



Wood Degrading Enzymes and their Decay Strength: A Review

Priya Anand^{a++} and Phulan Rani^{a#*}

^a Department of Agriculture, G.G.D.S.D College Haryana, Hoshiarpur, Punjab, (PIN-144208), India.

Authors' contributions

This work was carried out in collaboration between both authors. Both authors read and approved the final manuscript.

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Review Article

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ABSTRACT

The degradation of wood is a major point of concern in the economy. The microbes that degrade the wood release various enzymes that decay the wood. In the present review article, we have collected the data for various decay strengths of different decay enzymes released by the various microbes from several peer-reviewed articles. The fungus basidiomycetes and some wood-degrading bacteria are responsible for the degradation of wood. The degraded wood is a major loss to the economy timber decay and many more. The degradation of wood or wood decay is also a major loss to the ecosystem by losing some precious plant species. Various data mining techniques have been used in this review to collect the data from the publications. The data in this article covers the various fields, the Name of the plant being degraded, the name of the wood degrading microbe, the Enzyme released by the microbe, the Decay strength of that enzyme, and the total loss to the economy by that decay. The unwanted decay of plant wood can be minimized if the causative agent and the enzyme released by it are found.

⁺⁺ Assistant Professor;

[#] Assistant Professor & Head;

^{*}Corresponding author: E-mail: phulanranisyal@gmail.com;

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1. INTRODUCTION

“Crop losses due to microbial attacks even after excessive use of chemical antifungals and antibacterials, are major concerns for humanity and environmental protection. By the virtue of unique properties possessed by micro and nano-structures, their implementation in Agri-biotechnology is largely anticipated. Hence, traditional Wood degrading microbial management strategies are now forestalling the potential of micro and nanotechnology as an effective and viable approach to alleviate problems about wood-degrading microbial control. These technological innovations hold promise to contribute to enhanced productivity by providing novel agrochemical agents. The present work contributes to the data collection of wood degrading enzymes and their decay strength. The intensity with which the enzymes degrade the wood is the decay strength. Fungal pathogens are proven to be a common and popular contaminant of agroecosystems that approximately causes 70–80% of total microbial plant loss reported worldwide” [1]. It is estimated that nearly one-third of global plant production is destroyed annually due to the degradation of wood, pests, microorganisms, natural disasters, soil infertility, etc. [2] Reported that “to degrade the polysaccharides, wood-decay fungi secrete a variety of glycoside hydrolases (GHs) and carbohydrate esterases (CEs) classified into various sequence-based families of carbohydrate-active enzymes (CAZs) and their appended carbohydrate-binding modules (CBM). The enzymes released by the fungi are carbohydrate-degrading enzymes called CAZymes. Oxidative enzymes, such as cellobiose dehydrogenase (CDH) and lytic polysaccharide monooxygenase (LPMO, formerly GH61), also have been implicated in cellulose degradation”. [3] reported “prokaryotes are also involved in wood degradation. Recent developments in powerful meta-omic techniques are making it possible to mine the incredible genetic diversity of prokaryotic communities of lignocellulose-enriched environments, such as compost, for new robust lignocellulose degrading enzymes that could potentially perform well under industrial conditions. Lytic polysaccharide monooxygenases (LPMOs) are copper enzymes that catalyze oxidative cleavage of glycosidic bonds”. “These enzymes are secreted by many microorganisms to initiate infection and wood

degradation processes” [4]. “In marine waters wood degrading organisms can be divided into two groups. The first group consists of macro-organisms (mainly bivalves and crustaceans) that physically gnaw and feed on wood material. The second group is micro-organisms, fungi, and bacteria, which by enzymatic processes dissolve and utilize the carbohydrates within the wood cell wall” [5].

2. PURPOSE OF THE REVIEW

It is estimated that nearly one-third of global plant production is destroyed annually due to the degradation of wood, pests, microorganisms, natural disasters, soil infertility, etc. To overcome these problems, various modern technological strategies are implemented. Among these technologies is the use of nanotechnology, biotechnology, and bioinformatics in the management of wood-degrading microbes to answer global resin output. The wood submerged in saline and oxygenated marine waters are degraded by molluscs and crustaceans. And the cold coastal waters of the Antarctic the degraders are absent and no other wood-degrading organisms are there [6]. Hardwood species have much lower recalcitrance to enzymes than softwood [1].

3. ORGANISMS THAT CAUSE WOOD DEGRADATION

There is no report of viruses and algae degrading the wood. The viruses inhibit fungus to degrade the wood, As presented in the publication [1,8,9,10]. “The uptake of water is an integral factor associated with wood’s ability to be attacked by fungi and to decay, but moisture also impacts wood by moving into the cellular structure to associate with the cellulose, causing dimensional changes” [22]. [18] Created “a database named as eLignin that map the diversity of microbial lignin catabolism”. “Waterlogged archeological wood degradation is a prolonged process that completes over a very long period” [11]. “Fungi are considered to cause grapevine trunk diseases such as esca that result in wood degradation. Bacteria that colonize plants enhance the fungal degradation of wood” [12]. “Fungi are generally known to degrade lignocellulose. several fungal species like *Trichoderma reesei*, *Phanerochaete chrysosporium*, *Fomitopsis palustris*,

Orpinomyces sp etc, were found to degrade cellulose by inhabiting the gastrointestinal tracts of several ruminating animals" [13]. [14] "The authors in cited paper isolated an insect-associated fungus, *Daldinia decipiens oita*, as a potential symbiotic fungus of female *Xiphydria albopicta* captured from Hokkaido forest". "There are Structural variations in the pine and birch LCC(Lignin carbohydrate complex) preparations of different types (Milled Wood Lignin, Cellulolytic Enzyme Lignin and LCC extracted from MWLc with acetic acid (LCC-AcOH)) [15]. The decomposition of wood is influenced by invertebrates" [11].

4. SCOPE

"Several natural compounds of plant and animal origin have fungicidal properties, including essential oils, tannins, wood extractives, alkaloids, propolis, or chitosan" [16]. "Since the growth of wood-degrading fungi depends on water availability, one of the methods is moisture control using natural hydrophobicity agents, such as resins and waxes of plant or animal origin, or plant oils. The antifungal properties of various plant extracts make them interesting also as a potential source of natural substances that may be used as alternative wood preservatives against decay. Scot's pine heartwood is known to have resistance to wood decay due to the presence of extractives, namely stilbenes and resin acids. Even Scots pine heartwood can be degraded by the fungus *Rhodonia placenta*, which can degrade the extractives namely stilbenes due to which the pine woods can also be degraded" [17]. "The biological control of fungal diseases through biocontrol agents such as antagonistic fungi (AF) and other microorganisms can be done. AF includes various genera of fungi that cure fungal diseases in plants effectively. Furthermore, they play a regulatory role in various plant physiological pathways and interactions. AF is highly host-specific having negligible effects on non-target organisms and has fast mass production capability" [18]. "Some antagonistic bacilli inhibited the growth and development of wood-decay fungi in vitro and led to the formation of spheroplasts on growing hyphae" [19].

5. MICROBIAL METABOLITES THAT DEGRADE WOOD AND KILL WOOD DEGRADING FUNGUS

Trichoderma is identified as the genus with the greatest potential comprising 25 biocontrol

agents that have been used against several plant fungal diseases [20]. Scientists have found that several bacterial genera including *Bacillus* and *Pseudomonas* have antimicrobial activity against numerous pathogenic bacterial and fungal plant pathogens [21]. It is well established that the white-rot basidiomycetes can be distinguished by their decay patterns. One group includes the model ligninolytic fungus *Phanerochaete chrysosporium*, which degrades cellulose, hemicellulose, and lignin simultaneously. Another group, exemplified by *Ceriporiopsis subvermispora*, can selectively remove lignin in advance of cellulose degradation [22]. Rigid tubular structures are required in higher plants to transport water and nutrients yet, at the same time cellulose microfibrils together with lignin and hemicellulose form a natural biocomposite that allows trees to support their enormous weight. This natural biocomposite allows trees to withstand hostile weather—very strong winds and consequently live for many thousands of years [23]. Fungi produce a broad range of extracellular enzymes to facilitate the depolymerization of plant biomass, most of which are classified in the Carbohydrate-Active enZymes (CAZy) database (www.cazy.org) [24].

6. CHEMISTRY OF WOOD DEGRADING ENZYMES AND ANTAGONISTIC ENZYMES

Angiosperms have more complex lignin including a higher relative abundance of syringyl units with the C3 and C5 positions of the aromatic ring blocked by methoxyls, compared with most gymnosperms that results in a predominance of non phenolic (C4- etherified) units [25]. Numerous strains from the *Trichoderma* species have high cellulose and xylan degradation potential and could be useful for lignocellulose biomass conversion [26]. Most brown rot fungi are generalists or gymnosperm specialists, whereas most white rot fungi are angiosperm specialists [7]. Lytic polysaccharide monoxygenases (LPMOs), a class of copperdependent enzymes might be associated with a lignin degradation pathway . The enzymatic biodegradation of structural polysaccharides is affected by the degree of delignification of lignocellulose during the white-rot fungal decay process [27]. Plant biomass utilization by fungi requires the secretion of extracellular enzymes to degrade the polymeric components, transporters for the sugars released from the plant biomass, and intracellular catabolic enzymes [28]. Nanotechnology can

offer green and eco-friendly alternatives for plant disease management, a diverse range of fungi have been screened for their ability to create silver nanoparticles [29]. The various tunneling bacteria cause the degradation of wood in various plants [30]. Enzymes of the GH27 family also show α -N-acetylgalactosaminidase activity in *Aspergillus niger*, suggesting that members of this family could be involved in processes other than hemicellulose degradation [31].

7. METHODOLOGY

The study was selected based on commercial loss in wood and timber due to wood degradation. The various wood-degrading enzymes were the focus. The data was collected from the last 10 years of peer-reviewed journals. The publications were downloaded from PubMed and Google Scholar. The various fields were created including the name of the organism, the name of the enzyme, decay strength, etc. The data has been collected in the database format

creating various tables from the various publications in peer-reviewed journals [32–36]. The keywords used during the PubMed search were “Wood degrading enzymes” from which 150 papers were downloaded, Out of which 68 papers were cited in the present manuscript. The phylogenetic relationship for the various wood-degrading fungus species is done to get the genetic relationship between the various fungus species. The phylogenetic analysis is done using the Clustal Omega software. The wood-degrading enzyme sequences were downloaded from NCBI, and RCSB-PDB databases.

8. RESULTS AND DISCUSSION

The various wood degrading enzymes and their decay strength has been collected from various peer reviewed journals. The collection has been tabulated in tabular format. The various plants or plant parts which has been used as substrate for the study are included in the table. The plants



Fig. 1. Overview of the methodology followed to generate review

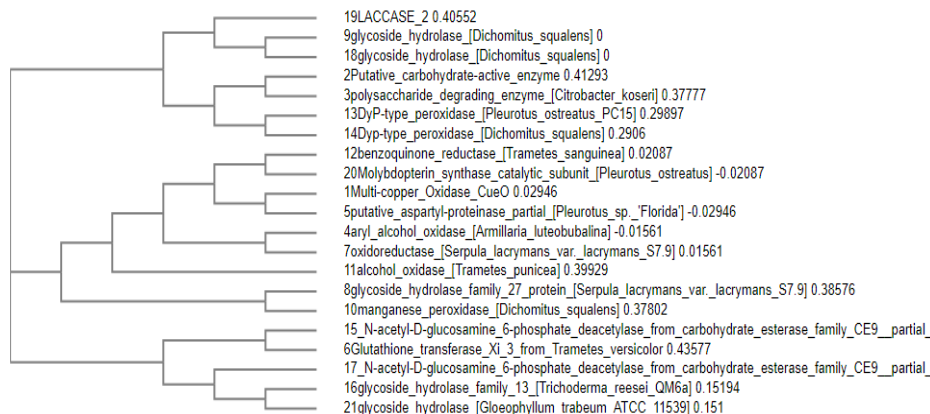


Fig. 2. The phylogenetic analysis for wood degrading enzymes

Table 1. List of Wood degrading enzymes with their decay strength and site of release

Sr. No	Substrate being degraded	Name of the organism causing wood degradation	Name of the Enzyme/Protein	Site of release	Decay Strength	Reference
1.	softwood species balsam fir (<i>Abies balsamea</i>), lodgepole pine (<i>Pinus contorta</i>), or white spruce (<i>Picea glauca</i>) or the hardwood species sugar maple (<i>Acer saccharum</i>)	White rot fungus <i>Phanerochaete carnos</i>	lignin-degrading peroxidases (manganese peroxidase (MnP))	Extracellular	High	[37]
2.	softwood species balsam fir (<i>Abies balsamea</i>), lodgepole pine (<i>Pinus contorta</i>), or white spruce (<i>Picea glauca</i>) or the hardwood species sugar maple (<i>Acer saccharum</i>)	White rot fungus <i>Phanerochaete carnos</i>	carbohydrate-active enzymes	Extracellular	Low	[38]
3.	<i>Arabidopsis thaliana</i>	Basidiomycetes	Polysaccharide degrading enzymes (Cytochrome P450 Monooxygenase)	Cytochrome complex	High	[39]
4.	Aspen Wood	<i>Ceriporiopsis subvermisp</i> (fungus), <i>Phanerochaete chrysosporium</i>	Manganese peroxidases and an aryl alcohol oxidase ,glycoside hydrolase (GH) family 51 arabinofuranosidase, GH10 endoxylanase, GH5_5 endoglucanase, and GH7 cellobiohydrolase, Cellobiosedehydrogenase	Cytochrome complex	High	[40]
5.	<i>Populus trichocarpa</i> (Viridiplantae)	<i>Aplysia californica</i> (Mollusca) and <i>Bankia setacea</i>	carbohydrate-active enzymes (CAZymes)	Gills	High	[41]
6.	Timber and wood	<i>Pleurotus sp.</i>	Proteases	Extracellular	High	[41]
7.	Sapwood, Heartwood, knotwood	<i>Trametes versicolor</i> , <i>Phanerochaete chrysosporium</i> (White rot fungus)	oxidoreductases	Extracellular	High	[42]

Sr. No	Substrate being degraded	Name of the organism causing wood degradation	Name of the Enzyme/Protein	Site of release	Decay Strength	Reference
8.	Hardwood and Softwood	<i>Myceliophthora thermophila</i> (white rot fungus)	lignocellulolytic	Extracellular	High	[43]
9.	Downed wood	<i>Postia placenta</i> , <i>Serpula lacrymans</i> , <i>Gloeophyllum trabeum</i> (Brown rot fungi)	Oxidoreductase	Extracellular	Low	[44]
10	Downed wood	<i>Postia placenta</i> , <i>Serpula lacrymans</i> , <i>Gloeophyllum trabeum</i> (Brown rot fungi)	glycoside hydrolase	Extracellular	High	[45]
11	Torreya Nucifera	Proteobacteria, Xanthomonas, Psuedomonas, and Stenotrophomonas	GH16 and GH53 proteins (hemicellulolytic enzymes)	Soil	High	[46]
12	Softwood, Hardwood, Barley straw, Oat straw, Wheat straw, Switchgrass, Muscathus, Corn Stalks, Cereals.	(Actinomycetes) <i>Streptomyces viridosporus</i> , <i>S. paucinobilis</i> and <i>Rhodococcus jostii</i> , (α-Proteobacteria) <i>Brucella</i> , <i>Ochrobactrum</i> , <i>Sphingobium</i> and <i>Sphingomonas</i> genera and (γ - Proteobacteria) <i>Pseudomonas fluorescens</i> , <i>Ps. Putida</i> , <i>Enterobacter lignolyticus</i> and <i>Escherichia coli</i>	Galactoglucomannan, Arabinoglucoronoxylan, Glucunoroxylan, Glucomamnan (Hemicelluloses), Multi-copper Oxidase CueO.	Soil	High	[47]
13	Spruce wood	<i>Fomitopsis pinicola</i> (Brown rot species)	Carbohydrate active enzymes (CAZymes), auxiliary oxidoreductases and protein-active enzymes	Extracellular	High	[48]
14	Plant Biomass	<i>Dichomitus squalens</i>	Carbohydrate active enzymes (CAZymes)	Extracellular	High	[49]
15	Heartwood	<i>Trametes versicolor</i>	Glutathione transferases	Extracellular	High	[50]
16	Hardwood and softwood	<i>Fomitopsis pinicola</i>	Peroxidases, laccases, ligninolytic oxidases, Carbohydrate- active enzymes, glycoside	Extracellular	High	[51]

Sr. No	Substrate being degraded	Name of the organism causing wood degradation	Name of the Enzyme/Protein	Site of release	Decay Strength	Reference
17	<i>Pinus contorta</i> , <i>Pinus taeda</i>	White rot fungi	hydrolases (GHs), carbohydrate esterases (CEs), and lytic polysaccharide monoxygenases (LPMOs), cellulose-binding modules Manganese peroxidase, Alcohol oxidase, Benzoquinone reductase, Dyp-type peroxidase	Extracellular	High	[52]
18	Wood	Brown rot fungus <i>Postia placenta</i> , non-brown-rot fungus, <i>Trichoderma reesei</i>	Carbohydrate active enzymes	Extracellular	High	[53]
19	Woody Biomass	Basidiomycetes, <i>Postia placenta</i>	Hydrolytic and Carbohydrate active enzymes	Extracellular	High	[54]
20	Decorticated and Sapwood	<i>Auriculariopsis ampla</i>	CAZymes (Carbohydrate active enzymes)	Extracellular	High	[55]
21	Spruce wood	White rot fungus <i>Trichaptum abietinum</i> , <i>Phlebia radiata</i> , Brown rot fungus <i>Fomitopsis pinicola</i>	Hydrolytic enzymes	Extracellular	High	[56]
22	Plant Biomass	<i>Dichomitus squalens</i>	Carbohydrate active enzymes CAZymes, intracellular catabolic enzymes	Extracellular and intracellular	High	[57]
23	Woody plant material	<i>Cerrena unicolor</i>	Cellobiose dehydrogenase	Cellulose-based medium	High	[58]
24	Media Agar	Basidiomycota (Class I) and Ascomycota (Class II and Class III)	Cellobiose dehydrogenase	Extracellular	High	[59]
25	Plant Biomass	<i>Cortaritermes fulviceps</i> and <i>Nasutitermes aquilinus</i>	Lignocellulose-degrading enzymes	Termite gut	High	[60]
26	Wood or timber <i>Malus domestica</i> , <i>Fraxinus excelsior</i> , <i>Juglans regia</i>	<i>Schizophyllum commune</i>	Lytic enzymes	Extracellular	High	[61]

Sr. No	Substrate being degraded	Name of the organism causing wood degradation	Name of the Enzyme/Protein	Site of release	Decay Strength	Reference
27	Dead organic matter	<i>P. cinnabarinus</i> , <i>P. coccineus</i> and <i>P. sanguineus</i>	CAZymes	Extracellular	High	[62]
28	<i>Populus alba</i>	<i>Pleurotus ostreatus</i>	Glycoside hydrolases, Redox enzymes, Intracellular Cont., Proteases, Esterases, Lyases	Extracellular	High	[63]
29	Japanese cedar <i>Cryptomeria japonica</i>	<i>Gloeophyllum trabeum</i>	Carbohydrate Active enzyme (CAZyme) glycoside hyrolase family 12 (GH12), GH131, carbohydrate esterase family 1 (CE1), auxiliary activities family 3 subfamily 1 (AA3_1), AA3_2, AA3_4 and AA9	Extracellular	High	[64]

with various decay strength are tabulated. The organism responsible for wood degradation is also listed in the table. The protein sequences for the wood degrading enzymes are collected from NCBI and various peer reviewed journals. For those collected sequences the phylogentic analysis is done. The phylogenetic relationship done for the various wood degrading enzymes exhibits the various wood degrading microbes having same ancestor and also the closely related microbes. Fig. 2 shows some of the closely related microbes that degrade the wood. The enzymes released by these microbes have similar functional activity. These enzymes react with similar compounds having the same functional activity.

9. WOOD DEGRADING MICROBES AND PATHOGENICITY

The bacterial community in wood degrading plants is very dynamic. Bacteria community in the fruiting body attached to the living standing tree gets suppressed compared with those associated with dead wood. The very interesting thing that can be seen in plants under wood degradation is that the wood degrading microbes are present in the wood as well as in the fruiting body upto the time the plant is standing alive. After the death of the plant the wood degrading microbes moves to the degrading dead wood and leave the fruiting body [66]. On the other hand, the Oxalate secretion by fungi provides advantages for their growth and colonization of substrates. The role of oxalic acid in pathogenesis is through acidification of host tissues and sequestration of calcium from host cell walls. The cell wall gets weakened because of the formation of calcium oxalate crystals. Thereby allowing polygalacturonase to effect degradation more rapidly in a synergistic response [67].

10. IMPACT ON SOIL NITROGEN CONTENT

The high carbohydrate availability in white-rotted wood promotes the activity of Nitrogen-fixing bacteria to fix the atmospheric Nitrogen in the soil. On the other hand, the Brown rotted wood is unattractive to the saproxylic communities due to the high recalcitrance of the accumulated lignin, low nutrient content, and low pH [65].

11. NITROGEN IN WOOD AND ITS ROLE IN DETERIORATION

Nitrogen is present in xylem cylinders of tree stems. Nitrogen gets diluted by the apposition of

cell wall contents. When the wood fiber cells mature the Nitrogen content gets eluted into the transpiration stream. The maximum Nitrogen content in the cytoplasm gets removed when the xylem parenchyma cells die during the aging of sapwood and the formation of heartwood [68]. The trees have a recycling mechanism for the conservation and reuse of the Nitrogen in the cytoplasm of the xylary cells.

12. CONCLUSION

The wood-degrading enzymes are the enzymes secreted by the wood-degrading microbes i.e fungi or bacteria. The enzymes show the characteristic decomposition of the wood. Various termites and wood borer organisms contain various cellulose degrading microbes in their gut. These microbes release the enzymes in organism's gut and the cellulose from the wood gets degraded by these microbes and excreted out in the soil. That soil again contains those wood degrading microbes and enzymes too. Then from soil these organisms are again able to degrade the wood content, timber, or direct wood. The main purpose of this study is to bring all the wood-degrading microbes and wood-degrading enzymes in front. Further investigation regarding wood-degrading microbes and the enzymes secreted by them can be done to bring to light the solution for minimizing the loss of wood and timber by degradation.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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