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Lignocellulose Degrading Enzymes from Fungi and Their Industrial Applications

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ABSTRACT

The rich diversity of fungi and diverse range of enzymes produced by them together make researchers to exploit their potential for various industrial applications. Few of the fungal enzymes have already been harnessed and many other are to be explored and brought into use. Recent studies suggested that the lignin degrading fungi can be used in the bioremediation of aromatic hydrocarbons including dioxins, dibenzofuran, aromatic dyes, etc. Employing fungal enzymes for the treatment of pollutants has gained attraction recent days for their selectivity, specificity and eco-friendly nature. Of these enzymes, peroxidases (lignin peroxidase and manganese peroxidase) and laccases are the two major classes of enzymes involved in biodegradation of lignin and recalcitrant xenobiotics. In addition, cellulase and hemicellulase were found to play a role in the management of lignocellulosic wastes. The present review gives a detailed account on the various lignocelluloses degrading enzymes, their fungal sources and their industrial applications.

Key Words: Peroxidases, Lignocelluloses degradation, Xenobiotics, Fungal sources, Industrial applications

INTRODUCTION

Lignocelluloses are the main structural component of all plants and most of the industries including forestry, agriculture, food, pulp and paper are producing large amount of lignocellulosic wastes[1-4]. Most of the agricultural residues are rich in non-edible lignocelluloses and serve as renewable sources for the production of various value added products including biofuel which can act as the replacement for the fossil fuels[5]. Alternative fuels of petroleum solve many of the current social problems and concerns, from air pollution and global warming to other environmental improvements and sustainability issues[6] In order to exploit the uses of lignocellulosic biomass, several physical and chemical processes have been developed for the separation of cellulose, hemicellulose, and lignin from them. The separation processes include chemical viz. alkali, acid, ammonia and lime and microwave pre-treatments (physical)[7]. The commercial pre-treatment process carries respective drawbacks including decrease in the quality of the polymers, release of by-products that inhibit the fermentation of resulting sugars, etc.

In order to overcome these drawbacks, biocatalysts (enzymes) can be used to improve the superiority of the pre-treatment process[8,9]. In turn, enzymes produced by wood decaying fungi serve as an important factor for the conversion of organic debris into humus and helps in the carbon and nitrogen cycling. The lignocellulytic activity of the fungi is also facilitated with the help of extracellular enzymes, such as cellulases, hemicellulases, MnP (Manganese peroxidase), LiP (Lignin Peroxidase) and Lac (Laccase). These enzymes can be used in the management of environmental pollutants such as textile effluents, pulp effluents, organochloride agrochemicals and crude oil residues[10,11]. The filamentous fungi are rich in the production of extracellular lignocellulolytic enzymes, when compared to bacteria and yeast[12]. Since, today's world demand for more constant, active and specific enzymes, wood decaying fungi serve as an ideal candidate for the management of lignocellulosic wastes. In order to exploit the uses of lignocellulosic biomass, enzymes produced

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by wood decaying fungi can be used as an important factor for the conversion of organic debris into humus and helps in production of value added products. Even though many fungal species are involved in the biodegradation of pollutants including xenobiotics, it is essential to investigate their sources, diversity and mode of action. The present review will aid to acquire knowledge of different lignocellulosic enzymes, the fungal strains responsible for their production and their industrial applications.

Plant cell wall

Plant cell wall is a multifaceted composite of polysaccharides, aromatic compounds, proteins, etc. The plant cell wall consists of three important lingocellulosic components which include cellulose, hemicelluloses and lignin. In a plant, the lingocellulose materials comprise 30-50% of cellulose, 15-30% hemicelluloses and 15-35% of non-carbohydrate aromatic polymers the composition vary based on the species, morphology and age of the plant[13,14]. The secondary cell wall is synthesized and differentiated by cellulose microfibrils with superior crystallinity and altered hemi-cellulose content[15]. The large quantity of lingo-cellulosic materials present in cell wall make them the abundantly present, potentially inexpensive and easily available natural resources for the production of biofuels and high value compounds[16]. The use of lignocellulosic materials primarily involves the separation of the polymeric compounds into cellulose and hemicelluloses. In the absence of potential enzymes, the natural degradation of such lignocelluloses is very slow: however, microorganisms in the soil are capable to degrading the compounds and converting them into sugars at faster rate. Microorganisms capable of growing on lignocellulosic materials produce a wide range of enzymes that could be of scientific and industrial importance. Moreover, the alcohols produced by the utilization of ligocellulosic wastes could be utilized as a biofuel. Also, chemicals like vanillin, xylitol, and furfural obtained from lingocellulosic wastes can be used in industrial products including herbicides, pharmaceuticals, and household products[17,18].

Wood decaying fungi

The omnipresent fungi are the extensive producers of hydrolyzing enzymes which are responsible for the degradation of carbohydrate present in dead plant biomass[19,20]. Generally, fungi require favorable temperatures (32˚ - 90˚ F), nutrients and sufficient source of oxygen for them to survive and multiply. Since forests represent the major biome of the earth, fungi inhabiting the forests are able to degrade and mineralize the major chunk of ligno-cellulosic substrates. Fungi can be differentiated into different classes based on their distinct spore structures including Ascomycetes, Basidiomycetes and Deuteromycetes[21]. The wood decaying fungi use both enzymatic and non-enzymatic system for the degradation and complete decomposition of wood. In the wood decay process, wood turns discolored and loses weight, strength and density by the action of fungi. Most of the fungi involved in degradation of lignin and hemicelluloses fall into three broader groups namely, brown-rot, white-rot and soft-rot fungi[22].

Brown-rot fungi

The brown-rot fungi generally reduce the strength of wood upto 75% by decomposing the cell wall polymers such as cellulose and hemicellulose leaving behind the lignin[23]. Brown rot fungi make the wood fragile, dry and crumble into cubes due to the formation of longitudinal and transverse cracks[24]. The brown rot fungi dry out, makes wood into to powder when crushed and it is characterized by reddish brown color and dry, crumbly and brittle consistency . Brown rot is often referred as “dry rot”. *Poria incrassate* is one of the water conducting brown rot fungi having specific rhizomorphs based on root-like water-conducting tubes to transport water from the soil to the wood and can be decayed by the fungus. Once the brown rot fungus infected, it can rapidly multiply from side to side building and destroying large areas of floor covering and walls in one or two years. Examples of such wood decaying brown-rot fungi include *Gloeophyllum trabeum, Fomitopsis lilacino-gilva, Laetiporus portentosus, Postia placenta* and *Serpula lacrymans*[24,25]. In contrast, the numerous enzymes secreted by brown-rot and white-rot fungi enhance the wood degradation[26].

White-rot fungi

White-rot fungi belong to the family, Basidiomycetes which gradually utilize all major cell wall components such as carbohydrates, lignin and aromatic compounds[27,28]. *Ceriporiopsis subvermispora* and *Phlebia radiata* are the two best studied white rot fungi to elicit white-rot decay[29,30]. The white rot fungi produce three classes of extracellular ligninolytic enzymes: laccase, lignin peroxidase and manganese peroxidase that produce H_2O_2 needed for peroxidase activities. The white rot fungi *Rigidoporous lignosus* is known to produce two oxidative enzymes such as MnP and laccase which is capable breaking down the lignin in a synergistic system[31]. The mixed cultures of white-rot fungi are also found to improve laccase production[32]. *Dichornitus sqiualenis* appeared to delignify early wood cells, whereas, *Phellinuis pini* delignifies latewood cells effectively. Otjen[33] observed decay patterns in oak caused by *Inonotits diyophillis* which demonstrated that the fungus has a preference of early wood fibers and parenchyma cells but not latewood fibers.

Soft rot fungi

Soft rot fungi otherwise referred to as micro fungi were characterized by cavity formation in the secondary walls of the wood cells[34]. Generally, soft rot fungi utilize cellulose and

hemicellulose. Soft rot fungi degrade wood at slower rate compared to brown rot fungi and white rot fungi. In general they are found in wet floor boards, rotting window frames and fence posts. Some of these fungi are common decomposers of cellulose in soil and they are the least specialized wood decaying fungi.

Enzymes involved in lignocellulose degradation

Laccases and peroxidases are major lignolytic enzymes involved in enzymatic lignin degradation[35,13]. In addition, cellulose, hemicellulase and pectinase also play role in lignocellulosic waste degradation. Particular significance is attached to fungi producing the lignocellulosic enzymes (Table. 1) and their role in the process will be discussed.

Cellulases

Cellulase hydrolyses the glycoside bond present between the glucose residues in the organic polymer cellulose (Fig.1). Cellulose can be hydrolyzed by β-1,4-endoglucanases, exoglucanases or 1,4-β-cellobiosidase, and β-glucosidase [36-38]. Immanuel[39]reported cellulase production by *Aspergillus niger* and *Aspergillus fumigates* and optimized the parameters including pH, inoculums size, temperature, presence of inducers, etc. *Trichoderma reesei* is identified as the efficient cellulase producer by many researchers to degrade the cellulose[40-42]. Elyas[43] and Dubrovskaya[44] have isolated β-glycosidase enzyme from marine derived fungi such as *Aspergillus* sp. and *Penicillum canescens*. The amount of β-glucosidase in the *Trichoderma* cellulase system is reported to be lower than that needed for the efficient saccharification of lingocelluloses[45]. In a recent study, the cellulose produced by the *Aspergillus* sp. was used for the enzymatic saccharification of lignocellulosic agrowaste[7]. In addition, the production of cellulase has been widely studied in *P. chrysosporium*, *Sclerotium rolfsii*, *Aspergillus* sp., *Penicillium* sp., *Schizophyllum* sp. and *Trichoderma* sp.[46-48].

Hemicellulase

Hemicellulase such as xylanase are hydrolyses the xylan(Fig. 2) are extensively studied and applied on industrial scale with higher pulp brightness resulting in a lower chemical input[49]. In a recent study, a cold active xylanase was isolated from a marine fungus, *Cladosporium* sp[50]. In addition, the xylanase and endo-xylanase production has been widely studied in fungi such as *Penicillium thomii*[51], *P. pinophilum*[52,53], *A. niger*[54]and *Ceratocystis paradoxa*[55]. From an industrial point of view, an alkaline xylanase producing fungi, *A. niger*[56]and *P. canescens*[57]were isolated from marine sources.

Pectinase

The pectinolytic enzymes are produced by both plants and microorganisms. In plants, the pectinases are concerned with fruit ripening and softening whereas, pectinase produced by microorganisms helps in the degradation of the dead vegetable biomass for their utilization in soil fertilizer and nutrient recycling[58,59]. The pecinases degrade the pectins (Fig. 3) via depolymerization and de-esterification reactions[60]. Pectinase production has been studied in the following group of microscopic fungal species: *Aspergillus*, *Penicillium*, *Colletotrichum*, *Sclerotina*, *Fusarium*, *Trichoderma*, *Verticulum*, *Sclerotium*, *Geotrichum*[61-66]. Among them *A. niger* was found to be a good producer of commercial[67,68]. Many industrial firms are involved in the commercial production of pectinases used in protoplast isolation whose purity and activity vary from one source to another. Pectinase production has also been studied in phytopathogenic Ascomycetes including, *Neurospora crassa*, *Thermoascus aurantiacus*, *Rhizoctonia* sp[69,70] yeast like *Saccharomyces cerevisiae*[71]and Zygomycetes such as *Mucour* sp. and *Rhizopus* sp.[72,73].

Lignin Peroxidase

Lignin peroxidases are the heme glycoprotein that plays a vital role in lignin degradation (Fig. 4), which cleaves C-C bonds and oxidizes benzyl alcohols to aldehydes or ketones[74,75]. Lignin peroxidases act on both phenolic (e.g. syringic acid, guaiacol, catechol, vanillyl alcohol, acteosyringone) and non-phenolic lignin substrates[25]. Mostly, basidiomycetes are shown to produce efficient lignin peroxidases[76,25]. Extracellular lignolytic enzymes are prominently produced by *P. chrysosporium* and *P. radiata*[77]whereas *Coriolus tersicolor*, are capable of producing intracellular lignolytic enzymes[78]. Researchers have studied the lignin peoxidase producing ability of different fungi including *P. chrysosporium*[79], *T. versicolor*[80], *Pleurotus ostreatus*[81], *Panus* sp., *P. coccineus*, *Perenniporia medullapanis*, and *P. sanguineus*[82].

Manganese peroxidase

Manganese peroxidase degrades the lignin mainly by attacking phenolic lignin component[83]. In the presence of H_2O_2, manganese peroxidase oxidizes the phenolic structures by converting Mn^{2+} to Mn^{3+}. Oxalate and malonate are the mediators that produce carbon centered radicals, peroxyl radicals and superoxide radicals which improves the effective lignin-degrading system[83,25]. Manganese peroxidase is an essential component to certain basidiomycetes and some wood decaying white-rot fungi, which secrete manganese peroxidase in several forms into their environment. Among the basidiomycetes, *Agaricus bisporus*[84], *Lenzites betulinus*[85], *Panus tigrinus*[86]and *Nematoloma frowardii*[87]are identified to produce more stable manganese peroxidases. Järvinen[88] have studied MnP production on selected lignin degrading organisms *P. chrysosporium*, *Physisporinus rivulosus*, *P. radiata* and *Bjerkandera* sp. and found *P. chrysosporium* as best manganese peroxidase producer. Bonugli santos[89] isolated marine fungi, *Mucor racemosus* which possess the ability to produce salt tolerant manganese peroxidase.

Laccase

Laccases are the copper containing polyphenol oxidases which enable degradation of phenolic compounds and also reduce molecular oxygen to water (Fig. 5)[90-92]. Laccases oxidize the phenolic units in lignin to phenoxy radicals, which can lead to aryl-C cleavage[93]. Laccase can also oxidize non-phenolic substrates in the presence of certain auxiliary substrates[94]. A large variety of fungal strains isolated from several sea grasses, algae and decaying wood samples possess the ability to produce laccase enzyme. Atalla[95] have isolated *Trematosphaeria mangrovei* from mangrove ecosystem which produces laccase enzyme at significant quantity. A thermo stable, metal-tolerant laccase is reportedly produced by marine-derived fungi, *Cerrena unicolor*[96]. Various researchers have isolated laccase producing fungi from different sources including *Trichoderma harzianum*[97], *Trichoderma atroviride*[98] and *Trichoderma longibrachiatum*[99], *Trametes versicolor*[100], *Lentinus tigrinus*[101], *Trametes pubescens*[102], *Cyathus bulleri*[103], *Paecilomyces* sp.[104], *P. chrysosporium*[105], *Lentines edodes*[106] and *Pleurotus ostreatus*[107,81], *Ganoderma lucidum*[91], *Alternaria tenuissima*[108] and *Trichoderma* sp.[92].

Applications of lignocellulytic enzymes

Lignocellulytic enzymes are industrially very useful and the fungal cellulases are having emerging applications in various industries like fruit juice processing, ruminant nutrition for improving digestibility and de-inking of paper[109,110]. A cellulase produced by *Aspergillus* sp. was used as refining aid for cotton comber pulp, and was changed into value added security paper[111]. The cellulase obtained from fungal sources also plays a key role in the preparation of household detergents and are also used in textile industry for bio-polishing of fabrics, stonewashing of denims[112]. The cellulase is also used in the animal feeds for increasing the nutritional quality, to develop digestibility[113-115]. Fungal hemicellulases are used in the production of chemical pulps and improving pulp beat ability of unbleached pulps[116-117].

Fungal pectinases are being used in other industries such as textiles, plant fiber processing, tea, coffee, oil extraction, treatment of industrial wastewater, paper making, etc.[119-120]. Among the fungal sources, *A. niger* produces commercial pectinases which are used in the fruit juice and wine making industries. Pectinase accounts for 7.5% in the global enzyme market costing approximately 75 million USD[72]. The major applications of the pectinase enzymes are found in vegetable and fruit processing, where the removal of undesired pectin during extraction and clarification of fruit juice, wine, and cider is carried out.

There is an enormous interest in wood decaying fungi for large scale biodegradation applications due to their ability to produce large amount of extracellular lignocellulolytic enzymes[28]. Mtui and Masalu[121] have isolated a lignocellulolytic fungus, *Laetiporus sulphureus,* from mangrove forest having the ability to degrade cellulose, hemicellulose and lignin presented in the mangrove litter. Immobilized enzymes are employed in the pharmaceutical, food and chemical industries [122]. Immobilization also facilitates the efficient recovery and reuse of costly enzymes, and enables their use in continuous, fixed-bed operation[123]. The enzyme produced by the fungi was also employed for the detoxification of aromatic pollutants like agrochemicals and industrial effluents. The lignolytic white rot fungi have found their potential applications in the fields such as decolorization of industrial dyes, bleaching of pulp from textiles and paper, and degradation of organo pollutants, etc.[28,124]. The salt tolerant lignin degrading enzymes from fungi can be used for the effective bioremediation of environment pollutants[125]. The MnP finds their major applications in biomechanical pulping, dye decolorization, biorefineries, bioremediation and pulp bleaching [126,127]. In modern sensitive studies involving plant protoplast fusion and gene transfer processes, purified cellulases and pectinasers find immense use and Japanese are the pioneers in this field.

Sahadevan[128] reported lignin-degrading enzymes, LiP, MnP and Laccase from MVI.2011 an alkalophilic fungus to afford an appropriate biological substitute to treat highly alkaline effluents like pulp, paper industry and waste water. Indira Priyadarsini[129]described that the ability of fungi to produce laccase was linked with the effective decolorization of azo dyes which can be exploited for the screening of laccase producers. The fungal laccases are widely used in the industries such as food, textile, wood processing, pharmaceutical and chemical industries. In recent years, laccases are widely studied for textile industry in denim bleaching[130,131]. Another important application of laccase is the bioremediation of poisonous organic pollutants like chlorophenols and polycyclic aromatic hydrocarbons from the soil[132,133]. The stable laccase enzyme produced by *A. tenuissima* is being used in several bioprocesses, such as biopulping, biobleaching, bioremediation, food technological uses, and treatment of industrial waste water[134-136].

CONCLUSION

Among the three groups Ascomycetes, Basidiomycetes and Deuteromycetes organisms producing lignocellulosic enzymes, Basidiomycetes group of fungi are considered as the promising candidates for the degradation lignocellulosic biomass. Even though many fungal species are involved in the biodegradation of pollutants, it is essential to augment the reactions by the development of new strains and employing microbial consortium or enzymatic cocktails for industrial applications. The enzyme production by the filamentous fungi are having biotechnological importance due to their applications in different fields including plant protoplast culture and

protoplast fusion. The typical ecosystems present a veritable emporium of such organisms which are as yen poorly understood and commercially less exploited. When compared to cellulose and hemi-cellulose, lignin is found to be most difficult to degrade. For the hydrolysis of lignin, in addition to physical and chemical elements, addition of enzyme will be effective in terms of economic use as well as eco-friendly and sustainable use. The present review will aid to acquire knowledge of different lignocellulosic enzymes, the fungal strains responsible for their production and their industrial applications. Further studies are necessary to investigate the industrial applications of these enzymes for emerging production and innovation of new fungal strains.

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Conflict of interest

There is no conflict of interest.

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Table 1: List of fungi producing lingo-cellulolytic enzymes

ORGANISM	ENZYME PRODUCED	REFERENCES
A. niger, *A. fumigates*	Cellulase	Immanuel *et al.*[39]
T. reesei	Cellulase	Stricker *et al.*[40]; Kubicek *et al.*[42]
Aspergillus sp.	Cellulase	Elyas *et al.*[43]
P. canescens	Cellulase	Dubrovskaya *et al.*[44]
Aspergillus sp.	Cellulase	Bhavsar *et al.*[7]
P. chrysosporium	Cellulase	Saratale *et al.*[48]
Trichoderma viride	Cellulase	Iqbal *et al.*[146]
Cladosporium sp.	Xylanase	Del-Cid *et al.*[50]
P. thomii	Xylanase	Palaniswamy *et al.*[51]
P. pinophilum	Xylanase	Li *et al.*[52]; Lee *et al.*[53]
A. niger	Xylanase	Sharma *et al.* [54]
C. paradoxa	Xylanase	Dekker and Richards[55]
A. niger	Xylanase	Raghukumar *et al.*[56]
P. canescens	Xylanase	Burtseva *et al.*[57]
A. niger	Pectinase	Sakai *et al.*[58]; Martens and Schaap[68]
N. crassa	Pectinase	Marcus *et al.*[69]

T. aurantiacus	Pectinase	Rombouts and Pilnik[63]
Rhizoctonia sp.	Pectinase	Martins *et al.*[70]
S.cerevisiae	Pectinase	Poondla*et al.*[71]
Mucour sp.	Pectinase	Kashyap *et al.* [72]
Rhizopus sp.	Pectinase	Kolarova and Augustin[73]
P. radiate	Lignin peroxidases	Lee *et al.*[77]
C. tersicolor	Lignin peroxidases	Lobarzewski [78]
Schizophyllum commune	Lignin peroxidases	Asgher *et al.*[137]
P. chrysosporium	Lignin peroxidases	Zeng *et al.*[138]; Junnarkar *et al.*[139]
T. versicolor	Lignin peroxidases	Johansson *et al.*[80]; Asgher *et al.*[140]
P. ostreatus	Lignin peroxidases	Sivakami *et al.*[81]
P. sanguineus	Lignin peroxidases	Pointing *et al.*[82]
A. bisporus	Manganese peroxidase	Lankinen *et al.*[84]
L. betulinus	Manganese peroxidase	Hoshino *et al.*[85]
T. suaveolens	Manganese peroxidase	Knezevic *et al.*[141]
P. tigrinus	Manganese peroxidase	Lisov *et al.*[86]
Trametes villosa	Manganese peroxidase	Silva *et al.*[142]
N. frowardii	Manganese peroxidase	Hilden *et al.*[87]
P. chrysosporium	Manganese peroxidase	Järvinen *et al.*[88]
P. rivulosus	Manganese peroxidase	Hakala *et al.*[143]
P. radiate	Manganese peroxidase	Hilden *et al.*[144]
Bjerkandera sp.	Manganese peroxidase	Järvinen *et al.*[88]
M. racemosus	Manganese peroxidase	Bonugli santos[89]
T. mangrovei	Laccase	Atalla, *et al.*[95]
C.unicolor	Laccase	D'Souza-Ticlo *et al.*[96]
T. harzianum	Laccase	Holker *et al.*[98]
T. atroviride	Laccase	Velazques *et al.*[99]
T. longibrachiatum	Laccase	Kiiskinen *et al.*[10]
T. versicolor	Laccase	Han *et al.*[100]; Asgher *et al.*[154]
L. tigrinus	Laccase	Ferraroni *et al.*[101]
T. pubescens	Laccase	Shleev *et al.*[102]
C. bulleri	Laccase	Salony *et al.*[103]
Paecilomyces sp.	Laccase	Liang *et al.*[104]
P. chrysosporium	Laccase	Viswanath *et al.*[105]
L. edodes	Laccase	Shanmugam *et al.*[106]
P. ostreatus	Laccase	Patel *et al.*[107]; Sivakami *et al.*[81]
G. lucidum	Laccase	Li *et al.*[91]
T. suaveolens	Laccase	Knezevic *et al.*[141]
A. tenuissima	Laccase	Abd El Aty *et al.*[108]
Trichoderma sp.	Laccase	Divya *et al.*[92]

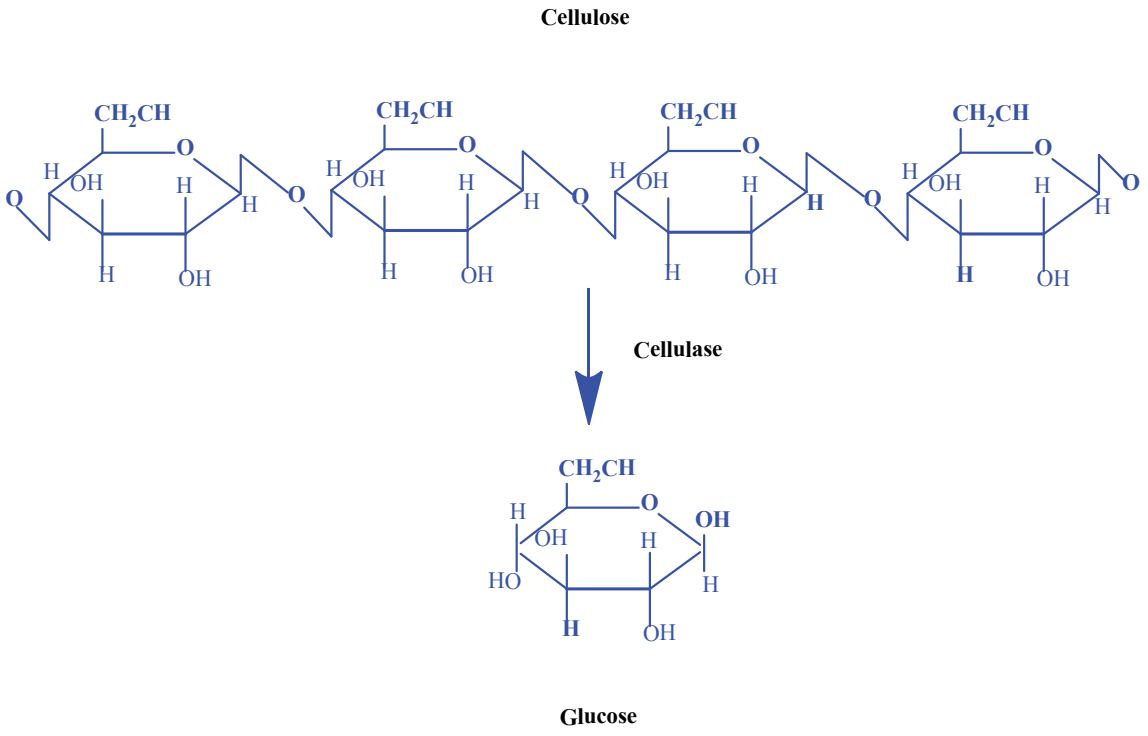

Figure 1: Mechanism of action of Cellulase.

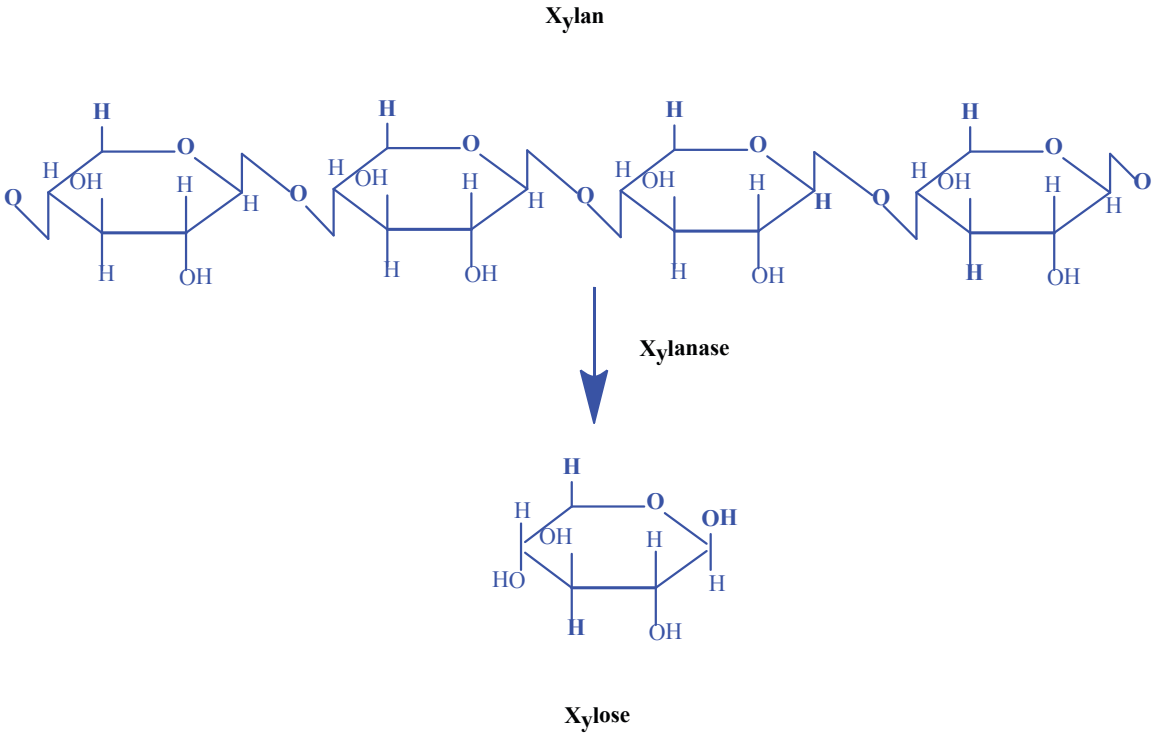

Figure 2: Mechanism of action of Xylanase.

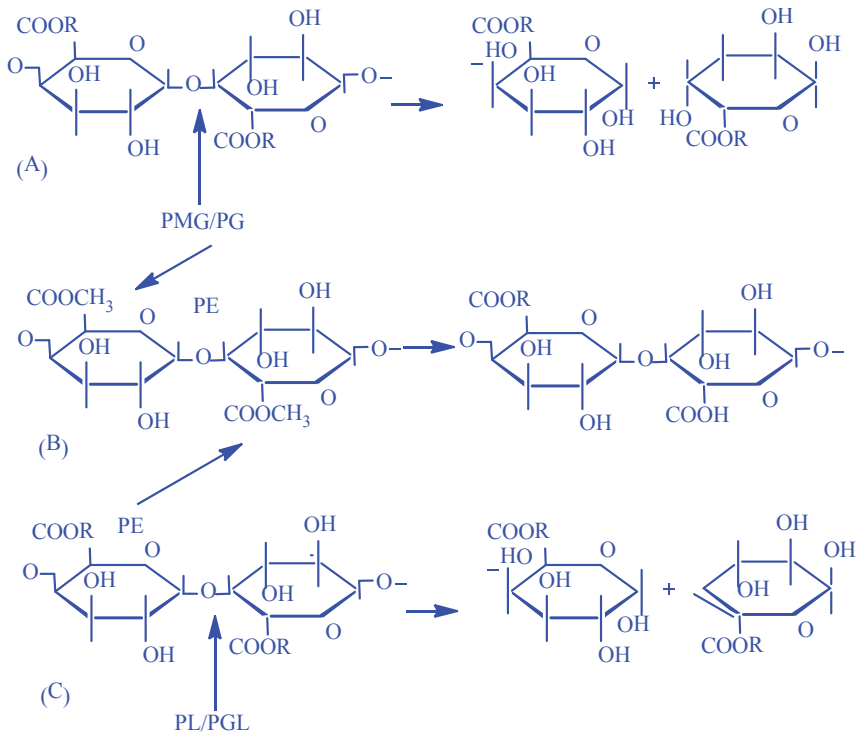

Figure 3: Mechanism of action of Pectinases[147].
PMG, polymethylg- alacturonases; PG, polygalacturonases; PE, pectinesterase; PL, pectin lyase

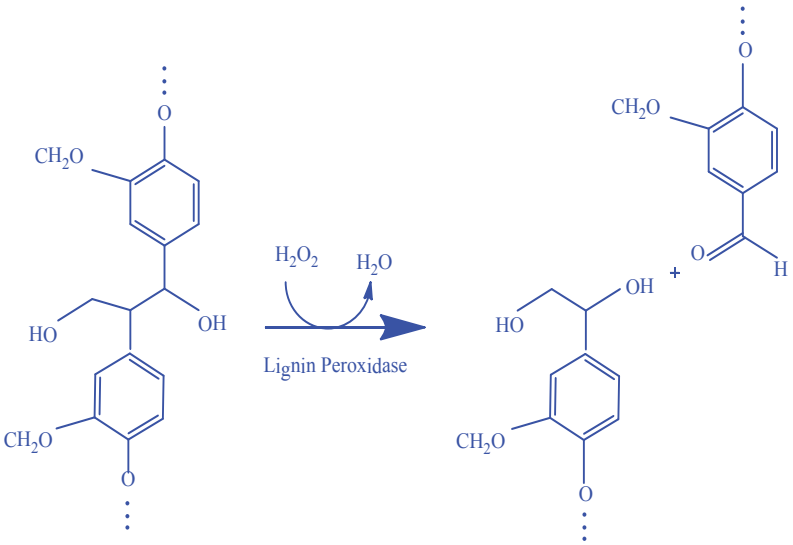

Figure 4: Mechanism of action of Lignin peroxidase.

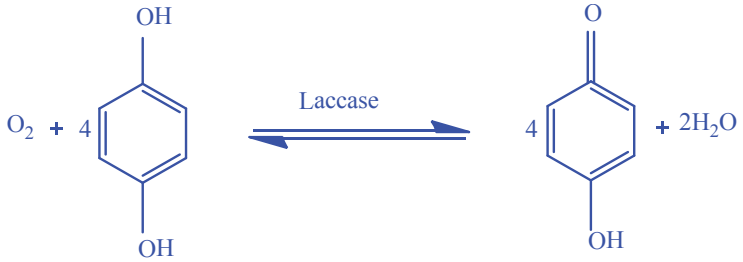

Figure 5: Mechanism of action of Laccase.