JETIR.ORG ISSN: 2349-5162 | ESTD Year : 2014 | Monthly Issue
JOURNAL OF EMERGING TECHNOLOGIES AND INNOVATIVE RESEARCH (JETIR)
An International Scholarly Open Access, Peer-reviewed, Refereed Journal

MICROBES IN LIGNOCELLULOSE DEGRADATION

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Abstract: Lignocellulosic biomass is the most abundant renewable organic resource on Earth. It consists of cellulose, hemicellulose, and lignin. Microorganisms, including fungi and bacteria, are the main decomposers of lignocellulose in nature. They produce lignocellulolytic enzymes that break down these complex polysaccharides into fermentable sugars. This process has the potential to revolutionize waste management and bioconversion industries. Lignocellulolytic enzymes can be used to convert lignocellulosic waste into biofuels, biochemicals, and biomaterials. Fungi, particularly white-rot and brown-rot fungi, have been widely explored for lignocellulolytic enzyme production. Bacteria are gaining increasing attention due to their faster growth rates and ability to survive in harsh environments. Accessory proteins play a crucial role in enhancing the efficiency of lignocellulolytic enzymes by modifying the structure of lignocellulose, making it more susceptible to enzymatic breakdown. Continued research on optimizing enzyme production, tailoring enzyme properties, and improving conversion processes is vital for realizing the full potential of lignocellulolytic enzymes in building a sustainable bioeconomy.

Index Terms - Cellulose, hemicellulose, lignin, cellulase, ligninase, laccase, pectinase

I. INTRODUCTION

Microorganisms, encompassing bacteria and archaea, are the most ancient and minute cellular life forms on Earth. Their fossil record, including stromatolites, indicates an origin around 3.8 to 3.9 billion years ago, predating the rise of plants and animals. These ubiquitous, single-celled organisms were the pioneer inhabitants of Earth's diverse ecosystems. Despite their diminutive size, microorganisms collectively contribute the most biomass on Earth. Recent estimates suggest a staggering diversity among prokaryotes, with 0.8 to 1.6 million predicted species. Their remarkable adaptability allows them to thrive in virtually every conceivable environment, from the fertile depths of soil to the Frigid Polar Regions, scorching hot springs, and hypersaline seas (Benatti et al., 2023). Currently, microorganisms, particularly bacteria and fungi, serve as the primary source of industrially relevant enzymes. Their rapid growth and ease of cultivation in large-scale fermentation processes enable the efficient and cost-effective production of these biocatalysts in significant quantities (Choi et al., 2015). Lignocellulolytic enzymes are a specialized group of enzymes produced by microbes that have the remarkable capacity to degrade lignocellulosic biomass. The building block of plant cell walls, this abundant and renewable resource is also the most common organic material on Earth. It consists primarily of three major components-

a) **Cellulose**: The main structural polysaccharide, accounting for 40-50% of lignocellulosic biomass. Cellulose microfibrils are made of β-1,4-glycosidic bonds between D-glucose units, forming a highly crystalline and recalcitrant structure.
b) **Hemicellulose:** The second most abundant component (20-30%), hemicellulose is a heteropolymer polysaccharide composed of various sugars (arabinose, mannose, and xylose) linked together by different glycosidic bonds. Hemicellulose acts as a matrix that encases cellulose microfibrils and binds them to lignin.
c) **Lignin:** An aromatic biopolymer (10-20%) that acts as a "glue," providing rigidity and structural support to the cell wall and hindering the enzymatic breakdown of cellulose and hemicellulose (Zoghlami et al., 2019).

In lignocellulosic membrane or biomass, cellulose is the main component which constitutes about 30-50%, while hemicellulose is the second highest component found in lignocellulosic biomass or membrane which constitutes about 20-30% and the third important component is the lignin which makes about 10-20% of membrane (Srivastava et al., 2019). Lignocellulolytic enzymes can be broadly classified based on their mechanism of action they are hydrolytic enzymes and ligninolytic enzymes. Hydrolytic enzymes contain cellulases and hemicellulases while ligninolytic enzymes contain oxidases, peroxidases, and so on (Mtui et al., 2012). Cellulases are enzymes that specifically target cellulose, breaking down β-1,4-glycosidic linkages to release sugars like glucose while hemicellulases are diverse group acting on various glycosidic bonds within hemicellulose, releasing a mixture of sugars like xylose and arabinose. Enzymes are complex biological molecules composed primarily of a protein portion (apoenzyme) and, in some cases, a non-protein cofactor. The protein part provides the enzyme's structure and catalytic machinery, while the cofactor, if present, can participate directly in the catalytic reaction. Enzymes are classified into six functional classes based on the type of chemical reaction they catalyze: which are oxidoreductase, transferase, hydrolase, lyase, isomerase, and ligase. The ligninolytic enzyme and hydrolytic enzyme fall under oxidoreductase and hydrolase respectively (Singh et al., 2019). Lignocellulolytic enzymes are a diverse group of enzymes produced by a wide range of microorganisms, encompassing bacteria, archaea, and fungi. These enzymes play a critical role in the biodegradation of lignocellulosic biomass, the most abundant renewable organic resource on Earth. The requirement for oxygen varies among lignocellulolytic enzyme producers. While some fungi and bacteria function optimally in aerobic environments, others, particularly anaerobic bacteria and archaea, thrive in

oxygen-limited conditions like the gut or waterlogged soils. Their enzymes have adapted to function efficiently in these oxygen-depleted environments. This diversity in microbial producers and enzyme specificities highlights the remarkable biological versatility harnessed for lignocellulose breakdown in nature. Several bacterial genera, including *Bacillus*, *Clostridium*, and *Streptomyces*, are known producers of lignocellulolytic enzymes. These enzymes often exhibit a high degree of specialization, targeting specific components of lignocellulose like cellulose or hemicellulose. While less studied compared to bacteria and fungi, some archaea, particularly those belonging to the phylum Euryarchaeota, have been shown to possess lignocellulolytic capabilities. Research suggests their enzymes might play a role in synergistic degradation alongside bacterial enzymes in natural environments. Considered the key decomposers in many ecosystems, fungi are prolific producers of lignocellulolytic enzymes. White-rot and brown-rot fungi utilize distinct enzyme sets to deconstruct lignocellulose. White-rot fungi employ a broader repertoire of enzymes, including cellulases, hemicellulases, and ligninolytic enzymes (oxidases and peroxidases) for complete degradation. Brown-rot fungi primarily target cellulose through the action of cellulases (Benatti et al., 2023).

II. MICROBES HAVING LIGNOCELLULOLYTIC ENZYMES

Major components of lignocellulosic materials include cellulose, hemicellulose, and lignin in combination with minor amounts of pectin, nitrogenous compounds, ash, salts, and minerals. Lignocellulose's potential to produce useful products remained underutilized. Pretreatment and enzymatic degradation of lignocelluloses obtained from anthropogenic solid waste can sustainably yield enzymes, biofuel, organic acids, animal feed, and feedstock for different industries. Lignocellulolytic enzymes secreted by various organisms sustainably degrade lignocellulose biomass and are employed in industries such as biofuel, textile, pharmaceutical and health sector, solid waste treatment, food and beverage, etc. It may result in lowering pretreatment costs and improve the adoption of biomass (Chukwuma et al., 2020). Nature harbors a diverse array of lignocellulolytic microbes, including fungi and bacteria. Both groups play essential roles in the biodegradation of lignocelluloses. Fungi, particularly filamentous ascomycetes like *Trichoderma*, *Penicillium*, and *Aspergillus*, have been widely explored for lignocellulolytic enzyme production. These fungi are known for their efficient extracellular secretion of a broad spectrum of enzymes, including cellulases, hemicellulases, and ligninolytic enzymes (oxidases and peroxidases). This diverse enzymatic arsenal allows them to effectively deconstruct the complex structure of lignocellulose. While fungi have traditionally been the focus of lignocellulolytic enzyme research, bacteria are gaining increasing attention. Bacteria generally have faster growth rates compared to fungi. This can be advantageous for large-scale enzyme production using fermentation processes. Some bacteria produce enzyme complexes (multi-enzyme systems) that can degrade several lignocellulosic components simultaneously. This can potentially enhance the overall efficiency of biomass deconstruction. Certain bacteria exhibit remarkable adaptability to various environmental conditions, including extremes of pH, temperature, and salinity. This could be advantageous for specific industrial applications (Woo et al., 2014).

III. ORGANISMS INVOLVED IN LIGNOCELLULOSE DEGRADATION

Being recalcitrant lignocelluloses are difficult to degrade by most organisms, especially lignin cannot be hydrolyzed by hydrolytic enzymes (hydrolases) due to heterogeneity in its chemical linkages. Primarily fungi are the most studied organisms that degrade lignocelluloses by secreting hydrolases and ligninases. Recently a shift of research towards bacteria using high-throughput technologies opened novel avenues for lignocellulose degradation at laboratory as well as at industrial levels.

3.1 Degradation of lignin by fungal candidates

Fungi mainly the white rot and brown rot fungi extensively explored for their potential to degrade lignocelluloses almost completely. Here are summarized examples of both categories.

White rot fungi: White rot fungi (Class- Basidiomycetes) are efficient delignifying agents as they form a set of extracellular lignin-degrading enzymes. White rot fungi like *Phanerochaete chrysosporium*, *Pleurotus ostreatus*, *Coriolus versicolor*, *Cyathus stercoreus*, and *Ceriporiopsis subvermispora*, have been extensively studied for their lignolytic performances (Martinez et al., 2004; Wan and Li, 2012). Wood ravaged by white rot takes on a whitish hue and a fibrous texture. Some white rot candidates degrade lignin preferentially in comparison to cellulose and hemicellulose components of lignocellulosic biomass. These include *C. subvermispora*, *Phellinus pini*, *Phlebia* spp., and *Pleurotus* spp. meanwhile, *Trametes versicolor*, *Heterobasidion annosum*, and *Irpex lacteus* degrade cellulose, hemicellulose, and other cell wall constituents simultaneously (Wong, 2009).

3.2. Ligcellulose degrading enzymes

Over a dozen extracellular lignocellulolytic enzymes have been discovered and are used industrially belongs hydrolytic and lignin-degrading enzymes. Hydrolytic enzymes are responsible for degrading complex carbohydrates like cellulose, hemicelluloses, pectins, chitin, etc. On the other hand, ligninases (peroxidases and oxidases) degrade lignin to produce the monomers and constituent components. Lignin Peroxidase (LiP), manganese Peroxidase (MnP), and versatile peroxidase (VP) are some of the many peroxidases used by fungi to break down wood. Laccase, another key player, belongs to the oxidase family with a different enzymatic function. Copper-containing phenolic oxidases are another assemblage of enzymes made and secreted by wood-rotting fungi and bacteria involved in lignin degradation. Many oxidoreductases such as glyoxal oxidase, aryl alcohol oxidase or veratryl alcohol oxidase, pyranose 2-oxidase or glucose 1-oxidase, cellobiose/quinone oxidoreductase, and cellobiose dehydrogenase are produced by various fungi help in lignin degradation (Ander and Marzullo, 1997).

LiP and MnP were discovered from *Phanerochaete chrysosporium, and* various iso-forms of LiP have been isolated and characterized from *T. versicolor*, *Phanerochaete sordida*, *Phlebia radiata*, and *Phlebia tremellosa* (Sugiura et al., 2009). White rot fungi produce MnP in several forms *e.g. C. subvermispora* is known to secrete 11 isoforms (Lobos et al., 1994). *Trichoderma reesei* secrete an array of enzymes that make it an efficient lignocellulolytic enzyme. VP was first isolated from *Pleurotus eryngii*and found restricted to species of two genera *Pleurotus* and *Bjerkandera* (Moreira et al., 2009). VP catalyzes the reactions of both LiP and MnP. DyP obtained from *Auricularia auricula-judae* is used to remove natural and synthetic dyes. Laccases are found distributed widely in wood-rotting fungi such as *Trametes versicolor*, *T. hirsuta*, *T. ochracea*, *T. villosa*, *T. gallica*, *Cerrena maxima*, *C. subvermispora*, *Pleurotus radiata*, *P. ostreatus* and *P. eryngii* (Baldrian, 2006) *Ganoderma lucidum* (Hariharan and Nambisan 2012), *Irpex lacteus* (Zhou et al., 2013), *Coriolus versicolor* (Nasreen et al., 2015), *Funalia trogii* (Boran and Yesilada 2011), *Marasmius* sp. (Hendro et al. (2012), *Oudemansiella radicata* (Balaraju et al. 2010), *Trichoderma harzianum* (Huiju et al., 2013), *Trichoderma muroiana* (Jaber et al., 2017). Almost all the white rot fungi make laccase with LiP

and/or MnP. Although *Pycnoporus cinnabarinus* lacks LiP as well as MnP but efficiently degrades lignin alone (Eggert et al., 1997). Some other important fungal genera naturally equipped with extracellular digestion of lignocellulolytic potential are *Aspergillus, penicillium, Schizophyllum, Trichoderma, Phanerochaete, and Sclerotium* (Saadeddin et al., 2012).

Hydrolytic enzymes producing micro-organisms have been reported by different workers such as *Aspergillus niger, and Trichoderma viride* produce cellulase used for bleaching, deinking of paper, hydrolysis of cellulose for ethanol, and biofuels production. *Aspergillus niger*, *Aspergillus terreus*, and *Penicillium verruculosum* secrete mannanase employed in the textile and paper industry. *Penicillium sp.* and *Cerrena unicolor* produce xylanase and laccase respectively employed in bleaching and deinking of paper (Ravindran and Jaiswal, 2016). Mushroom cultivation is another way of solid-state fermentation that leads to the degradation of lignocellulolytic materials and generates useful food and feedstock (Kumla et al., 2020).

Brown rot fungi: The groups of wood rotting fungi attack the wood polysaccharides and hydrolyze them into components. Brown rot fungi such as *Gloeophyllum trabeum*, *Laetiporus portentosus*, and *Fomitopsis lilacinogilva* especially attack conifers wood to degrade cellulose and hemicelluloses. They partially degrade lignin resulting in brown coloration, hence the name (Monrroy et al., 2011).

Soft rot Fungi: These fungi are known to be present under high-temperature habitats but are almost found where white rot and brown rot fungi are prohibited from growing due to high temperature, high moisture, low oxygen concentrations, and the presence of preservatives. Soft rot fungi do not produce ligninases, hence no lignolytic activities. They produce cellulases and degrade cellulose inside the wood resulting in microscopic cavities. Sometimes soft rot fungi induce discoloration and cracking patterns in the same manner as brown rot fungi (Abdel-Hamid et al., 2013).

3.3. Degradation of lignocelluloses by bacteria and archaea

Lignocellulolytic bacteria are more advantageous and less explored than their fungal counterparts as they multiply more rapidly and consist of multi-enzyme complexes enabling them to survive under adverse environmental conditions (Woo et al., 2014). Search for lignocellulolytic enzymes from bacterial sources is in its beginning phase it needs more studies to isolate and culture such bacteria and then can be used in the laboratory or industry.

Along with the advent of advanced strategies such as meta-genomics and meta-transcriptomics analyze the bacterial populations involved in lignocellulose degradation. In meta-genomics labeled probes and group-specific primers are used to detect novel enzymes. The limitation of this qualitative method is that metabolic potential cannot be determined. However, it is useful to screen a large number of species and strains in a very short period. Transcriptome and proteome studies further explore the expression potential of such strains.

Culture, culture-independent meta-genomic approach led to finding a diverse world of microorganisms in operational and non-operational landfills. It revealed that non-operational landfills exhibit higher diversity as compared to the close ones. The observations indicate proteobacteria most abundant phylum followed by Bateroidetes, Firmicutes, and Tenericutes respectively in both landfills. Acidobacteria, Actinobacteria Gemmatimonadetes, Nitrospirae, and Verrucomicrobia predominantly occur in closed landfills. Archaea are represented by few genera making it a minor phylum in active landfills while nearly absent in closed landfills (Kochling et al., 2015; Zainun and Simarani 2018). Bacteria isolated from active and closed landfills are efficiently run biodegradation and bioremediation (Azari et al., 2017). Enzymes like azoreductases and depolymerases isolated from *Bacillus* spp., *Pseudomonas* spp., *Nocardia* spp., *Streptomyces* spp., *Aspergillus* spp., and *Alternaria* spp. through enrichment, cultivation methods are reported to be employed in xenobiotic degradation (Jain et al., 2011).

Municipal solid wastes (MSW) are predominantly rich in biodegradable organic materials and can harbor a variety of lignocellulolytic bacteria. As a result of fermentation methane and other greenhouse gases are generated and cause nuisance to the environment. The lignocellulolytic potential can be utilized for the generation of biofuel and other industrial products. Studies based on analyses of 16S rRNA sequence revealed that *Proteobacteria* are most abundant followed by *Actinobacteria*, *Firmicutes*, *Bacteriodetes*, and *Chloroflexi*. Other phyla including *Verrucomicrobia, Acidobacteria, Parcubacteria, and Tenericutes* were abundant at different sites. In landfills great number of microbial communities although less abundant but metabolically more active than communities present in great proportions. These include *Sulfurimonas, Pelagibius*, *Halomonas, Paraburkholderia tropica, Moheibacter, Luteimonas, Rhizobium, Paracoccus, Norcardioides,* and *Woodsholea* (Thakur et al., 2020). Landfills are good breeding grounds for a variety of microbial communities having a broad range of biodegradation capabilities. At landfill sites, the cocktail of enzymes reduces the time for the degradation of solid wastes. *Acinetobacter pittii* MASK25 isolated from landfills produces methodical xylanase that can degrade rice straw and corn cob to yield xylo-oligosaccharides. Cellulases and laccases have been isolated from microbes in landfill samples and can hydrolyze rice straw into glucose (Chownk et al., 2019). *Woodsholea* isolated from certain landfill sites is a sulfur-oxidizing bacteria and grows on reduced sulfur compounds. Pulp and paper mills, sewage treatment plants, landfills, and oil refineries are good sources of reduced sulfur compounds (Borrás et al., 2016).

Among herbivores, termites bear efficient lignocellulolytic potential and act like microscale bioreactors (Brune, 2014). There is a microbiota living in symbiotic association with termite gut and secrete lignocellulolytic enzymes. Cellulolytic and hemicellulolytic groups of bacteria such as *Bacteroides* and *Enterobacteriaceae* have been isolated and cultured (Azizi-Shotorkhoft et al., 2016). Metagenomic studies of termite gut revealed the abundance of phyla Spirochaetes, Bacteroidetes (*Bacteroides* and *Prevotella),* Fibrobacteres, and Firmicutes. Fibrobacteres and Firmicutes are capable of degrading lignocelluloses as they code glycoside hydrolases (Brune, 2014). These microbiome candidates can be good inoculums for lignocellulolytic bioreactors for the industrial production of methane and volatile fatty acids. *Clostridia* isolated from biogas plants found cellulose and hemicellulose degrading potentials (Thomas et al., 2014).

Many researchers using different strategies determined the lignocellulolytic enzyme production potential of bacteria. For instance, *Streptomyces viridosporus, S. badius, S. albus, Amycolatopsis* sp., and *Thermobifida fusca* are known to produce LiP and MnP. DyPA and DyPB were isolated and characterized from *Rhodococcus jostii* (Ahmad et al., 2011). Bacterial laccases are obtained from *S. cyaneus, Streptomyces ipomoea, S. coelicolor, T. thermophilus,* and *Bacillus licheniformis. Streptomyces actuosus* produce a good quality xylanase. While traditionally considered less prominent producers compared to bacteria and fungi, some archaea hold promise for lignocellulose breakdown. Genera like *Pyrococcus*, *Sulfolobus*, *Thermogladius*, and *Thermofilum* are known extremophiles, thriving in harsh environments with high temperatures, acidic pH, or high salinity. The extremophilic nature of these archaea raises interesting possibilities for industrial applications (Suleiman et al., 2020).

IV. Role of accessory proteins and enzymes in degradation

Lignocellulolytic enzymes, while powerful, don't operate in isolation. Accessory proteins play a crucial role in enhancing their efficiency and facilitating the complete breakdown of lignocellulosic biomass. These accessory proteins function through various mechanisms to modify the complex structure of lignocellulose, making it more accessible to enzymatic attack (Ezeilo et al., 2017). Some accessory enzymes, like Lytic Polysaccharide Monooxygenases (LPMOs), can disrupt the crystalline structure of cellulose. LPMOs are a particularly well-studied group that utilizes a unique oxidative mechanism. They incorporate molecular oxygen into the cellulose structure, introducing breaks in the β-1,4-glycosidic bonds. This weakens the tight packing of cellulose microfibrils, making them more susceptible to hydrolysis by cellulases. Other accessory proteins may loosen or swell the lignocellulosic matrix. This can involve breaking hydrogen bonds or non-covalent interactions within the structure, allowing better penetration of lignocellulolytic enzymes to their target substrates (cellulose, hemicellulose). LPMOs represent just one example of a diverse group of accessory enzymes involved in lignocellulose breakdown. Some accessory proteins are Swollenins and expansins. Swollenins are proteins that can disrupt hydrogen bonds within cellulose microfibrils, leading to increased accessibility for cellulases. Another one is expansins which target non-covalent interactions within hemicellulose, loosening the matrix and facilitating enzymatic access. The other one is Carbohydrate-binding modules (CBMs) which are not strictly enzymes; CBMs are attached to some cellulases and hemicellulases. They act by specifically binding to cellulose or hemicellulose, bringing the catalytic domain of the enzyme closer to its substrate for more efficient hydrolysis (Agger et al., 2014). The combined action of lignocellulolytic enzymes and accessory proteins is crucial for efficient lignocellulose deconstruction. Accessory proteins modify the substrate, making it more susceptible, while the enzymes then cleave the glycosidic bonds within cellulose and hemicellulose. This synergistic interaction is essential for the complete breakdown of lignocellulosic biomass into fermentable sugars for biofuel production or other industrial applications.

V. Conclusions and Future Prospects

Enzymes are indeed fundamental biological catalysts playing crucial roles in various cellular processes. Among these, lignocellulolytic enzymes hold immense promise for sustainable waste management and bioconversion applications. Lignocellulosic biomass, the most abundant renewable organic resource on Earth, comprises plant cell wall components like cellulose, hemicellulose, and lignin. Lignocellulolytic enzymes possess the remarkable ability to degrade these complex polysaccharides. This breakdown unlocks the potential of lignocellulosic waste streams, transforming them into valuable products (Chukwuma et al., 2020). By facilitating the breakdown of lignocellulosic waste materials, these enzymes offer a sustainable approach to waste management. This can divert waste from landfills, reducing greenhouse gas emissions associated with decomposition. The breakdown products of lignocellulosic biomass by these enzymes can be utilized for various purposes: a) Fermentable sugars released from cellulose and hemicellulose can be converted into biofuels like ethanol and biodiesel, offering a renewable alternative to fossil fuels. b) Lignocellulose breakdown products can also serve as precursors for the production of bio-based chemicals and materials, promoting a more sustainable bioeconomy. Lignocellulolytic enzymes represent a powerful tool with immense potential for sustainable waste management, biofuel production, and the development of a bio-based economy. Continued research and development efforts focused on optimizing enzyme production, tailoring enzyme properties, and improving conversion processes are crucial for realizing their full potential.

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