 A phenylpropanoid unit and precursors of lignin. Names in parentheses refer to the corresponding phenylpropanoid units in a lignin molecule. *Source:* Buswell et al. 1987

13.1.2 Papermaking Process

The papermaking process takes place in three significant steps: wood pulping, pulp bleaching and papermaking (Fig. 13.5).

13.1.2.1 Wood Pulping

Wood pulping is the initial stage of the papermaking process in which the wood is processed to form the pulp. All the impurities like soil, dust, bark, cellulose, hemicellulose, lignin, etc. are removed during the pulping process. The pulping process is the primary source of the most pollutant of the paper industry. A large amount of water is needed during the pulping process, causing the generation of high amounts of wastewater (Pokhrel and Viraraghavan 2004).

The wood pulping process is followed by several steps described below.

1. Wood preparation

In this step, all the impurities like soil, dirt, bark, etc. are removed from woods and are then chipped, separated and cleaned by water.

2. Wood pulping

The cleaned wood chips cooked at high temperature, pressure and high alkaline pH solution of sodium hydroxide (NaOH) and sodium sulphide (Na_2S). Approximately 95% of the total lignin is dissolved in pulping liquor (black liquor).

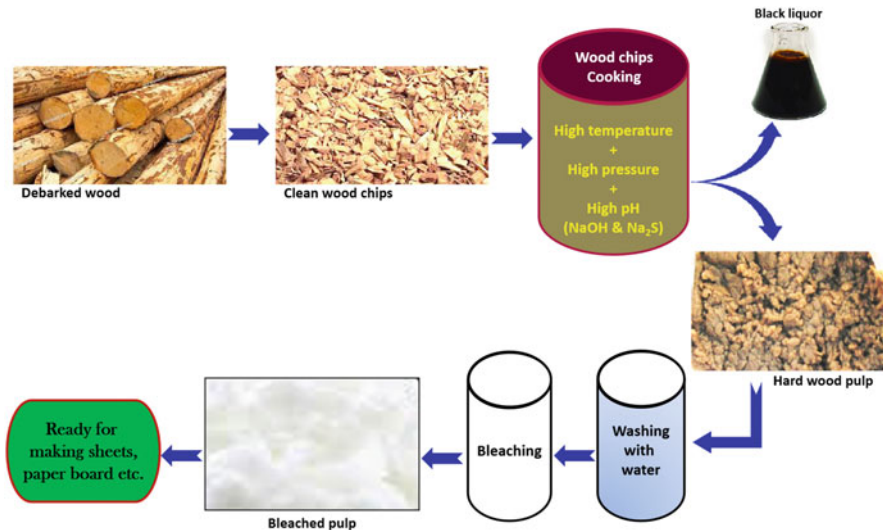


Fig. 13.5 Process of transformation of wood to paper

3. *Pulp washing*

The cooked pulp contains cooking chemicals, lignin and other extractives from the wood which is removed by washing with water.

4. *Pulp screening*

Pulp screening involves sieving of formed pulp to remove pulp knot and uncooked fibres clumped together from the wood pulp.

13.1.2.2 Pulp Bleaching

Pulp bleaching is the process to whiten and brighten the pulp and is done in two steps. Initially, pulp is treated with sodium hydroxide (NaOH) in the presence of oxygen, which removes hydrogen ions from the lignin and then oxygen breaks down the polymer. Subsequently, the pulp is treated with chlorine dioxide (ClO₂), a mixture of NaOH, oxygen (O₂) and peroxide and finally with ClO₂ again to expel remaining lignin.

During the bleaching process, chlorine molecules react with a phenolic constituent of the wood pulp leading to the formation of a large number of toxic chlorinated organic contaminants. High energy and freshwater is required for bleaching process and generate effluents containing a high concentration of compounds like chlorophenols, extractable organic halogens (EOXs) and absorbable organic halogens (AOXs), as well as a small proportion of extremely toxic PCBs (polychlorinated biphenyls) and PCDDs (polychlorinated dibenzodioxines) (Suntio et al. 1988). Chlorinated organic compounds formed due to chlorine compounds used for the bleaching process are released into the environment, which is known to have toxic, mutagenic and carcinogenic effects (Bajpai and Bajpai 1997).

13.1.2.3 Papermaking

This is the final stage of papermaking process in which pulp fibres are mechanically treated to make unique properties as per requirements, and finally pass through continuous moulds/wires to shape smooth and dried sheets.

13.1.3 Environmental Pollution

Lignin is the primary source of pollution in the wastewater formed in pulp and papermaking industries. Lignin is one of the important components of wood, and its degradation by-products, built during the process of cooking and bleaching, are major wastewater contaminants. The pulp is rinsed to free from residues of the liquors and discarded from the mills after preliminary treatments, and is generally runoff into local streams or rivers. To remove all the lignin from the crude pulp, the pulp must be bleached, and the bleaching solutions and washings lead to chlorinated lignin, which are major pollutants when released in the environment. To reduce load of pollution formed during the pulping process, researchers are trying to find

alternatives of wood pulping and bleaching methods to avoid chlorine or pollutants. Poorly treated or untreated effluents are responsible for a considerable amount of pollutants when discharged to watercourse such as a river, lake, ponds, etc. These pollutants can be described by total solids (TS), total dissolved solids (TDS), total suspended solids (TSS), chemical oxygen demand (COD), biochemical oxygen demand (BOD), metals, toxicity and colour (Pokhrel and Viraraghavan 2004). The higher amount of water is utilized in wood pulping and paper production, which causes the generation of large amounts of wastewater (Nemerow and Dasgupta 1991). Industrial effluents are accountable for the thermal impacts, slime growth, scum formation, and furthermore the aesthetic beauty loss in the environment (Pokhrel and Viraraghavan 2004). Paper and pulp mill processes water, contains high chemical diversity of organic pollutants causing high toxicity effects on aquatic communities (death to zooplankton and fish), as well as profoundly affecting the terrestrial ecosystem when discharged into the recipient watercourses (Yen et al. 1997; Pokhrel and Viraraghavan 2004).

Establishment of stringent government rules for controlling pollution, and due to public awareness, paper mills are under pressure to ensure a decrease in the level of chlorinated lignin residue in the effluent through changing the production process and applying improved treatment technologies. Although total chlorine-free (TCF) bleaching using ozone, oxygen and hydrogen peroxide is found to be an alternative to replace conventional chlorine bleaching, implementation of these methods involves high capital investment for process change and also would be economically unfeasible for small-scale pulp paper industries. Increasing awareness about environmental concerns has led the paper industry to look for cleaner production option aimed at the reduced consumption of chlorine and its compounds in the bleaching sequence, which thereby minimizes the discharge of chlorinated compounds in the effluent.

13.2 Biobleaching

The problems caused by chemicals used in bleaching forced industries to consider alternative and new environmentally friendly methods. One such a biological alternative to traditional bleaching was found through the discovery of oxidative enzymes termed as biobleaching. Utilization of lignin-degrading organisms and their enzymes became the highly attractive alternative methods. The ability of microorganisms to break down the lignin molecules has paved the way for providing environmental friendly technologies for the pulp and paper industry.

Biobleaching is an alternative process for chemical bleaching in which microbes or their enzymes are used to remove residual lignin and hemicellulose contents from the cellulosic pulp. Recently, biological methods have been paid more attention to lignin degradation (Mathews et al. 2016; Ebanyenle et al. 2016). Different types of ligninolytic microorganisms such as bacteria, actinomycetes and filamentous fungi are able to biodegrade lignin components to some extent. The high recalcitrant complex structure and the presence of irregular hydrolysable bonds in the lignin

are the cause for restricted metabolization by most of the microorganisms. However, there are microorganisms possessing unique strategy and advantage to overcome the restriction and limitations for degradation of lignin. These ligninolytic microorganisms are known to degrade the lignin, and among them, the fungus is the most efficient lignin-degrading microbes. Apart from the ligninolytic fungal species, several bacterial and actinomycetes also exhibit the ligninolytic activity.

13.3 Fungus and Lignin Degradation

Fungi are well-described microorganisms for lignin degradation, however, among more than one million known species only a few are wood-rotting fungi belonging to the phyla Basidiomycota and Ascomycota and grouped in white-rot, brown-rot and soft-rot fungi (Paliwal et al. 2015) as per their wood degradation capability (Tables 13.1, 13.2, and 13.3). Recently, several basidiomycetous fungal species have been studied intensively, and on the basis of lignin removal and degradation ability, white-rot fungi are the most efficient microbes able to mineralize the lignin extensively. Most of the white-rot fungi grow on hardwoods, while few species such as *Phellinus pini*, *Heterobasidion annosum* and *Phlebia radiata* grow on softwoods (Blanchette 1995).

Lignin degradation requires extracellular enzymes and fungal species have secreted a wide range of ligninolytic enzymes including lignin peroxidase (LiP), manganese peroxidase (MnP) and laccase, which can degrade lignin and another recalcitrant compound (López et al. 2017; Hatakka 2001; Kirk and Farrell 1987). Attack of fungi to lignin is an oxidative and non-specific process leading to decrease in the phenolic, methoxy and aliphatic content of lignin, breaking the aromatic rings, and forms new carbonyl groups. Such changes lead to depolymerization of lignin molecule and production of carbon dioxide (Kirk and Farrell 1987).

13.3.1 White-Rot Fungi

White-rot fungi are widely explored and studied organism for depolymerization of wood components like cellulose, hemicelluloses and lignin (Paliwal et al. 2015). About 60 years ago, Fukuzumi has studied the degradation of lignin through white-rot fungi and confirmed the degradation through *Poria subacida* (Peck) Sacco (Fukuzumi 1960). White-rot fungi and related litter-decomposing fungi can degrade lignin more rapidly and extensively than any other microorganisms (Kirk and Farrell 1987; Hatakka 2001) (Table 13.1). The growth substrates of white-rot fungi are cellulose and hemicelluloses, and lignin is not used as a carbon source. However, they have developed a complex system for the production of the extracellular enzyme, which helps in lignin degradation. Thus, lignin degradation is essentially a secondary metabolic process and occurs at the end of primary growth by secondary metabolism in deficiency of nutrients, such as nitrogen, carbon or sulphur (Kirk and Farrell 1987; Hatakka 2001; Paliwal et al. 2015).

Table 13.1 Studies on activities of white-rot fungi in the treatment of lignocellulosic biomass

Microorganisms	Activities	References
<i>Phanerochaete sordida</i> YK-624	High lignin degradation ability by secretion of lignin peroxidase and manganese peroxidase enzymes	Wang et al. (2020)
<i>Phanerochaete chrysosporium</i> , <i>Lentinula edodes</i> , and <i>Trametes versicolor</i>	Synergistic action of electro-Fenton processes and these fungi are superior for lignin degradation (82–89%).	Hou et al. (2020)
<i>Pleurotus ostreatus</i> 3004 CCBAS 278 and <i>Irpex lacteus</i> 617/93	Have capability of biodegradation of dental care antimicrobial agents Chlorhexidine and octenidine	Linhartová et al. (2020)
<i>Trametes</i> , <i>Spongipellis</i> , <i>Dichomitous</i> , <i>Calocybe</i> , <i>Lepista</i> and <i>Panus</i>	Presence of versatile peroxidase	Chaurasia and Bhardwaj (2019), Chen et al. (2010), Moreira et al. (2007), Ruiz-Dueñas et al. (2008)
<i>Pleurotus ostreatus</i>	Degrade lignin through ligninolytic enzymes laccase, LiP, MnP	Metri et al. (2018), Fitria (2008)
<i>Ganoderma applanatum</i>	About 40.9% lignin degradation	Čilerdžić et al. (2016)
<i>Porodaedalea pini</i>	Lignin-degradation activity through the production of xylanase and endoglucanase	Sunardi et al. (2016)
<i>Lentinus tigrinus</i> LP-7 and <i>Irpex lacteus</i> KB-1.	Kappa number reduction and enhancement of brightness	Afrida et al. (2014)
<i>Pholiota adipose</i> – <i>Armillaria gemina</i>	1:2 ratio most effective	Dhiman et al. (2015)
<i>Pycnoporus sanguineus</i>	Biobleaching of kraft pulp of <i>Eucalyptus globulus</i> by laccase	Martin-Sampedro et al. (2015)
<i>Trametes versicolor</i> , <i>Trametes hirsute</i> , <i>Trametes velutina</i> , <i>Trametes villosa</i>	Potent lignin-degrading white-rot fungi	Quintana et al. (2015), Bourbonnais et al. (1995), Jönsson et al. (1995), Wu et al. (2011), Wang et al. (2013a), Ahn et al. (2007)
<i>P. ostreatus</i> <i>P. Pulmonarius</i>	20-fold increase in hydrolysis	Castoldi et al. (2014)
<i>Irpex lacteus</i>	43.8% of lignin degradation, saccharification efficiency increases sevenfold	Song et al. (2013)
<i>Trametes velutina</i> D10149	85% of lignin removal	Wang et al. (2013a)
<i>Pleurotus eryngii</i>	Versatile peroxidase (VP) was the first time described	Martinez et al. (1996)
<i>Phlebia</i> sp. MG-60	40.7% of lignin degradation after 56 days aerobic incubation	Kamei et al. (2012)

(continued)

Table 13.1 (continued)

Microorganisms	Activities	References
<i>Punctularia</i> sp. TUF20056	53.3% lignin removal from bamboo	Suhara et al. (2012)
<i>T. versicolor</i> , <i>Pycnoporus coccineus</i> , <i>T. hirsute</i>	High laccase production	Wu et al. (2011), Bourbonnais et al. (1995), Jaouani et al. (2005)
<i>Phanerochaete chrysosporium</i> , <i>Phanerochaete sordida</i> YK-624, <i>Trametes versicolor</i> , <i>Coriolus versicolor</i> , <i>Schizophyllum commune</i> , <i>Tinctoporia borbonica</i> , <i>Phlebia radiata</i> , <i>Dichomitus squalens</i> , <i>Bjerkandera</i> sp.	Lignin degradation in pulp and paper mill wastewater	Mäkelä (2009), Katagiri et al. (1997), Eaton et al. (1982), Hirai et al. (1995), Archibald et al. (1997), Kirk et al. (1976), Belsare and Prasad (1988), Fukuzumi (1980), Palma et al. (2000)
<i>Phanerochaete sordida</i> YK-624	Novel lignin peroxidases (YK-LiP2)	Hirai et al. (2005)
<i>Ceriporiopsis subvermispora</i>	11 different isoforms of manganese peroxidase (MnP)	Hofrichter (2002)
<i>Phlebia</i> sp. MG-60	Strong lignin degradation capability especially in a hypersaline environment	Li et al. (2002)
<i>P. chrysosporium</i> and <i>T. versicolor</i>	Produce laccase and manganese peroxidase (MnP)	Katagiri et al. (1997)
<i>P. chrysosporium</i> , <i>T. versicolor</i> , <i>P. sordida</i> YK-624, <i>Ceriporiopsis subvermispora</i> and <i>Bjerkandera</i> sp. BOS55	Delignify kraft pulp	Moreira et al. (1997), Katagiri et al. (1995), Reid et al. (1982), Hirai et al. (1995), Christov et al. (1996)
<i>Heterobasidion annosum</i> , <i>Phlebia radiata</i> and <i>Phellinus pini</i> ,	Grown on softwoods, involved in lignin degradation	Blanchette (1995)
<i>P. Chrysosporium</i>	Manganese peroxidase (MnP) discovered	Glenn and Gold (1985), Kuwahara et al. (1984), Paszcynski et al. (1985), Paszczyński et al. (1986)
<i>Phanerochaete chrysosporium</i>	First ligninolytic enzyme lignin peroxidase (LiP) isolated	Tien and Kirk (1984)
<i>Pleurotus ostreatus</i>	35% of lignin reduction	Hatakka (1983)
<i>Poria subacida</i> (peck) Sacco	Lignin degradation reported	Fukuzumi (1960)

13.3.1.1 Ligninolytic Enzyme

White-rot fungi are involved in the degradation of cellulose, hemicellulose and lignin by the production of a number of extracellular enzymes including cellulases, xylanases, hemicellulases, laccases and peroxidases, such as lignin peroxidase (LiP),

Table 13.2 Studies on activities of brown-rot fungi in the treatment of lignocellulosic biomass

Microorganisms	Activities	References
<i>Phellinus noxius</i>	Brown root rot pathogen, secretes enzymes for potential degradation of diverse wood substrates	Ibarra Caballero et al. (2020)
<i>Gloeophyllum trabeum</i> , <i>Piptoporus betulinus</i> , <i>Schizophyllum commune</i> , <i>Serpula lacrymans</i> , <i>Postia placenta</i> , <i>Coniophora puteana</i> and <i>Fomes fomentarius</i>	Typical wood degrading species, commonly found in nature	Peralta et al. (2017)
<i>Serpula lacrymans</i> and <i>Coniophora puteana</i>	Most harmful brown-rot fungi	López et al. (2017), Blanchette (1995)
<i>Gloeophyllum trabeum</i> <i>Postia placenta</i> , <i>Piptoporus betulinus</i>	Strongly degrade the cellulose, hemicellulose and demethoxylated lignin left behind	Mäkelä et al. (2015), Dey (2014)
Co-transformant strain L#61 of <i>Gloeophyllum trabeum</i> KU-41	Most potent strain for high laccase activity	Arimoto et al. (2015)
<i>Fistulina hepatica</i> and <i>Cylindrobasidium torrendii</i>	Proved the evolution of brown-rot fungi from white-rot fungi	Floudas et al. (2015)
<i>Gloeophyllum trabeum</i> , <i>Laetiporus portentosus</i> , and <i>Fomitopsis lilacinogilva</i>	Primarily attack on softwoods	Abdel-Hamid et al. (2013), Sigoillot et al. (2012), Hatakka (2005), Gilbertson (1980)
<i>Gloeophyllum trabeum</i>	Presence of the laccase gene-specific sequences	D'Souza et al. (1996)
<i>Coniophora puteana</i> , <i>Serpula lacrymans</i> , <i>Gloeophyllum trabeum</i> and <i>Meruliporia incrassata</i>	Strongly destructive to wood used in building material	Blanchette (1995)
<i>Polyporus ostreiformis</i>	Expression of LiP and MnP, 18.6% lignin removed from rice straw within 3 weeks	Dey et al. (1994)

manganese peroxidase (MnP) and versatile peroxidase (VP) (Hatakka 2001; Datta et al. 2017). Lignin-degrading enzymes are generally classified into two classes: heme peroxidases and phenol oxidases. Lignin peroxidase (LiP), manganese peroxidase (MnP) and versatile peroxidase (VP) are heme peroxidase enzymes depending on the heme (Fig. 13.6), while phenol oxidases include laccases containing copper (Bugg et al. 2011a.; Falade et al. 2017). Ligninolytic enzymes activity of laccase and peroxidase occurs through depolymerization of the phenolic and non-phenolic lignin polymer, degradation through low molecular weight free radicals such as OH, and by mineralizing the insoluble lignin (Datta et al. 2017).

Manganese peroxidase (MnP) and laccase are the most common lignin-modifying and degrading enzymes produced by almost all species of white-rot

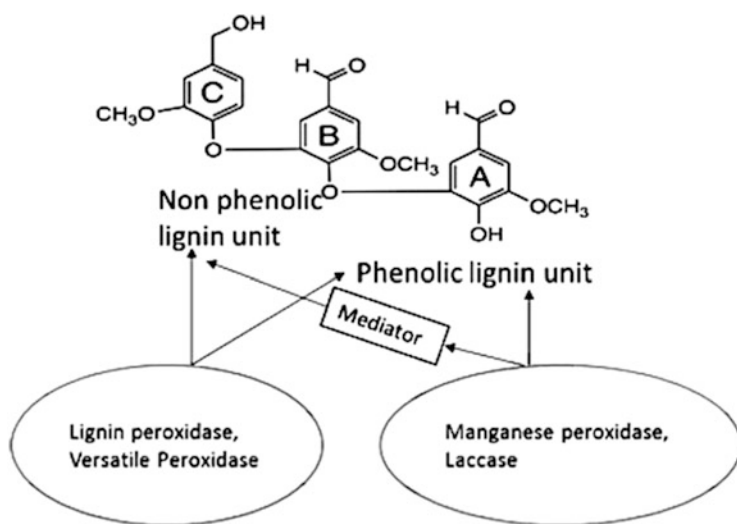
Table 13.3 Studies on activities of soft-rot fungi in the treatment of lignocellulosic biomass

Microorganisms	Activities	References
<i>Daldinia eschscholtzii</i> (SA2 80), <i>Daldinia eschscholtzii</i> (SA2 85), <i>Hypoxylon</i> sp. (SA2 146), <i>Hypoxylon investiens</i> (SA2 149), <i>Nemania primolutea</i> (KT2 106)	Lignin degradation range between 5% and 15%. Among all <i>D. eschscholtzii</i> exhibited highest degradation capability	Ramadhani et al. (2019)
<i>Neopestalotiopsis</i> sp. B2B	Production of laccase	Kang et al. (2019)
<i>Chrysonilia sitophila</i>	Ligninolytic activity, 20% weight loss of pine wood	Madadi and Abbas (2017), Hatakka (2005)
<i>Neurospora discreta</i>	Two times more degradation of lignin in sugarcane bagasse compared to <i>P. chrysosporium</i>	Pamidipati and Ahmed (2017)
<i>Thermoascus aurantiacus</i>	Thermophilic ascomycete, grow in heated parts of wood chip piles	López et al. (2017)
<i>Trichoderma asperellum</i>	Produce ligninolytic enzyme, Xylanase even at alkaline pH	Sridevi et al. (2017)
<i>Aspergillus niger</i> , <i>A. flavus</i>	Xylanase enzyme production, reduced kappa number and enhanced brightness	Sridevi et al. (2016), de Alencar Guimaraes et al. (2013)
<i>Trichoderma viride</i>	Lignin removal ability increased by 15% and 11%, respectively, by addition of wet milling and surfactant (Tween 80)	Ghorbani et al. (2015)
<i>Chaetomium globosum</i> , <i>Ustilina deusta</i> , <i>Alternaria alternata</i> , <i>Thielavia terrestris</i> and <i>Paelomyces</i> sp.	Common soft-rot fungi, mainly degrade non-woody biomass	Mäkelä et al. (2015), Daniel (1994), Haider et al. (1980), Martínez et al. (2005), Nilsson and Daniel (1989)
<i>Aspergillus niger</i> and <i>Penicillium chrysogenum</i>	Biodegradation ability	Hamed (2013)
<i>Alternaria alternata</i>	Cause soft-rot decay	Sigoillot et al. (2012)
<i>Xylaria</i> spp. and <i>Coccomyces</i> spp.	Ligninolytic activity with selective delignification	Koide et al. (2005), Liers et al. (2010), Osono and Takeda (2001)
<i>Penicillium chrysogenum</i> , <i>Fusarium solani</i> , <i>F. oxysporum</i> and <i>F. proliferatum</i> in soil, compost and forest litter.	Exhibited lignin degradation ability, but their degradation efficiency is low and mineralized 14 C-labelled lignin up to 27.4%	Rodríguez et al. (1996), Tuomela et al. (2000), Kirk and Farrell (1987)
<i>Thermoascus aurantiacus</i>	Brazilian strain produced high levels of phenol oxidase (PO) and efficiently degraded <i>Eucalyptus grandis</i> extractive substances	Machuca et al. (1998)
<i>Botrytis cinerea</i>	Production of extracellular laccases	Thurstun (1994)

(continued)

Table 13.3 (continued)

Microorganisms	Activities	References
<i>Aspergillus niger</i> , <i>Trichoderma</i> sp.	Lignin degradation in pulp and paper mill wastewater	Kannan and Oblisami (1990), Prasad and Joyce (1991)
<i>Daldinia</i> , <i>Hypoxyton</i> , and <i>Xylaria</i>	Common wood degrading fungi, but <i>D. concentrica</i> was most potent and caused highest lignin losses (44%)	Nilsson and Daniel (1989)
<i>Fusarium</i> sp.	Degrade lignin components	Higuchi (1980), Iwahara (1980), Buswell et al. (1987)
<i>Graphium</i> sp., <i>Paecilomyces</i> sp., <i>Monodictys</i> sp., <i>Thielavia terrestris</i> , <i>Papulospora</i> sp., and <i>Allescheria</i> sp.	Lignin depletion characteristics and decayed the standardized blocks of alder, poplar and pine wood	Eslyn et al. (1975)

**Fig. 13.6** Schematic representation of ligninolytic enzymes and their selective activity on the components of lignin. *Source:* Datta et al. 2017

fungi, while only a few of them produce lignin peroxidase (LiP) (Hatakka 2001). Recently, Su et al. (2018) have reported *Myrothecium verrucaria* as a potent ligninolytic enzyme secreting fungi with high activity levels of laccase (6.61 Ug^{-1}), lignin peroxidase (0.78 Ug^{-1}) and manganese peroxidase (1.31 Ug^{-1}) dry biomass.

Lignin peroxidase (LiP) was the first ligninolytic enzyme isolated from *Phanerochaete chrysosporium* in 1984 (Tien and Kirk 1984). Lignin peroxidase (LiP) exhibited the highest redox potential activity compared to other peroxidases and can directly oxidize the phenolic and non-phenolic structures of lignin without

any mediator (Datta et al. 2017). Haem in peroxidases enzymes (LiP, MnP and VP) make them high redox potential. At the same time, two other research teams (M. Gold's and R. Crawford's groups) have discovered manganese peroxidase (MnP) in the same white-rot fungal species, *P. chrysosporium* (Kuwahara et al. 1984; Paszcynski et al. 1985; Glenn and Gold 1985; Paszczyński et al. 1986). During MnP enzymatic activity, manganese acts as a mediator, and due to its high redox potential, it highly degraded the phenolic compounds of lignin compared to laccase (Datta et al. 2017).

Later on, the third ligninolytic enzyme, versatile peroxidase (VP) was for the first time described in *Pleurotus eryngii* (Martinez et al. 1996). For the first time, VP was purified from the *Bjerkandera*, a wood-rotting fungus and was described to have the ability to transform lignin even without any external mediator (Moreira et al. 2007). It was also recognized to be present in other white-rot fungal species including *Trametes*, *Spongipellis*, *Dichomitus*, *Calocybe*, *Lepista* and *Panus* (Moreira et al. 2007; Ruiz-Dueñas et al. 2008; Chen et al. 2010; Chaurasia and Bhardwaj 2019). Versatile peroxidase (VP) has the combined catalytic activities of both LiP and MnP and shows the high-redox potential activity for non-phenolic compounds like LiP and also able to oxidize Mn^{2+} like the MnP (Abdel-Hamid et al. 2013).

Laccase is a copper-containing enzyme, belonging to the oxidoreductase group of enzyme and oxidizes a wide variety of organic and inorganic substances, including lignin (Datta et al. 2017). In 1883, Yoshida for the first time isolated laccases from the *Rhus vernicifera*, commonly known as Japanese lacquer tree (Yoshida 1883; Thurston 1994; Viswanath et al. 2014) and subsequently in 1896 it was reported as a fungal enzyme by Bertrand and Laborde (Bertrand 1896; Laborde 1896). Laccase is reported in several organisms, but it is highly produced by white-rot fungus and is also reported from some bacterial species (Datta et al. 2017). Among the white-rot fungi, *P. chrysosporium* has deeply studied due to their potent lignin degradation properties. A total of 16 candidate genes have been reported in *P. chrysosporium* in correspondence with lignin degradation which are ten LiP enzymes, five MnP enzymes and one NoP (novel peroxidase) (Levasseur et al. 2008). Ten structurally related genes family *lipA* to *lipJ* encodes the lignin peroxidase (LiP) enzyme. The presence of multiple *lip* genes in the *P. chrysosporium* is not clearly described; however, oxidation-reduction potential difference among isoenzymes of LiP has been observed (Macarena et al. 2005). Most of the white-rot fungi produce laccase enzyme, interestingly *P. chrysosporium* does not provide it (Larrondo et al. 2003). However, in 2004, Larrondo et al. have described a cluster of four multicopper oxidase genes (*mco1* to *mco4*) in *P. chrysosporium* (Larrondo et al. 2004). Crystal structures study of LiP and MnP determines that both these enzymes and other peroxidases are structurally related to each other indicating the divergent evolution (Edwards et al. 1993; Sundaramoorthy et al. 1994; Banci et al. 1999). Manganese peroxidase (MnP) is often produced in multiple forms and is only a single fungal species *Ceriporiopsis subvermispora* and up to 11 different isoforms have been described (Hofrichter 2002).

Earlier studies have reported that several white-rot fungi such as *Phanerochaete chrysosporium* (Eaton et al. 1982; Katagiri et al. 1997), *P. sordida* YK-624 (Hirai

et al. 1995), *Trametes versicolor* and *Coriolus versicolor* (Kirk et al. 1976; Archibald et al. 1997), *Schizophyllum commune* (Belsare and Prasad 1988), *Tinctoporia borbonica* (Fukuzumi 1980), *Phlebia radiata* and *Dichomitus squalens* (Mäkelä 2009) and *Bjerkandera* sp. (Palma et al. 2000) degrade the lignin in pulp and paper mill wastewater but, only some of them such as *P. chrysosporium* (Katagiri et al. 1995), *Trametes versicolor* (Reid et al. 1982), *P. sordida* YK-624 (Hirai et al. 1995), *Ceriporiopsis subvermispora* (Christov et al. 1996) and *Bjerkandera* sp. BOS55 (Moreira et al. 1997) have been claimed to possess the ability to delignify kraft pulp.

Hirai et al. (2005) isolated and characterized a novel lignin peroxidase (YK-LiP2) from white-rot fungus *P. sordida* YK-624. The absorption spectrum of identified enzyme YK-LiP2 from *P. sordida* YK-624 was same as LiP from *P. chrysosporium*. However, the degradation capacity of YK-LiP2 from *P. sordida* for dimeric lignin model compounds was higher than the LiP from *P. chrysosporium*. *P. chrysosporium* has produced several ligninolytic enzymes, but it is not capable of producing the versatile peroxidase (Chaurasia and Bhardwaj 2019). It has been reported that *P. chrysosporium* and *Trametes* species could secrete the oxidative enzyme and make them highly selective towards lignin (Zhang et al. 2012; Knežević et al. 2013; Zeng et al. 2013). Katagiri et al. (1997) have investigated the production of ligninolytic enzyme for biobleaching of unbleached softwood kraft pulps by *P. chrysosporium* and *Trametes versicolor* and described that both the fungal species were able to produce the laccase and manganese peroxidase (MnP). However, production of lignin peroxidase was not observed (Katagiri et al. 1997). In comparison with *T. versicolor*, *P. chrysosporium* showed higher delignification activity for unbleached softwood kraft pulps. During delignification of softwood kraft pulps, MnP production by *P. chrysosporium* was much less than that of unbleached hardwood kraft pulp.

Apart from *P. chrysosporium* several other white-rot fungal species play a significant role in delignification (Table 13.1). Several species of *Trametes* such as *T. versicolor*, *T. hirsute*, *T. velutina*, *T. villosa* have also been reported as potent lignin-degrading white-rot fungi (Quintana et al. 2015; Wang et al. 2013a; Wu et al. 2011; Ahn et al. 2007; Bourbonnais et al. 1995; Jönsson et al. 1995). In 1989, Archibald et al. have described that *T. versicolor* have the capability of delignifying and substantially brightening the unbleached kraft pulps (Archibald et al. 1997). Archibald et al. (1997) investigated the delignification enzyme families secreted by *T. versicolor* which include lignin peroxidases (LiP), manganese peroxidases (MnP), laccases and cellobiose dehydrogenases (CDH). They have also purified two laccase isozymes (laccase I and II) and they have reported that in the presence of the mediator both laccase isozymes were able to delignify the kraft pulp (Archibald et al. 1997). The secreted MnP activity by *T. versicolor* and the presence of substantial available Mn (II) ions are necessary for lignin degradation and pulp brightening. They have also reported that purified MnP, supplied with Mn (II), H₂O₂ and Mn (II)-complexing agents can delignify pulp (Archibald et al. 1997).

Bourbonnais and Paice (1992) demonstrated that bleaching of Kraft pulp by laccase enzyme from fungus *T. versicolor* in the presence of 2,2'-azinobis-

(3-ethylbenzthiazoline-6-sulphonate) (ABTS) led to methanol release and delignification of the pulp. The methanol release was produced by demethylation of the pulp during the delignifying process. Several other researchers have also reported that *T. versicolor*, *Pycnoporus coccineus* and *T. hirsute* are high laccase enzyme-producing fungi (Bourbonnais et al. 1995; Jaouani et al. 2005; Wu et al. 2011). Quintana et al. (2015) have reported that an enzymatic biobleaching sequence was developed in a combination of laccase from *Trametes villosa* with violuric acid (VA) followed by pressured H₂O₂ treatment, and found better bleaching and desired dissolving pulp requirements such as improved brightness, reduced hemicellulose, insignificant cellulose degradation, brightness stability against moist heat ageing, etc. (Quintana et al. 2015; Chaurasia and Bhardwaj 2019).

Xylanase is a hemicellulase enzyme which hydrolyses xylan to xylose, widely used in feed processing and pulp and paper industry. Researchers have proved that pretreatment of agro-industrial residues pulp with xylanase produced by *Aspergillus niger* (de Alencar Guimaraes et al. 2013; Sridevi et al. 2016), *A. flavus* (de Alencar Guimaraes et al. 2013), *Lentinus tigrinus* LP-7 and *Irpex lacteus* KB-1.1 (Afrida et al. 2014) causes reduction of kappa number and enhancement of brightness (Chaurasia and Bhardwaj 2019). Song et al. (2013) have reported that 43.8% of lignin degradation was obtained after 42 days of non-sterile fungal pretreatment with *Irpex lacteus* of corn stover, saccharification efficiency was increased sevenfold after enzymatic hydrolysis (Song et al. 2013). Sunardi et al. (2016) have reported that *Porodaedalea pini* showed lignin-degradation activity through the production of xylanase and endoglucanase (Sunardi et al. 2016). Kappa number is a parameter for the bleaching ability, relative hardness, or degree of delignification of pulp.

In 2018, Metri et al. used *Pleurotus ostreatus* to degrade the lignin in palm midrib and reported that fungus used lignin for their growth, due to which the lignin level decreases (Metri et al. 2018). Their finding revealed the previous result confirming that *P. ostreatus* belong to such microbial group which can thoroughly degrade the lignin in CO₂ and water by producing a family of enzymes including the phenoloxidase laccase, lignin peroxidase (LiP) and manganese peroxidase (MnP) (Fitria 2008; Metri et al. 2018). An earlier study has proved that *P. ostreatus* can reduce lignin content about 34% in 5 weeks pretreated wheat straw with *P. ostreatus*. Still, only 12% lignin reduction was observed in untreated samples (Hatakka 1983). Scanning electron microscopy and Fourier transform infrared spectroscopy (FTIR) analysis evidenced that *P. ostreatus* and *P. pulmonarius* pretreatment *Eucalyptus grandis* sawdust enhanced the more extensively and selective lignin degradation (Castoldi et al. 2014). It has also been proved that *P. ostreatus* and *P. pulmonarius* are responsible for the improvement of hydrolysis and sugar reduction approximately 20-fold (Castoldi et al. 2014).

Li et al. (2002) isolated white-rot fungi *Phlebia* sp. MG-60 from mangrove stands in Okinawa, Japan and employed for the first time to bleach hardwood kraft pulp (UKP). They found that *Phlebia* sp. MG-60 was strongly capable to degrade lignin than *P. chrysosporium*, especially in a hypersaline environment (Li et al. 2002). Later on, Kamei et al. (2012) used *Phlebia* sp. MG-60 for aerobic delignification, anaerobic saccharification and fermentation of oak wood and found that *Phlebia*

sp. MG-60 selectively degrades lignin under aerobic solid-state fermentation conditions, and 40.7% of initial lignin was degraded after 56 days aerobic incubation. Under semi-aerobic liquid culture conditions, ethanol was directly produced from delignified wood (Kamei et al. 2012).

In 2015, beneficial effects of synergism between two or three fungal/bacterial cocultured lignocellulose-degrading microorganisms were explored and found that saccharification activity was significantly increased by cocultured fungal combination of *Neosartorya fischeri*–*Myceliophthora thermophila* and other fungal combination *Trichoderma longibrachiatum*–*Phanerochaete chrysosporium* by up to three- and ~sevenfold than their monocultures (Taha et al. 2015). Dhiman et al. (2015) also investigated the high saccharification yield by the cocktail of two fungal species. They reported that 1:2 ratio for *Pholiota adiposa*–*Armillaria gemina* was the best combination for better yield of cocktail characteristics.

Studies on the Mn-oxidizing peroxidases and laccases from *Ganoderma applanatum* have reported that enzymes expression was more excellent in submerged cultivation than solid-state and showed degradation of lignin (40.9%), hemicellulose (32.7%) and cellulose (27.4%) during the oak sawdust fermentation. Oak sawdust stimulated maximum activities of Mn-dependent and Mn-independent peroxidases while wheat straw favoured more significant laccase activity than Oak sawdust (Ćilerdžić et al. 2016). Suhara et al. (2012) isolated 51 fungal white-rot basidiomycete from decayed bamboo culms (*Phyllostachys pubescens*), among them *Punctularia* sp. TUF20056 showed high lignin degradation capability by removing 53.3% of lignin from bamboo.

13.3.2 Brown-Rot Fungi

Brown-rot is another group of most common and destructive wood decay fungi comprising of approximately 10% of all wood-rotting basidiomycetes. Typical wood degrading brown-rot fungi species are *Gloeophyllum trabeum*, *Piptoporus betulinus*, *Schizophyllum commune*, *Serpula lacrymans*, *Postia placenta*, *Coniophora puteana* (known as the ‘cellar fungus’) and *Fomes fomentarius* which are commonly found in nature (Peralta et al. 2017). Brown-rot such as *Gloeophyllum trabeum*, *Laetiporus portentosus* and *Fomitopsis lilacinogilva* are generally found in coniferous ecosystems and primarily attack softwoods (Gilbertson 1980; Hatakka 2005; Sigoillot et al. 2012; Abdel-Hamid et al. 2013). Comparative and functional genomics indicated that evolution of brown-rot fungi was accompanied by losses in key enzymes, especially cellulases and lignin-modifying enzymes implicated in biomass breakdown in white rot (López et al. 2017). Recently comparative studies on *Fistulina hepatica* and *Cylindrobasidium torrendii* have proved that the brown-rot evolved from white-rot fungi by losing multiple functional genes involved in cellulose and lignin degradation (Floudas et al. 2015) (Table 13.2).

Unlike white-rot fungi, brown-rot fungi are less efficient in lignin degradation (Datta et al. 2017), but the degradation of wood polysaccharides such as cellulose and hemicellulose is much quicker which rapidly loses its strengthening properties

(Madadi and Abbas 2017). Consequently, in advanced stage of wood decay through brown-rot fungi, wood shrinks, becomes crumbly and converts to brown colour due to the lignin oxidation and cracks into roughly cubical pieces (Gilbertson 1980; Monroy et al. 2011). Brown-rot fungi cannot degrade the lignin completely, and to some extent, the residual lignins can be dealkylated, demethoxylated and demethylated, however, their aromatic rings still remain without degradation (Sigoillot et al. 2012). Unlike white-rot fungi that produce different ligninolytic enzymes for lignin degradation, the brown-rot fungi do not produce lignin-degrading enzymes; however, they have other mechanisms for lignin modification and depletion from wood. Expressions of lignin-degrading enzymes such as LiP and MnP have also been reported in the brown-rot fungus *Polyporus ostreiformis*, revealing 18.6% lignin removal from rice straw within 3 weeks (Dey et al. 1994). D'Souza et al. (1996) have also detected the presence of the laccase gene-specific sequences in brown-rot fungus *Gloeophyllum trabeum*.

Due to the lack of exoglucanases, the digestion process of the plant wood by the brown-rot fungi is completely different, i.e. nonenzymatic process (Goodell 2003). In contrast to white-rot fungi, wood degradation process of brown-rot fungi such as *Gloeophyllum trabeum*, *Postia placenta* and *Piptoporus betulinus* actively degrade the cellulose and hemicellulose and demethoxylated lignin left behind (Dey 2014; Mäkelä et al. 2015). *G. trabeum* significantly releases alkali-soluble lignin mainly in the first week during its growth on pine sawdust (Agosin et al. 1989). *Gloeophyllum trabeum* is the most studied brown-rot fungi and plays an important role in the wood used in construction together with *Coniophora puteana* (Boletales) and *Serpula lacrymans* (Blanchette 1995). The brown-rot fungus *Gloeophyllum trabeum* KU-41 strongly degrades the Japanese cedar wood. Arimoto et al. have developed a gene transformation system for *G. trabeum* KU-41 for strong biofuel production from Japanese cedar wood and found that co-transformant strain L#61 was a potent strain for high laccase activity among all obtained 44 co-transformants (Arimoto et al. 2015).

The brown-rot fungi produce nonenzymatic, low molecular agents which are responsible for early stages of wood decay (Goodell 2003). These initiators are of low molecular weight compounds, diffusible, extracellular oxidants (free radicals), like phenolates, glycopeptides or iron-chelating compounds, e.g. siderophores, oxalate and simple aromatic compounds, etc. These initiators are capable of penetrating the wood cell wall and depolymerizing cellulose, making it accessible to further degradation (Wang and Gao 2003). The degradation of wood started by the readily diffusion of the initiators from hyphae and operating at a distance from the hyphae after penetration in wood (Shimada et al. 1997; Goodell et al. 1997; Evans et al. 1994; Wood 1994; Espejo and Agosin 1991; Fekete et al. 1989).

Brown-rot fungi start lignin degradation through nonenzymatic oxidation reaction process that produces hydroxyl radicals via Fenton chemistry ($\text{Fe} + \text{H}_2\text{O}_2 \rightarrow \text{Fe} + \text{OH}^\cdot + \text{OH}^-$) (Kirk et al. 1991; Kerem et al. 1998, 1999). Brown-rot fungi partially oxidize lignin via demethylation of the aromatic ring of phenolic and non-phenolic compounds (Blanchette 1984; Datta et al. 2017), resulting in aromatic

hydroxylation and splitting of the ring, and increase in the phenolic hydroxyl content of reaction mixture (Kirk and Farrell 1987; Hatakka and Hammel 2011).

Some brown-rot fungi are able to accumulate the oxalic acid, causing a significant reduction of pH and generating the hydroxyl radicals using the oxalic acid as a proton donor for enzymatic and nonenzymatic hydrolysis of polysaccharides and as a chelator for a Fe (II)-H₂O₂ system (Goodell et al. 1997). This process does not occur with *G. trabeum*, because it could be producing the enzymes that degrade oxalate (Espejo and Agosin 1991). *G. Trabeum* exhibited different attributes for rapid degradation of aliphatic polyether through extracellular one-electron oxidation (Jellison et al. 1991), resulting in simple aromatic compounds such as 4,5-dimethoxy-catechol and 2,5-dimethoxyhydroquinone (Enoki et al. 1997) and 2,5-dimethoxy-1,4-benzoquinone (Paszczynski et al. 1999). These compounds may serve as oxygen-reducing agents, ferric chelators and compounds of redox-cycling (Kerem et al. 1999).

Several brown-rot fungi such as *Coniophora puteana*, *Serpula lacrymans*, *Gloeophyllum trabeum* and *Meruliporia incrassata* are strongly destructive to the wood used in the building and other structures, and due to lignin modification, wood is converted to dark, shrink, typically broken into small cubical parts which can easily fragment into brown powder (Blanchette 1995). *S. lacrymans* and *C. puteana* are the most harmful brown-rot fungi mainly found in the wood of temperate regions which generally prefer softwood to hardwood as substrates (Blanchette 1995; López et al. 2017).

13.3.3 Soft-Rot Fungi

Soft-rot fungi such as *Chaetomium globosum*, *Ustulina deusta*, *Alternaria alternata*, *Thielavia terrestris* and *Paecilomyces* spp. belonging to Ascomycetes and Deuteromycetes (Haider et al. 1980; Nilsson and Daniel 1989; Daniel 1994; Martínez et al. 2005) mainly degrade non-woody biomass (Mäkelä et al. 2015). Wood degradation process in soft-rot fungi is not as well described as in the white-rot and brown-rot (Blanchette et al. 2002), and they follow the soft-rot decay processes which are their lifestyle characteristics. Soft-rot decay occurs by Ascomycetes and Deuteromycetes; however, facultative soft-rot decay has also been reported scarcely in some basidiomycetes (Sigoillot et al. 2012) (Table 13.3).

Several decades ago, different soft-rot fungi such as *Graphium* sp., *Paecilomyces* sp., *Monodictys* sp., *Thielavia terrestris*, *Papulospora* sp. and *Allescheria* sp. isolated from pulp chip storage piles were used to decay the standardized blocks of alder, poplar and pine wood. All these fungi were responsible for the depletion of lignin however; carbohydrates were depleted faster than lignin in the alder and poplars. In the case of pine both *Paecilomyces* sp. and *T. terrestris* removed lignin faster than carbohydrates, because both fungal species have more characteristic of white-rot fungi (Esllyn et al. 1975). Other soil fungi such as *Fusarium* sp. have also been reported to degrade the lignin components, however; their contribution to the biosphere's polymer conversion was not described in detail (Higuchi 1980; Iwahara

1980; Buswell et al. 1987). Wood degradation by the soft-rot fungi usually occurs in wet environmental condition following a characteristic decay patterns (Mäkelä et al. 2015). Several studies have been carried out to investigate the changes in the structural and chemical composition of degraded wood by soft-rot fungi (Hamed 2013; Blanchette 1995; Rodríguez et al. 1996; Tuomela et al. 2000; Hofrichter and Fritsche 1996).

Soft-rot fungi preferably degrade wood polysaccharides like cellulose and hemicellulose (Sigoillot et al. 2012); moreover, the ligninolytic activity has also been reported in the ascomycete fungi such as *Xylaria* spp. and *Coccomyces* spp. with selective delignification; however, their enzymatic system has not been explored broadly (Osono and Takeda 2001; Koide et al. 2005; Liers et al. 2010). Lignin degradation occurs very slowly (Nilsson and Daniel 1989; Daniel and Nilsson 1998), because their lignin-degrading enzyme LiPs or laccases may not show the potential oxidative activity on recalcitrant guaiacyl lignin, but on syringyl lignin (Rodríguez et al. 1996). In the wet environments, this limited action of the soft-rot fungi makes the wood consistently soft, while in the dry environment wood becomes brown and crumbly (Eriksson et al. 1990).

Soft-rot fungi most frequently prefer the hardwoods for the degradation, and only slightly degradation occurs in the softwoods. Degradation generally occurs in the moist and aquatic conditions area, due to which the soft-rot fungi is mainly found on waterlogged woods, utility poles and archaeological wood (Martínez et al. 2005). In comparison with white-rot and brown-rot fungi, soft-rot fungi can survive in adverse environmental conditions and tolerate a wide range of temperature, humidity, pH conditions and oxygen limitation (Aarti et al. 2015; López et al. 2017). It directly acts on a large number of wood substrates in soils and other environments (López et al. 2017). Soft-rot fungi are particularly active in such an adverse condition where the activity of white-rot and brown-rot fungi generally decreases, indicating they are more commonly found in the hardwood than in softwood (López et al. 2017).

Several Ascomycetes from the Xylariales order such as the genera of *Daldinia*, *Hypoxylon* and *Xylaria* previously were in the white-rot fungi group but due to the typical type II soft-rot activity currently, it is classified as soft-rot fungi and is primarily found on the hardwood (Hatakka 2005; López et al. 2017). Among all these, *Daldinia concentrica* was reported to be the most potent wood-degrading fungus and able to cause more than 53% weight loss in birch wood and highest lignin loss (44%) was observed when the weight loss was 77% in 4-month inoculation. However, low degradation was also reported by this fungus in the pinewood with only 2.5% weight loss (Nilsson and Daniel 1989). Sigoillot et al. have reported that common anamorphic fungi such as *Alternaria alternata* also cause soft-rot decay (Sigoillot et al. 2012). Other studies have also described that few species of *Eutypella* produce soft-rot decay in the early stage of wood decay, while white-rot decay in the late stages (Worrall et al. 1997; Pildain et al. 2005).

Deuteromycetes and certain ascomycetes microfungi such as *Penicillium chrysogenum*, *Fusarium solani*, *F. oxysporum* and *F. proliferatum* mainly degrade the polysaccharide in soil, compost and forest litter. They also exhibited the lignin degradation ability, but their degradation efficiency is low compared to white-rot

fungi (Kirk and Farrell 1987; Rodríguez et al. 1996; Tuomela et al. 2000) and mineralized 14 C-labelled lignin up to 27.4%, prepared from milled wheat straw. The red mould of bread (*Chrysonilia sitophila*) also has the lignin degradation capability, and 20% weight loss of pine wood was reported in 3 months, with 18% and 25% loss of carbohydrate and lignin, respectively (Madadi and Abbas 2017; Hatakka 2005). Recently, Pamidipati and Ahmed have reported that *Neurospora discreta* can degrade the lignin up to twice as much in sugarcane bagasse compared to well-known white-rot fungus *Phanerochaete chrysosporium* and produces about 1.5 times the amount of lignin degradation of products in the submerged culture (Pamidipati and Ahmed 2017; Madadi and Abbas 2017). The production of extracellular laccases in the plant pathogen *Botrytis cinerea* was observed by Thurston in 1994. This fungal species also shows the soft-rot like decay in several horticultural crop plants like *Cucumis* and *Daucus*, including ‘noble rot’ and ‘grey rot’ of *Vitis vinifera* (Thurston 1994).

Hamed in 2013 investigated the biodegradation ability of wood by two artificially infested soft-rot fungi, *Aspergillus niger* and *Penicillium chrysogenum* and through scanning electron microscope (SEM) evaluation they confirmed that in comparison with the hardwood, softwood is more resistant to fungal attack in early stages. However, in the later stage of infection degradation occurs rigorously (Hamed 2013). Recently, the biodegrading capability of the lignin through *Aspergillus flavus* and *Emericella nidulans* was studied and reported approximately 14.4–21% reduction of alkali lignin in different mediums (Barapatre and Jha 2017). The extracellular ligninolytic enzymes (peroxidases and oxidases) produced by soft-rot fungi may be effective than white-rot fungi, although they have some unique characteristics. For instance, the thermophilic ascomycete *Thermoascus aurantiacus* generally grow in heated parts of wood chip piles and also abundant in low-cost agro-industrial and forest residues/wastes (López et al. 2017). Another Brazilian strain of *T. aurantiacus* produced high levels of phenoloxidase (PO) and efficiently degraded the *Eucalyptus grandis* extractive substances and biobleached the kraft pulp of Eucalyptus wood. Furthermore, this fungal species grows rapidly on a solid medium that contains various compounds related to high lignin such as guaiacol, vanillin and tannic acid (Machuca et al. 1998). In 2015, Ghorbani et al. have reported that lignin degradation performance by soft-rot fungi can be improved by slight modification. Lignin removal by *Trichoderma viride* increases about 15% and 11%, respectively, by the addition of wet milling and surfactant (Tween 80) (Ghorbani et al. 2015). Another species *Trichoderma asperellum* have reported producing the ligninolytic enzyme, xylanase even at alkaline pH, and could be an effective biobleaching agent for pulp (Sridevi et al. 2017).

13.4 Bacteria and Lignin Degradation

Bacteria generally show cellulolytic and pectinolytic activities and their performance of lignin degradation is low in comparison with fungi (Blanchette 1995; Daniel and Nilsson 1998). Lignin degradation mechanism of bacteria is more specific than

fungi, and they are able to cleave only one type of bond at a time in the lignin polymer (Vicuña et al. 1993). Lignocellulose degradation by bacteria commonly occurs in the mixed culture or in the culture of bacterial and fungal together (Vicuña et al. 1993; Daniel and Nilsson 1998). However, wood degradation by bacteria has some advantages over fungal degradation, such as the bacteria can tolerate a wider range of temperature, pH and oxygen limitations than fungi (Daniel and Nilsson 1998). Another advantage is that in bacteria, genetic manipulation for overexpression of gene for lignin-degrading enzyme production is easy compared to fungi (Suman et al. 2016). Several studies have been carried out on the biodegradation of lignin through bacteria. Recently, several lignin-degrading bacteria have been characterized, which comes under a broad taxonomic group from Qinling, China (Yang et al. 2017) (Table 13.4).

It has been reported that strains of *Streptomyces*, *Pseudomonas*, *Rhodococcus* and *Bacillus* have the capability to decompose the lignin (Lee et al. 2019). Several bacteria such as *Pseudomonas* sp., *Ochrobactrum* sp. and *Burkholderia* sp. strains have shown high value of ligninolytic enzyme activity, particularly, extremely high LiP activity in *Burkholderia* sp. H1 (Yang et al. 2017). It has been already reported that extracellular ligninolytic enzymes, including laccase (Lac), lignin peroxidase (LiP) and manganese peroxidase (MnP) are required for lignin degradation (Singh et al. 2013). Previously, these enzymes were reported in most of the fungal species mainly in white-rot fungi; however, increasing number of ligninolytic enzyme secreted by bacteria has also been reported in recent studies (Singh et al. 2013; Yang et al. 2017; Chaurasia and Bhardwaj 2019). Recently, Xu et al. (2018) have isolated *Klebsiella pneumoniae* NX-1, *Pseudomonas putida* NX-1 and *Ochrobactrum tritici* NX-1 from leaf mould samples which exhibited potential ligninolytic activities, among them *P. putida* NX-1 showed high laccase, lignin peroxidase and Mn-peroxidase activities. Rahman et al. (2013) have identified *Bacillus* Sp. SHC1, *Ochrobactrum* sp. SCH2 and *Leucobacter* sp. SHC3 from palm oil plantation soils, which were found to be producing all three ligninolytic enzymes, viz. laccase, lignin peroxidase and manganese peroxidase. *Bacillus* sp. SHC1 was reported as high amount of manganese peroxidase and lignin peroxidase producing; however maximum laccase production was observed in the *Ochrobactrum* sp. Scheme 2 (Rahman et al. 2013).

Lignin degradation ability of the *Pseudomonas* sp. has been studied broadly and has been proved that *Pseudomonas* sp. might be a potent lignin-degrading bacteria (Sasikumar et al. 2014; Yang et al. 2017). Salvachúa et al. (2015) found that *Pseudomonas* strains and *Acinetobacter* ADP1 have the ability for depolymerization of high molecular lignin species and catabolize a part of low molecular weight aromatics. In an earlier study, Yang et al. (2012) have demonstrated the lignin-degrading ability of *Pseudomonas putida* mt-2 through depolymerization of high molecular weight lignin (Yang et al. 2012). Three dyp-type peroxidases were reported in the *Pseudomonas fluorescens* Pf-5 strain which could cause release of the low molecular weight fragment of lignin (Rahmanpour and Bugg 2015). Another ligninolytic soil bacterium *Rhodococcus jostii* RHA1 has dye-decolorizing peroxidase (DypB) capable of catalysing the peroxide-dependent oxidation of divalent

Table 13.4 Studies on activities of bacteria in the treatment of lignocellulosic biomass

Microorganism	Activities	References
<i>Microbacterium phyllosphaerae</i> and <i>Agrobacterium sp.</i>	Lignin-oxidizing enzymes and aromatic degradation gene clusters are involved in lignin degradation	Granja-Travez et al. (2020)
<i>Bacillus cereus</i> WGB1	Ligninolytic bacterium, potential degradation of methylene blue	Mary et al. (2020)
<i>Paenibacillus lautus</i> strains S18, S20, S36	Grow with lignin as a sole carbon source	Tahir et al. (2019)
<i>Streptomyces griseorubens</i> LH-3	Pulp brightness increases by 14.5% after treatment with purified thermostable endoxylanase and kappa number reduction by 24.5%	Wu et al. (2018)
<i>Klebsiella pneumoniae</i> NX-1, <i>Pseudomonas putida</i> NX-1, <i>Ochrobactrum tritici</i> NX-1	Potential ligninolytic activities	Xu et al. (2018)
<i>Rhodococcus opacus</i> PD630	Sole carbon source for growth	Kosa and Ragauskas (2013), He et al. (2017)
<i>Clostridium thermocellum</i>	Decreased b-O-4 linkage and increased S/G index	Akinosho (2017)
<i>Bacillus ligniniphilus</i>	Release of monomeric aromatic compounds	Zhu et al. (2017)
<i>Pseudomonas sp.</i> , <i>Ochrobactrum sp.</i> , <i>Burkholderia ginsengisoli</i>	High value of ligninolytic enzyme activity	Yang et al. (2017)
<i>Burkholderia sp.</i> H1	Extremely high LiP activity	Yang et al. (2017)
<i>Pseudomonas monteilii</i> , <i>Raoultella planticola</i> , <i>Lelliottia amnigena</i> , <i>Lelliottia nimipressuralis</i>	Have laccase activity	Yang et al. (2017)
<i>Pseudomonas plecoglossicida</i> , <i>P. citronellolis</i> strain DSM 50332 and NBRC 103043, <i>P. monteilii</i> , <i>Ochrobactrum anthropic</i> , <i>Leclercia adecarboxylata</i>	Highest MnP activity in <i>Pseudomonas plecoglossicida</i> , however other strains also have high MnP activity	Yang et al. (2017)
<i>Burkholderia ginsengisoli</i> , <i>Ochrobactrum haematophilum</i> , <i>P. plecoglossicida</i> , <i>P. citronellolis</i> , <i>P. monteilii</i>	High LiP activity	Yang et al. (2017)
<i>Rhizobia sp.</i> YS-1r	15% lignin degradation of acid insoluble in switchgrass	Jackson et al. (2017)
<i>Cupriavidus basilensis</i>	Break down kraft lignin	Shi et al. (2017)
<i>Pseudomonas putida</i> KT2440	Extremely high lac activity	Mazurkewich et al. (2016), Yang et al. (2017)

(continued)

Table 13.4 (continued)

Microorganism	Activities	References
<i>Pseudomonas</i> sp.	High MnP activity	Yang et al. (2017), Rahmanpour and Bugg (2015), Salvachúa et al. (2015)
<i>Paenibacillus glucanolyticus</i>	Decreased average molecular weight of lignin	Mathews et al. (2016)
<i>Trabulsiella</i> sp.	Biodegradation of lignin, isolated from termite gut	Suman et al. (2016)
<i>P. glucanolyticus</i> SLM1	Facultative anaerobic, lignin degradation under aerobic and anaerobic conditions	Mathews et al. (2016)
<i>Acetoanaerobium</i> sp. WJDL-Y2	Maximum KL degradation capability is 24.9%	Duan et al. (2016)
<i>Burkholderia</i> sp. H1	High ligninolytic activity and degrade alkali lignin and Klason lignin	Kumar et al. (2015)
<i>Pseudomonas</i> strains and <i>Acinetobacter</i> ADP1	Depolymerize high molecular lignin	Salvachúa et al. (2015)
<i>P. fluorescens</i> Pf-5	Dyp-type peroxidases, release low molecular weight fragment of lignin	Rahmanpour and Bugg (2015)
<i>Bacillus tequilensis</i> SN4	Thermo-alkali-stable laccase potential to biobleach softwood pulp, active at high temperature (90 °C) and also stable at a higher pH (9.0–10.0)	Sondhi et al. (2015)
Bacterial cocultures <i>Aeromonas hydrophila</i> – <i>Pseudomonas poae</i> and <i>Klebsiella oxytoca</i> – <i>Bacillus amyloliquefaciens</i>	Degradation increase 6.6-fold and ~sevenfold, respectively	Taha et al. (2015)
<i>Acinetobacter</i> ADP1 <i>Rhodococcus jostii</i> RHA1 <i>Pseudomonas putida</i> <i>Amycolatopsis</i> sp.	Nearly 30% of initial lignin can be depolymerized and catabolized	Salvachúa et al. (2015)
<i>Bacillus</i> sp. CS-1 and CS-2	Capability of alkali lignin degradation	Chang et al. (2014)
<i>Klebsiella</i> sp. strain BRL6-2	Have small arsenal of genes encoding lignocellulolytic enzyme	Woo et al. (2014)
<i>Pseudomonas</i> sp.	Potent lignin-degrading bacteria	Sasikumar et al. (2014)
<i>Paenibacillus</i> sp. strain LD-1	Reduced the pollution parameters such as colour by 68%, lignin 54%, phenol 86%, BOD 83% and COD 78%	Raj et al. (2014)
<i>Bacillus</i> Sp. SHC1, <i>Ochrobactrum</i> sp. SCH2, <i>Leucobacter</i> sp. SHC3	Produce ligninolytic enzymes such as laccase (Lac), lignin peroxidase (LiP) and manganese peroxidase (MnP)	Rahman et al. (2013)

(continued)

Table 13.4 (continued)

Microorganism	Activities	References
<i>Rhodococcus jostii</i> RHA1	Dye-decolourizing peroxidase (DypB)	Singh et al. (2013)
Bacterial consortium LDC	Lignin break down up to 60.9% under static culture conditions within 15 days	Wang et al. (2013b)
Bacterial strain C6 (<i>Bacillus pumilus</i>) and strain B7 (<i>Bacillus atrophaeus</i>)	High laccase activity	Huang et al. (2013)
<i>Ochrobactrum</i> sp. and <i>Rhizobium</i> sp.	Depolymerize lignin and produce low molecular weight oxalic acid and protocatechic acid metabolites	Taylor et al. (2012)
<i>Pseudomonas putida</i> mt-2	Depolymerization of high molecular weight lignin	Yang et al. (2012)
<i>Streptomyces</i> , <i>Nocardia</i> , and <i>Rhodococcus</i>	Lignin peroxidase for lignin degradation	Leisola et al. (2012), Bugg et al. (2011b)
<i>Amycolatopsis</i> sp. 75iv2 ATCC 39116 (formerly <i>Streptomyces setonii</i> and <i>S. griseus</i> 75vi2)	Extracellular heme-dependent enzyme activity against lignin model	Brown et al. (2011)
<i>Pandoraea norimbergensis</i> <i>Bacillus</i> sp.	Degrade ligninolytic indicator dyes	Bandounas et al. (2011)
<i>Thermobifida fusca</i>	Thermophilic bacteria, dyp-type peroxidases	Adav et al. (2010)
<i>Streptomyces viridosporus</i> T7A	Best studied for production of lignin peroxidase (LiP) and lignin degradation	Niladevi and Prema (2008)
<i>Streptomyces psammoticus</i> , and <i>S. chromofliscus</i>	Produce extracellular LiP	Niladevi and Prema (2008)
<i>S. Psammoticus</i>	Have MnP activity	Niladevi and Prema (2008)
<i>Sphingomonas paucimobilis</i> SYK-6	Catabolic pathways for lignin components breakdown studied	Masai et al. (2007)
<i>Aneurinibacillus aneurinilyticus</i>	Reduced colour by 58% and lignin content by 43%	Raj et al. (2007)
<i>Burkholderia</i> sp. strain VE22	Isolated from lower termite (<i>Coptotermes formosanus</i>) gut, degrade the aromatics	Harazono et al. (2003)
Endospore coat protein CotA of <i>Bacillus subtilis</i> , <i>Azospirillum lipoferum</i> , <i>Marinomonas mediterranea</i>	Showed the laccase activity	Martins et al. (2002)
<i>Actinomyces</i>	Digest and modify the lignin structure	Buswell et al. (1987)

manganese (Singh et al. 2013). Recently, a second class of enzymes in the soil bacteria *Sphingobacterium*— a manganese superoxide dismutase (MnSOD1 and MnSOD2) partially purified extracellular fractions showed high lignin degradation activity (Rashid et al. 2015).

Yang et al. (2017) have identified different strains of *Pseudomonas*, and most of them had higher laccase activity. *Pseudomonas putida* KT2440 strain showed the highest Lac activity and catabolized the lignin. Their cleavage paths have also been studied (Mazurkewich et al. 2016). A bacterial consortium LDC was selected from reeds pond sludge which could degrade 60.9% lignin in reeds at 30 °C under static culture conditions within 15 days. This bacterial consortium was classified into various bacterial species such as *Pseudomonas* sp. (25.2%), *Desulfomicrobium* (10.9%), *Clostridiales* (9.1%), *Microbacterium* (7.8%), *Geovibrio thiophilus* (5.1%), *Azoarcus* sp. (5.1%), *Thauera* (5.1%), *Paenibacillus* sp. (5.1%), *Acinetobacter* sp. (3.1%), *Cohnellasp.* (2.2%) and uncultured bacterium (21.3%) (Wang et al. 2013b). The bacteria strain C6 (*Bacillus pumilus*) and strain B7 (*Bacillus atrophaeus*) isolated from soils of a rich biodiversity rainforest in Peru were reported to have high laccase activity (Huang et al. 2013). A novel extracellular thermo-alkali-stable laccase (SN4 laccase) enzyme was reported by Sondhi et al. (2015) from *Bacillus tequilensis* SN4 which has the potential to biobleach softwood pulp and is active at high temperature (90 °C) and also stable at a higher pH 9.0–10.0 (Sondhi et al. 2015). Martins et al. have reported the laccase activity in the endospore coat protein CotA of *Bacillus subtilis* and they have also found that apart from *B. subtilis* laccase activity was also in the *Azospirillum lipoferum* a soil bacterium and the marine bacteria *Marinomonas mediterranea* (Martins et al. 2002).

Raj et al. (2007) have identified a potent lignin removal bacteria *Aneurinibacillus aneurinilyticus* from sludge of pulp and paper mill and reported that these bacteria do not use the kraft lignin as a sole carbon source but, after 6 days, reduced colour by 58% and the lignin content by 43% from kraft lignin-mineral salt media supplemented with glucose at pH 7.6 and 30 °C. Later they have identified other potent laccase-producing bacteria *Paenibacillus* sp. strain LD-1 from the contaminated soil sample through lignin enrichment method. This bacterium showed potential bioremediation of highly hazardous pulp and paper mill effluent and it was found that this bacteria significantly reduced the pollution parameters such as colour by 68%, lignin 54%, phenol 86%, BOD 83% and COD 78% at 34 ± 1 °C and 120 rpm for 144 h (Raj et al. 2014). Mathews et al. have also isolated a facultative anaerobic bacterial strain *Paenibacillus glucanolyticus* SLM1 from pulp mill waste and can degrade the lignin under aerobic and anaerobic conditions (Mathews et al. 2016). Recently, Tahir et al. (2019) have confirmed the lignin degradation property of the *Paenibacillus lautus* strains S18, S20 and S36 isolated from decaying oil palm empty fruit bunches (OPEFB).

Some previous studies have confirmed that high MnP activity was in most of the *Pseudomonas* sp. (Rahmanpour and Bugg 2015; Salvachúa et al. 2015), later on it was also confirmed by Yang et al. (2017). Highest MnP activity was in *Pseudomonas plecoglossicida* strain NBRC 103162; however, other *Pseudomonas* sp. such as *Pseudomonas citronellolis* strain DSM 50332, *Pseudomonas citronellolis* strain

NBRC 103043 and *Pseudomonas monteilii* also have high MnP activity. Noteworthy, higher MnP activity was also found in *Ochrobactrum anthropic* strain ATCC 49188 and *Leclercia adecarboxylata* strain NBRC 102595 (Yang et al. 2017). Laccase activity has been reported in several bacterial strains such as *Pseudomonas monteilii*, *Raoultella planticola* strain NBRC 14939, *Lelliottia amnigena* strain JCM1237, *Lelliottia nimipressuralis* strain LMG 10245. In general, high LiP activity was reported in *Burkholderia ginsengisoli* strain NBRC 100965, *Ochrobactrum haematophilum* strain CCUG 38531 and several *Pseudomonas* sp. such as *Pseudomonas plecoglossicida* strain NBRC 103162, *Pseudomonas citronellolis* strain DSM 50332, *Pseudomonas monteilii* (Yang et al. 2017).

The bacteria *Burkholderia* sp. H1 isolated from rotten wood samples showed high ligninolytic activity and degrades alkali lignin and Klason lignin in wheat straw (Kumar et al. 2015). Another bacterial strain *Burkholderia* sp. strain VE22 isolated from lower termite (*Coptotermes formosanus*) gut could also degrade the aromatics (Harazono et al. 2003). In 2017, Jackson et al. have reported that *Rhizobia* sp. YS-1r also have lignin degradation activity and could degrade acid-insoluble lignin in switchgrass up to 15%. However, *Rhizobia* sp. YS-1r exhibited low potential for degradation of raw lignin compared to *Burkholderia* sp. H1 (Jackson et al. 2017). Moreover, lignin degradation activity of *Burkholderia* sp. H1 was lower than *Ganoderma applanatum* BEOFB 411 fungal strain that had a maximum rate of degradation about 35% during cultivation for 14 days in wheat straw (Ćilerdžić et al. 2016). The *Cupriavidus basilensis* B-8 has also been reported to break down the kraft lignin from 15.1 kDa to 1.65 kDa for 7 days, and degraded lignin fragments were used as a carbon source for bacterial metabolism (Shi et al. 2017).

Duan et al. isolated the lignin-degrading bacterial strain, *Acetoanaerobium* sp. WJDL-Y2 from the sludge of a pulp and paper mill (Duan et al. 2016). GC-MS analysis of kraft lignin-degraded products revealed that the bacterial strain oxidized the lignin structural units p-hydroxyphenyl, guaiacyl and syringyl, and low-molecular-weight aromatic compounds such as benzene-propanoic acid, syringic acid and ferulic acid (Duan et al. 2016). Apart from *Burkholderia* sp. VE22 strain, *Trabulsiella* sp. was the other termite gut bacteria isolated from termite (*Odontotermes obesus*) gut and has been reported to degrade the alkyl lignin which was confirmed by the presence of some aromatic compounds in GC-MS analysis of the degraded product (Suman et al. 2016).

Two bacterial strains of *Bacillus* sp. CS-1 and CS-2 were isolated from forest soils in Japan exhibiting the capability of alkali lignin degradation (Chang et al. 2014). The bacterial species *Ochrobactrum* and *Rhizobium* were isolated from woodland soil and have reported to depolymerize lignin molecules and produce low molecular weight oxalic acid and protocatechuic acid metabolites from wheat straw lignocellulose (Taylor et al. 2012). A small arsenal of genes encoding lignocellulolytic enzymes have been reported from the *Klebsiella* sp. strain BRL6-2, isolated from tropical forest soils in the USA (Woo et al. 2014). *Enterobacter aerogenes* ATCC 29007 was used to assess the effects on cell growth, 2,3-butanediol production and enzyme activity of compounds derived from lignocellulosic biomass (Lee et al. 2015). Salvachúa et al. (2015) have demonstrated that a

bacterial subset can depolymerize and catabolize lignin initially up to 30%, particularly by *Amycolatopsis* sp., *Acinetobacter* ADP1, two *Pseudomonas putida* strains, and *Rhodococcus jostii*.

Several decades earlier, Actinomycetes have reported to digest and modify the lignin structure extensively; however, their degradation pattern differed with that of white-rot fungi (Buswell et al. 1987). Actinomycetes are the strong ligninolytic enzyme producers and among them *Streptomyces viridosporus* T7A was best studied for the production of lignin peroxidase (LiP) and lignin degradation. Additionally, other strains of *Streptomyces* such as *S. psammoticus* and *S. chromofiscus* have also reported producing the extracellular lignin peroxidase (LiP) (Niladevi and Prema 2008). Apart from the LiP, *Streptomyces* strains are also a good source of laccase, but the information about the production of MnP is less. However, MnP activity has been reported in some actinobacterium such as *S. psammoticus* (Niladevi and Prema 2008). Other strains such as *S. coelicolor* A3(2) and *S. badius* ATCC 39117 also showed lignin decomposition activity (Majumdar et al. 2014; McCarthy 1987). Bacteria from some genera, such as *Streptomyces*, *Nocardia*, and *Rhodococcus*, have been shown to degrade lignin with bacterial lignin peroxidase by radiochemical assay ^{14}C -labelled lignins (Leisola et al. 2012; Bugg et al. 2011b). Masai et al. (2007) extensively studied the catabolic pathways for the breakdown of lignin components in *Sphingomonas paucimobilis* SYK-6. Later on dyp-type peroxidases have been reported in a secretome of cellulose-degrading thermophilic bacterium *Thermobifida fusca* belonging to Actinobacteria (Adav et al. 2010). Extracellular heme-dependent enzyme activity has been reported against lignin model in the soil bacterium *Amycolatopsis* sp. 75iv2 ATCC 39116 formerly *Streptomyces setonii* and *S. griseus* 75vi2 (Brown et al. 2011). Recently, a thermostable endo-xylanase enzyme from the *Streptomyces griseorubens* LH-3 for biobleaching of eucalyptus kraft pulp was studied and found that pulp brightness increased up to 14.5% after treatment with purified xylanase and kappa number by 24.5% (Wu et al. 2018).

Bandounas et al. (2011) identified three bacterial species *Pandoraea norimbergensis* LD001, *Pseudomonas* sp. LD002 and *Bacillus* sp. LD003 and allowed to grow on high- and low-molecular-weight lignin fractions and degradation of ligninolytic indicator dyes. They found that *Pandoraea norimbergensis* LD001 and *Pseudomonas* sp. LD002 were efficiently growing but their decolourizing capability of dye was low, during the growth of *Bacillus* sp. LD003 was slow but decolourized the dye efficiently (Bandounas et al. 2011).

Microbial synergistic effects on saccharification were also studied, and it was observed that dual and triple microbial combinations significantly affect the saccharification. Bacterial cocultures *Aeromonas hydrophila*–*Pseudomonas poae* and *Klebsiella oxytoca*–*Bacillus amyloliquefaciens* led to increased saccharification up to 6.6- and ~ sevenfold, respectively (Taha et al. 2015).

13.5 Research Gaps and Future Outlook

Wood is the basic raw material for paper production, comprising three essential constituents: cellulose, lignin and hemicellulose. The lignin presence in the paper leads to discolouration of paper on standing by the chemical changes in lignin in the presence of light. Therefore, pulp manufacturers prefer to dissolve and remove the lignin out of the wood by chemical solutions (Paliwal et al. 2015). Lignin and hemicellulose contents are removed from cellulose fibres during the wood to paper conversion. Since several decades, pulp and paper industries are converting ligno-cellulose into valuable fibres, lignin burning for energy. The second-generation biofuels production technology began commercialized in 2015, capable of producing the chemicals and biofuels from the cellulose and hemicellulose (Xu et al. 2019; Nguyen et al. 2017). The complex structure of lignin makes it very hard to transform into valuable products and is considered as waste in biorefineries and needs to be removed, due to its inhibitory effects on fermentative bacteria (Lee et al. 2019). Depolymerization and fragmentation of the lignin are predominant strategies for the production of any valuable product such as paper, biofuels, etc. (Xu et al. 2019). In the pulp and paper industries, most of the lignin content is removed during cooking stage at high alkaline and high temperature, and the remaining residue is decolourized during bleaching process leading to the generation of highly toxic, mutagenic and carcinogenic by-products which are released in the environment.

Biological treatment of the lignin is one of the most effective and environment-friendly approaches for lignin valorization. During the last several decades, wood-rooting fungi have reported as potential lignin-degrading microorganism belonging mainly to phyla Basidiomycota, Ascomycota. Progress on fungal degradation of lignin has been made, and few of them are in the commercial processes. However, the main issue with fungal delignification is the duration required to achieve higher delignification percentages, which is more than 13 days and can vary up to 40 or 50 days, depending on the strain involved. The effectiveness and reduction of the delignification process duration have been improved to some extent by treatment with alkali before initiation of fungal delignification, and are also reported to increase yield in the glucose and bioethanol production. Bacterial degradation has some advantages over fungal degradation, such as the bacteria can tolerate a wider range of temperature, pH, and oxygen limitations than fungi (Daniel and Nilsson 1998). Another advantage is that in bacteria genetic manipulation for overexpression of gene for production of lignin-degrading enzymes is easy compared to that in fungi (Suman et al. 2016). Lignin degradation through crude and purified/semi-purified ligninolytic enzymes such as laccase, MnP and LiP also is of great concern. Synergistic effects of the combination of two or more enzymes exhibited enhanced delignification. Alkali pretreatment facilitates and improves the delignification process, similar to the microbial delignification. The advantage of enzymatic delignification over fungal delignification is the duration of time required to achieve the same delignification which is less varying between 1 and 4 days. Nevertheless, the enzymatic degradation of lignin is a high-cost process due to difficulties in producing ligninolytic enzymes on a large scale.

Although the role of microorganisms in delignification has several advantages and is beneficial to the surrounding environment in reducing the pollutants, implementation of these environmentally friendly methods is hindered due to several factors. The different methodologies of delignification process have specific advantages; however, these delignification processes cannot compete with the conventional methods in terms of cost and duration required for delignification. Extensive research to explore and identify effective and potential strains is one of the key aspects which could play a significant role to replace the existing conventional methods. Whilst, improvement in the methodologies of utilizing these microorganisms for delignification, to bring down the cost and time-span involved in the process, is crucial for upbringing and implementation of such environmental friendly technologies. In addition, it may be emphasized that these ligninolytic enzymes produced by fungal species have the potential to produce second-generation biofuels. Research with a multidimensional approach to explore the lignin-degrading microorganisms, ligninolytic enzymes and synergetic relationship, for their role in delignification in the industrial process and biofuel production could pave the way for implementation effectively and provide insight in the economic efficiency.

13.6 Conclusions

This paper reviews on the microorganisms possessing properties to degrade lignin, a component removed through various processing methods by pulp and paper industries, leading to the generation of wastewater containing large number of chlorinated toxic organic contaminants, which are highly toxic, mutagenic and carcinogenic. This large amount of wastewater generated in the form of effluents contains high chemical diversity of organic pollutants causing high toxicity effects on aquatic communities, as well as profoundly affecting the terrestrial ecosystem when discharged in recipient watercourses. One among the alternatives is the use of microbes or their enzymes like laccase, lignin peroxidase and manganese peroxidase, which are potential to remove or break down the lignin residuals and hemicellulose contents from the cellulosic pulp. Microorganisms possessing these enzymes could be a potential source for environmentally friendly technologies for the pulp and paper industries in future. Wood rotting white-rot fungi have been widely studied and reported, and among them, *Phanerochaete* sp. and *Trametes* sp. have been shown to possess strong ligninolytic properties by several researchers. Apart from white-rot fungi, several species of brown-rot and soft-rot fungi are also involved in the biobleaching process. In addition, most of the bacteria and Actinomycetes have reported as strong ligninolytic enzymes producer, among them species of the *Pseudomonas*, *Klebsiella*, *Bacillus* and *Streptomyces* could play an important role in lignin breakdown. Microbial based bleaching is an eco-friendly, safe and free from the fear of toxicity, mutagenic and carcinogenic effects of effluents on environmental communities. Use of such microbial-based

applications is the need of today and could lead to a decrease in pollutants in wastewater generated and released into the natural environment by industry.

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