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Review

The Bacterial Degradation of Lignin—A Review

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Abstract: Microbial degradation of lignin, a natural complex biopolymer, a renewable raw material with a wide range of applications, has been mainly directed at fungal systems, nevertheless, recent studies have proposed the bacterial role in lignin degradation and modification since bacteria possess remarkable environmental adaptability, and various production of enzymes and biochemistry. An occurrence of a high proportion of lignin-degrading genes has been confirmed in actinobacteria and proteobacteria classes by bioinformatics analysis, which points to the probability of undiscovered pathways and enzymes. Because of that, bacterial lignin decomposition might be substantially different from fungal lignin decomposition. Bacteria capable of lignin modification and degradation belong to actinomycetes, some Firmicutes, α-proteobacteria, and γ-proteobacteria. The enzymes responsible for lignin degradation are lignin peroxidase, manganese-dependent peroxidase, versatile peroxidase, dye-decolourizing peroxidase, and laccases. One of the main lignin producers is the pulp and paper manufacturing industry. Lignolytic microorganisms have been identified from diverse habitats, such as in plants, soil, wood, and the gut. Bacterial strains *Bacillus*, *Rhodococcus*, *Sterptomyces*, and *Pseudomonas* have been reported to have lignin decomposition ability. This review aims to describe the role of bacteria in lignin degradation, bacterial species, and bacterial enzymes included in lignin degradation. Several reports about bacterial species involved in lignin degradation are also highlighted, and the current state of the knowledge on the degradation of lignin from the pulp and paper manufacturing industry are reported.

Keywords: lignin; bacterial degradation; bacterial species; bacterial enzymes

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1. Introduction

Lignin is the most widespread natural aromatic heteropolymer and one of the basic building blocks of lignocellulosic biomass. Lignin (15–30%), together with cellulose (30–50%) and hemicellulose (15–30%), forms part of the secondary cell wall of plants and contributes to the integrity of the cellulose/hemicellulose/pectin matrix [1]. Lignin is a complex highly branched three-dimensional phenolic structure that contains three basic monolignols, phenol derivatives, which make up almost all types of lignin: p-coumaryl alcohol (M1H), coniferyl alcohol (M1G), and sinapyl alcohol (M1S) [2] (Figure 1). Each monolignol produces p-hydroxyphenyl, guaiacyl, and syringyl subunits in the polymer [3]. Lignin has a variable molecular mass due to random cross-linking by polymerization of phenolic groups, which originate from radical coupling reactions between phenolic radicals [1]. Lignin contains functional groups such as phenol hydroxyl, methoxyl, carboxyl groups, and alcohol hydroxyl, which affect the reactivity of lignin [4]. The synthesis of lignin takes place by joining monolignol units using peroxidase-mediated dehydrogenation, whereby the structures of connected basic units are formed and connected to each other by C–C bonds and aryl ether linkages with aryl-glycerol and β-aryl ether. The largest proportion is β-O-4 aryl ether bonds, about 50–70%, followed by β-β, β-5, 5-5, and 5-O-4 bonds [3].

Carbon–carbon bonds are among the most resistant bonds to breaking [4]. Monolignols are connected to other polymers from the cell wall, such as cross-linking of polysaccharide and protein, and thus a complex three-dimensional matrix is formed [3], which provides the tissues and cell walls of all vascular plants rigidity, strength, and protection against degradation by microorganisms [5]. Lignin can be classified into four main groups according to the amount of basic phenol units such as guaiacyl (G), syringyl (S), and p-hydroxyphenyl (H) in the polymer into type-G, type-G-S, type-H-G-S, and type-H-G [3].

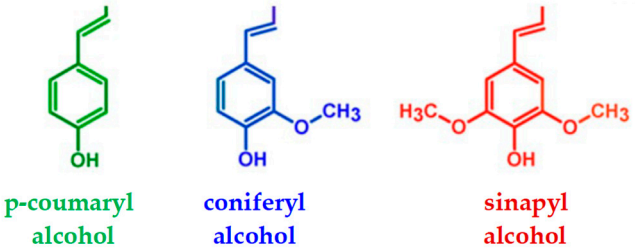

Figure 1. Basic phenol units.

Interest in lignocellulosic material is growing because of its potential replacement for high-value chemicals derived from petroleum derivatives [6], and its potential in the production of biofuels [5], the paper industry [3], the production of sorbents, activated carbon, carbon fibres with a very large surface area and pore volume [7], and in bioplastics production [3] (Figure 2).

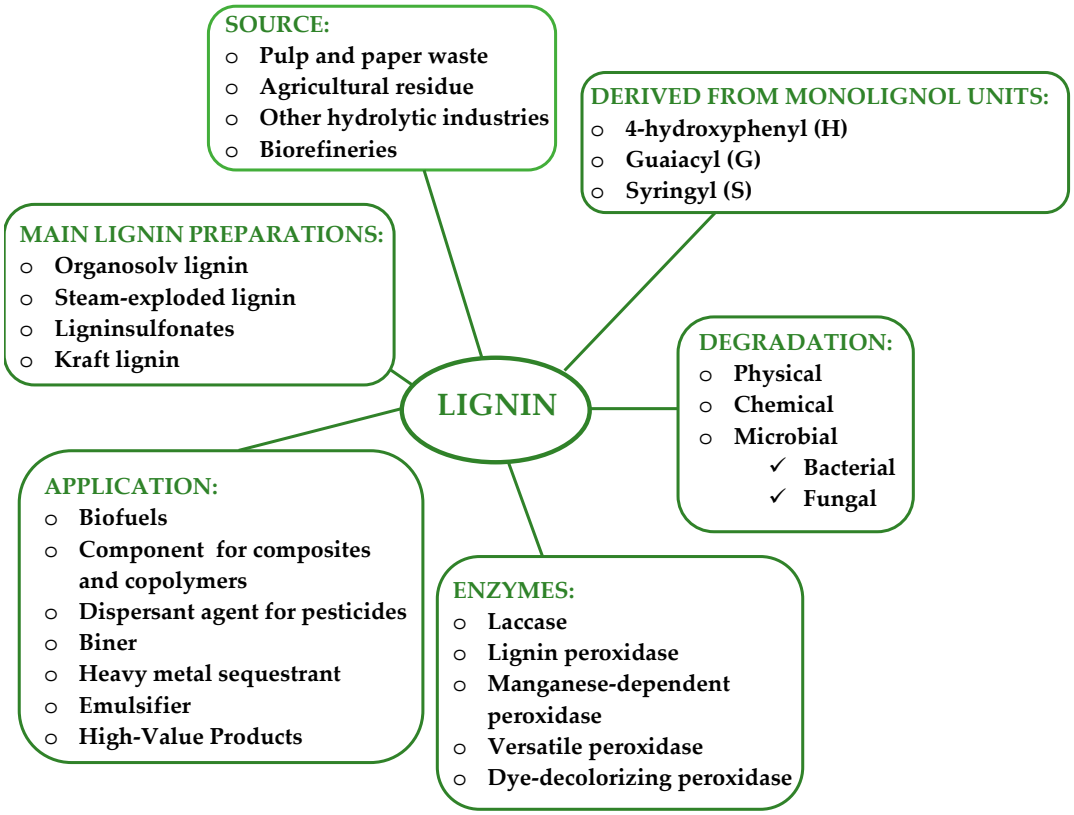

Figure 2. The source of lignin, monolignol units, main lignin preparations, application of lignin, degradation of lignin, and enzymes involved in lignin degradation.

One of the most important mechanisms for lignin utilization is via biotransformation and degradation [8] (Figure 2). Biodegradation of lignin is an economically and environ-

mentally friendly option [9], and key research on lignin degradation is based on biological methods, oxygen-dependency, and cometabolic methods.

Biological degradation or decomposition of lignin can be carried out by fungi [6,10] and bacteria [6,10–12] (Figure 2). Bacterial lignin breakdown is not as efficient as fungal, and bacterial delignification is more limited and slower than fungal [13], but bacteria can tolerate a wider range of pH values, temperature, and oxygen availability, and bacteria are easier to manage in comparison with fungus [8]. Ligninolytic bacteria have been found in soil [9,12], animals [12], compost [9], sediments [12], insect guts [12], and sewage [9]. Bacteria have the ability to modify and degrade lignin including actinomycetes, some Firmicutes, α-proteobacteria, and γ-proteobacteria [11,14–16].

The paper industry is one of the main producers of lignin (Figure 2). The pulp and paper manufacturing industry is responsible for the annual production of 50–70 millions m^3 of lignin [17,18]. The dark brown wastewater (the colour comes from the lignin and lignin derived compounds) resulting from the paper industry makes globally an amount of 695.7 million m^3 [19]. For the treatment of paper mill wastewater and for lignin removal, physical and chemical techniques can be applied [20]; however, in comparison with the biological approach, they are expensive, usually require intense process conditions, and result in sludge [21]. The removed lignin from the paper and pulp industry is not intended for application goals [22].

In this review, lignin biodegradation by bacteria, ligninolytic enzymes, as well as some reports of lignin degradation by bacteria, are highlighted. The current state of knowledge on the degradation of lignin from pulp and paper manufacturing industry is also highlighted.

2. Lignin Degradation

Lignin degradation can be carried out chemically [23] and thermally [7] by advanced oxidation processes: photocatalytic [24], pyrolysis, electrochemical [25], or enzymatically/biologically [9] (Figure 2).

Lignin cannot be degraded by most degradation methods [9] due to its complex and irregular structure and because it lacks standard repeating covalent bonds [12], which makes it a recalcitrant material [24,26]. Biological methods of lignin degradation are preferred over chemical processes because there is no yield loss in biological processes, such as in the case of thermal lignin decomposition, and because of the possibility of managing lignin biodegradation in biological methods by using selective ligninolytic enzymes and microorganisms, which avoids the formation of unwanted by-products. Biological processes are characterized by mild conditions, which reduce the energy input and the environmental impact [4].

The decomposition of lignin is carried out by ligninolytic enzymes in order to produce valuable chemicals, such as vanillin and vanillic acid, and other chemicals [27], for biofuel production [28]. During the operation of cellulose and paper mills, lignin ends up in the wastewater effluent and significantly contributes to environmental pollution with high values of organic compounds and the colour of the effluent, and therefore the decomposition of lignin is very important [24]. Such wastewater is a great challenge for treatment by conventional wastewater treatment processes [23]. Moreover, the essential point of closing the carbon cycle is microbial lignin degradation because the elimination of the lignin blockade allows the subsequent use of plant carbohydrates by other microorganisms [29].

3. Biological Lignin Degradation

Fungi and bacteria do not produce secondary pollution, and biological degradation or decomposition of lignin is considered a green and environmentally friendly process [8].

Hydrolytic enzymes cannot cleave lignin due to the branched three-dimensional structure, and C–C and C–O ether bonds [30]. Moreover, non-phenolic aromatic subunits of lignin cannot be oxidized by low-potential oxidoreductases such as plant oxidases that initiate lignin polymerization. Such lignin composition results in the evolution of fungi and bacteria that developed several groups of enzymes that have ligninolytic activity [14,15,30].

Biodegradation of lignin is an oxidative process that requires the production of extracellular ligninolytic enzymes, namely lignin peroxidase (LiP), manganese-dependent peroxidase (MnP), versatile peroxidase (VP), dye-decolourizing peroxidase (DyP), and laccases (LaC) [9] (Figure 2). The binding affinity of lignin-degrading enzymes is connected to the type and structure of lignin. The three main non-covalent bonds: electrostatic bonds, hydrophobic bonds, and hydrogen bonds, are included in interactions between lignin and amino acids in the enzymes [31] (Figure 3).

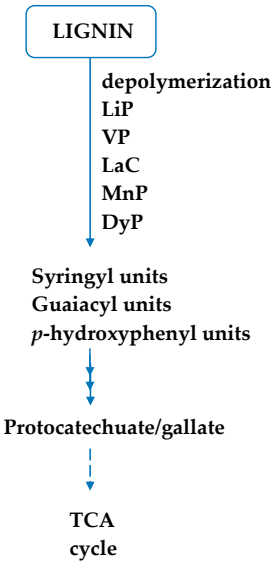

Figure 3. Microbial lignin degradation.

Since the chemical structure of lignin is highly variable, as well as the enzymes used to degrade lignin, the degradation products also vary [5]. During multiple biochemical transformations, C–C and C–O monomer bonds are split, and hydroxylation, demethylation, and modification of side chains and other transformations occur. All transformations occur mostly simultaneously [32].

Lignin degradation takes place in two phases [15]. During the first phase, homocyclic aromatic compounds are converted into protocatechuic acid and catechol [33]. The first phase of lignin degradation is mainly cleavage of the β-O-4 aryl ether bond in the phenylen unit [8]. During the second phase, a series of intermediates are formed due to the cleavage of the central ring. The produced aromatic compounds, catechol, and protocatechuic acid, are the predominant intermediates during the lignin biochemical conversion [33]. Bugg et al. [15] described catabolic pathways for the breakdown of lignin components: by β-aryl ether degradation pathways (bacteria and fungi), biphenyl degradation pathways (bacteria), diarylpropane degradation pathways (bacteria and fungi), degradation of phenylcoumarane and pinoresinol lignin components (bacteria and fungi), bacterial degradation of ferulic acid, and oxidative cleavage of protocatechuic acid (bacteria).

One of the processes in which biodegradation of lignin takes place is composting. During the composting, the mixed microbial community present in the compost pile is active and microorganisms convert organic material into compost (humus), carbon dioxide, water, and heat. It is assumed that humus is formed mainly from lignin, polysaccharides, and nitrogenous compounds, so that the complete mineralization of lignin does not occur during the composting process. During composting, thermophilic microfungi and actinomycetes are responsible for lignin degradation [34,35].

Lignin degradation and modification has been mostly studied in basidiomycetes [5]. White and brown rotting fungi play an important role in the degradation of lignocellulosic biomass due to the secretion of extracellular ligninolytic enzymes [32]. Different white-rot fungi produce different combinations of enzymes, for example LiP and MnP, MnP and LaC,

and LiP and LaC. Brown-rot fungi are able to successfully degrade cellulose and hemicellulose, but lignin only to a limited extent [35]. Aerobic white-rot fungi basidiomycetes can carry out complete degradation of lignin [36]. Due to the strict fungi growth conditions, their industrial application is limited, since high yields and productivity are required [8].

4. Lignin Degradation by Bacteria

Bacterial lignin metabolism has not been studied in as much detail as fungal lignin metabolism [12]. Bacteria can also be applied for lignin degradation due to their exceptional environmental adaptability, diverse biochemistry and enzyme production [37], and some bacteria are listed in Table 1. Many bacteria with the capability of degrading lignin can be found in soil since those bacteria have a catabolic pathway for metabolizing aromatics due to the quantity of lignin, an aromatic material, present in soil [15]. The bacterial pathways for lignin-derived components catabolism are proposed regarding the bacterial metabolism of aromatics since they are not fully investigated [38], with model bacteria for aromatics catabolism *Sphingomonas paucimobilis* SYK-6 [5]. Bioinformatic analyses in actinobacteria and proteobacteria classes confirmed the occurrence of a high proportion of lignin-degrading genes [15] and suggest the possibility of undiscovered pathways and enzymes [5], and therefore the bacterial strategies for lignin decomposition might significantly differ from fungal strategies [39]. Laccase genes were mostly identified in strains belonging to Firmicutes, Proteobacteria, Actinobacteria, and in a much lower extent in strains belonging to Bacteroidetes, and Cyanobacteria [40].

Examples of lignin-degrading bacteria belonging to the *Actinomycetes* are *Streptomyces viridosporus* T7A, *Sphingomonas paucimobilis* SYK-6, *Comamonas*, *Nocardia*, *Rhodococcus*, and sulfate-reducing bacteria. When these bacteria are grown on lignocellulose, they secrete extracellular peroxidases and degrade both the lignin and the carbohydrate components of lignocelluloses [9]. A wide group of bacteria can degrade lignin and 'C-labelled dihydroxyl phenol, such as eubacteria (*Bacillus*, *Acinetobacter*, *Xantomonas*, *Aeromonas*, and *Pseudomonas*) and actinomycetes (*Micromonospora*, *Thermomonospora*, *Nocardia*, and *Streptomyces*) [9]. Some bacteria that show the ability to degrade lignin are *Pandoraea* sp. B-6, *Novosphingobium* sp. B-7, *Bacillus* sp. strains CS-1 and CS-2, *Citrobacter freundii* (FJ581026), *Citrobacter* sp. (FJ581023), *Pandoraea* sp., *Streptomyces* spp. strains F-6, and *Streptomyces* spp. strains F-7 [6]. The most studied lignin-degrading bacterium, *Streptomyces viridosporus* T7A, produces several extracellular peroxidases that depolymerize lignin by breaking the β-aryl ether bond which results in the release of phenols of low molecular weight [41]. *Rhodococcus jostii* RHA1 [42] and *Pseudomonas putida* mt-2 [16,42] are also recognized as species capable of lignin degradation.

Although fungal systems are more efficient in degrading lignin than bacterial systems, bacterial systems have some abilities to modify lignin and release smaller aromatic compounds that can be imported into the cell and metabolized via aromatic catabolism [14].

Actinomycetes are bacteria that resemble fungi due to the formation of multicellular filaments. This group of bacteria tolerates higher pH and temperature values than fungi. Actinomycetes can break down cellulose and solubilize lignin. However, the ability of actinomycetes to degrade lignin and cellulose is lower than that of fungi. Actinomycetes degrade lignin as part of primary metabolism and at high nitrogen concentrations, compared with white-rot fungi, which mainly degrade lignin as part of a secondary metabolism [35].

Lignin degradation is oxidative, although reduction reactions can contribute similarly [43]. Genomic and proteomic studies of lignin-reducing bacteria have shown the existence of bacterial laccases and DyP peroxidases, and the lack of LiP, MnP, and VP enzymes [44].

Different bacteria use different lignin degradation pathways [16]. For example, there are bacteria that possess oxidative enzymes for modifying lignin by means of demethylation or hydroxylation, such as cytochrome P450 monooxygenase (P450s), manganese superoxide dismutase, DyP, and laccase [45]. Some bacteria in the absence of hydrogen peroxide use the β-ketoadipate pathway (β-KAP) to degrade lignin, such as *Rhodococcus jostii* RHA1 [16].

The β-KAP pathway involves enzymatic degradation of the aryl ring, whereby aromatic compounds are converted to metabolites of the tricarboxylic acid cycle by nine essential enzymes and intermediates [46].

Some bacteria need another carbon source for lignin degradation, such as *Enterobacter lignolyticus* SCF1 which requires xylose [47]. Since lignin degradation is too slow for lignin to serve as an energy source, microbial degradation of lignin requires an energy source, despite the fact that complete lignin degradation is highly exothermic. Because of this, numerous microorganisms are not able to use lignin as the sole source of carbon or energy [12].

The use of psychrotrophic bacteria that have the ability to degrade lignin is a promising way to degrade lignin in cold climates to return agricultural residues to the land [27].

Bacterial laccases are more stable at higher pH and temperature values compared with fungal laccases. Bacterial laccases have a higher optimal pH than fungal laccases, which are more suited to an acidic pH value. Bacterial laccases are mainly intracellular, and fungal laccases are both intra- and extracellular [4]. Bacterial laccases have a lower redox potential than fungal laccases [5].

Table 1. Bacteria capable of lignin degradation and/or modification.

Bacteria	Reference
Bacillus	[11]
Bacillus ligniniphilus L1	[12]
Bacillus sp.	[48,49]
Bacillus sp. ITRC-S8	[37]
Bacillus magnetrium	[50]
Bacillus altitudinis SL7	[51]
Bacillus flexus RMWW II	[52]
Bacillus pumilus	[53]
Bacillus atrophaeus	[53]
Bacillus cereus	[54]
Bacillus megaterium	[55]
Bacillus sp. (AY952465)	[56]
Bacillus endophyticus	[48]
Bacillus subtilis	[48,57]
Arthrobacter sp. C2	[27]
Planococcus sp. TRC1	[58]
Pseudomonas	[11]
Pseudomonas sp. Q18	[59]
Pseudomonas putida NX-1	[60]
Pseudomonas putida KT2440	[61]
Pseudomonas putida A514	[62]
Pseudomonas fluorescens	[40]
Pseudomonas aeruginosa	[63]
Pseudomonas plecoglossicida	[50]
Brevibacillus thermoruber	[8]
Microbacterium sp.	[6]
Streptomyces	[11]
Streptomyces sp.	[6]
Streptomyces badius ATCC 39117	[64]
Streptomyces viridosporus T7A	[65]
Streptomyces coelicolor A3(2)	[66]
Streptomyces cinnamoneus	[39]
Rhodococcus	[11]
Rhodococcus opacus PD630	[67,68]
Rhodococcus jostii RHA1	[16]
Rhodococcus opacus DSM 1069	[68]
Rhodococcus erythropolis	[69]

Table 1. *Cont.*

Bacteria	Reference
Amycolatopsis sp. 75iv2	[70,71]
Enterobacter	[11]
Enterobacter lignolyticus SCF1	[47,72]
Enterobacter soil sp. nov.	[73]
Enterobacter aerogenes	[74]
Paenibacillus sp. (AY952466)	[56]
Paenibacillus glucanolyticus	[75]
Paenibacillus sp. strain LD1	[76]
Caldicellulosiruptor bescii	[77]
Thermobifida fusca	[78]
Clostridium thermocellum	[79]
Brucella	[40]
Ochrobactrum	[40]
Sphingobium	[40]
Sphingomonas	[40]
Sphingobacterium	[45]
Escherichia coli	[40]
Aneurinibacillus aneurinilyticus (AY856831)	[56]
Azotobacter	[55]
Citrobacter sp.	[80]
Citrobacter freundii	[81]
Klebsiella pneumonia	[57,80]
Pantoea sp.	[82]
Pseudochrobactrum glaciale	[82]
Serratia marcescens	[55,80]
Serratia liquefaciens	[83]

5. Reports of Lignin Degradation by Bacteria

5.1. Lignin Degradation by Bacillus ligniniphilus L1, Halotolerant Bacterium

Zhu et al. [12] investigated lignin degradation and colour removal from alkaline lignin using the alkaline halotolerant bacterium *Bacillus ligniniphilus* L1 during a 7-day experiment. Degradation metabolites were monitored using the Gas Chromatography-Mass Spectrometry (GC-MS) analysis. The experiments were performed at 50 °C as the optimal temperature for the investigated strain for lignin degradation, with lignin as the only carbon source and with the combination of glucose-lignin as the carbon source. After 7 days of incubation of the investigated strain with lignin as the only carbon source, they recorded 38.9% lignin degradation and 30% colour removal [12]. As manganese peroxidase and laccase are hypothesized to decolourize lignin [84], Zhu et al. [12] suggested that *Bacillus ligniniphilus* L1 can secrete laccase or manganese peroxidase to degrade lignin. GC-MS analysis showed that 15 aromatic compounds were identified during 7 days of incubation of the investigated strain with lignin, and nine aromatic compounds were identified in the control sample (non-inoculated sample). The lignin metabolite that was detected the most was vanillic acid, accounting for 44.2% of all produced aromatic metabolites. This is followed by 4′-hydroxyacetophenone with 14.5%, vanillin with 8.7%, and 4-hydroxyphenylacetic acid with 7.2%. The authors believe that the L1 strain degraded lignin, but also that it degraded aromatic compounds from lignin or used it as a source of carbon or energy. In addition to the detected 15 aromatic compounds with one phenyl ring, the authors assume that there can be many other aromatic compounds that were not detected by GC-MS because they were present in low concentrations below the detection limit. In the whole genome of the L1 strain there were no observed LiP or MnP genes. The results obtained by the combination of GC-MS and genome data suggest that there can be three pathways of lignin degradation in the L1 strain: the gentisate pathway, the benzoic acid pathway, and the β-ketodiapate pathway [12].

5.2. Lignin Degradation by Arthrobacter sp. C2, Psychrotrophic Bacterium

Jiang et al. [27] investigated the biodegradation of lignin (sodium lignin sulfonate) using the psychrotrophic bacterium *Arthrobacter* sp. C2 isolated from soil. *Arthrobacter* species can be found and isolated in contaminated environments, and they play an important role in the biodegradation of organic substances [27]. This species is ubiquitous due to its diverse diet and resistance to environmental stress, such as long-term starvation, changes in osmotic pressure, temperature changes, oxidative stress, high concentrations of heavy metal ions, and toxic chemicals [85,86]. *Arthrobacter* sp. C2 shows the activity of LiP and MnP. The authors used sodium lignin sulfonate as a substrate. The conditions for the enzyme activity of the strain were optimized using Response Surface Methodology (RSM) based on Box–Behnken Design (BBD). For enzymatic activity, the optimal conditions were initial pH 6.47, temperature 14.9 °C, incubation time 6.87 days, and inoculum size 2.23%. Lignin peroxidase and manganese peroxidase were responsible for lignin degradation, and 40.1% of lignin degradation was achieved. The rate of lignin degradation was determined using ultraviolet (UV) spectrophotometry and the biodegradation products were monitored using GC-MS and Fourier Transform Infrared Spectroscopy (FTIR), and acids, phenols, aldehydes, and alcohols were detected. Decomposition of lignin using psychrotrophic bacteria enables the decomposition of lignin even in cold climates, but also represents energy savings during the production of useful chemicals [27]. Cold-adapted enzymes from psychrotrophic bacteria, compared with the same type of mesophilic and thermophilic enzymes, show higher catalytic efficiency and poor thermal stability [87]. Processes in which cold-adapted enzymes are applied are fast and economical, so savings in energy and production costs can be realized [88].

5.3. Lignin Degradation by Pseudomonas sp. Q18

Yang et al. [59] investigated the biodegradation of lignin, namely alkaline lignin and raw lignocellulosic material (switchgrass, corn stalk, and wheat straw), using the bacterium *Pseudomonas* sp. Q18, isolated from rotten wood in China. The decomposition of alkaline lignin was monitored after 3 and 7 days of incubation. The process of lignin degradation was monitored by Gel-Permeation Chromatography (GPC), Field-Emission Scanning Electron Microscope (FE-SEM), and GC-MS. In raw lignin samples, after treatment with *Pseudomonas* sp. Q18, the amount of residual lignin was reduced, with the amount of residual material in relation to total lignin being lower for switchgrass than for corn stalk and wheat straw. The treatment of switchgrass resulted in the greatest loss of mass from dry biomass, almost 25%, compared with corn stalks and wheat straw. FE-SEM analysis of wheat straw after treatment with *Pseudomonas* sp. Q18 showed a damaged stalk structure and numerous small fragments on the surface compared with the appearance of wheat straw before decomposition. FE-SEM analysis of alkaline lignin showed that after treatment, the smooth surface of lignin was completely eroded. GPC analysis of alkaline lignin showed a decrease in molecular weight after treatment with the investigated strain, which coincides with the lignin content after treatment. The GPC results suggest that the high molecular weight alkaline lignin particles are depolymerized into smaller particles after treatment. Analysis using GC-MS showed that after the incubation of lignin with *Pseudomonas* sp. Q18 the concentration of aromatic compounds with a phenolic ring significantly increased, which indicates the degradation of lignin [59]. The strain Q18 can use the compounds of low molecular weight as energy or carbon source, as shown by substantial consumption and catabolism of aromatic compounds [12]. Depolymerisation of lignin, aromatic catabolism, and production of co-products occurred simultaneously. During the alkaline lignin decomposition process, the amount of organic acids and esters increased, such as oxalic acid, ethyl acetate, and 3-acetyloxybutanoic acid ethyl ester. This increase possibly reflects chemical reactions among primary microbial metabolites or cleavage of lignin intermediates after degradation. The authors of the research assume that the Q18 strain possesses DyP peroxidase (PmDyP) based on the analysis of lignin-derived

metabolites, which belongs to the B-type subfamily of DyP. This strain has the potential for use in a refinery for lignocellulose biodegradation [59].

5.4. Lignin Degradation by Brevibacillus thermoruber

Niu et al. [8] investigated the degradation of lignin using *Brevibacillus thermoruber*, at temperatures of 37 °C and 55 °C. The bacterium *Brevibacillus thermoruber* has the ability to secrete MnP, LaC, and LiP, and was isolated from aerobic corn stalk and food factory sludge compost. *Bacillus* possess broad physiological characteristics, high adaptability, a short cycle of proliferation, and can produce thermostable enzymes. Atomic Force Microscopy (AFM), FTIR, and UHPLC-QTOF/MS were used to analyse lignin before and after decomposition. During the biodegradation of lignin, 81.97% of lignin degradation was achieved during 7 days using the bacterium *Brevibacillus thermoruber*, similar to what is achieved by lignin degradation using fungi. At 37 °C, the lignin degradation pathway (G and H monomers) took place via the β-ketodiapate pathway. At 55 °C, the product of lignin degradation (S monomer) was mainly benzoic acid, that is, the path of lignin degradation took place via the path of benzoic acid. Extracellular enzymes secreted by *Brevibacillus thermoruber* were adsorbed on the lignin surface, which disrupted the lignin structure, increased the surface roughness, decreased the surface size, increased the specific surface area, and increased the number of active sites, which helped the lignin degradation. The degradation products of lignin were analysed and compared with the Metlin database, where 40 compounds were identified. The amount of lignin decomposition products changed over time and depending on the temperature at which the decomposition took place. The efficiency of lignin degradation increased with an increase in temperature [8].

5.5. Lignin Degradation by Bacteria Streptomyces sp. and Microbacterium sp., White-Rot Fungi Coriolus versicolor and Trametes gallica, and Purified Laccase Enzyme

Asina et al. [6] conducted experiments on the degradation of a high lignin concentration (industrial lignin) of 13.3 g/L during 54 days using the white-rot fungi *Coriolus versicolor* and *Trametes gallica*, the bacteria *Streptomyces* sp. and *Microbacterium* sp., and a purified laccase enzyme. The expression of lignin-modifying enzymes depends on the growth phase of the microorganism and on the occurrence of a secondary metabolism, so subtle changes in the balance between actively growing and dying biomass can lead to variations in the extent of activity of extracellular enzymes over time [89]. Laccase activity in both fungal strains was significantly higher compared with bacterial strains [6]. Most bacterial laccases are expressed intracellularly, but some strains of *Streptomyces* sp. produce extracellular laccases [90]. The activity of extracellular laccase varies significantly depending on the pH value of the solution and the composition as a result of the interference of electrostatic interactions and hydrogen bonds within the tertiary structure of the protein [91]. During the entire experiment, all four investigated strains showed significant MnP activity, and LiP activity was not recorded in any strain [6]. Contrarily, Adhi et al. [92] noticed significant LiP activity in numerous *Streptomyces* strains. The *Streptomyces* bacterial strain did not show apparent laccase activity [6]. The extent of lignin decomposition and observed enzyme activity are not directly correlated [93]. Asina et al. [6] suggested that some other enzymes besides the investigated ones might be engaged in the biodegradation of lignin. Mineralization of kraft lignin was more significant by fungi, and bacteria partially decomposed and modified lignin. The highest mass loss was obtained with fungal treatment, especially with *C. versicolor*, 45 ± 8% at the end of the experiment, or 25 ± 15% when taking into consideration lignin mass loss in the control. The slight weight loss was observed with bacterial and laccase treatment. The extent of repolymerization is more pronounced during the decomposition of lignin by laccase and fungi. Fungi have shown the ability to cleave highly cross-linked fractions of lignin, with a fine balance between cross-linking by polymerization and degradation. After bacterial degradation of lignin, the accumulation of phenolic monomers was recorded without their further catabolism [6].

Effective degradation of kraft lignin (the most numerous form of lignin, obtained by acid dissolution of black liquid, which is formed as a by-product of alkaline sulphide treatment of lignocellulose characteristic of the paper industry [94]) during a short incubation time was achieved mainly by bacterial strains (30–81.4%) because the treatment with fungi is often unstable when carried out by rough industrial treatments [95].

6. Ligninolytic Enzymes

Lignin degradation enzymes can be classified as: (i) lignin-modifying enzymes (LMEs), and (ii) lignin-degrading auxiliary (LDA) enzymes. LDA enzymes are important in completing the degradation process and cannot perform the lignin degradation process alone [96]. Ligninolytic enzymes LMEs primarily include the peroxidase families (heme-containing peroxidases: lignin, manganese, and versatile peroxidase), and laccases (phenol oxidase) [5,39]. Lignin-modifying peroxidases (LMPs: VP, LiP, and MnP) are a part of the superfamily of catalase-peroxidases and a part of class II peroxidases [39]. A new group of enzymes, LDA enzymes, heme-thiolate haloper-oxidases, has been proposed for lignin degradation. Within the heme protein family, it is the most versatile biocatalysts [39,97]. The members of the auxiliary enzymes (LDAs), usually produced by white-rot fungi, are: glucose oxidase, glyoxal oxidase (GLOX), cellobiose dehydrogenase (CDH), pyranose 2-oxidase (POX), and aryl alcohol oxidases (AAOs) [98].

LaC, multi-copper oxidases, are produced by many organisms: insects, bacteria, fungi, and plants [5]. Laccase is a secondary metabolite that is produced under growth-limiting conditions, especially under nitrogen limitation, which has a negative effect on the enzyme yields. The laccases have many different functions, such as lignin biosynthesis and lignin degradation, among others [4]. The majority of laccases have four atoms of copper that mediate the redox process in their active site. Regarding laccases' spectroscopic and magnetic characteristics, they are divided into three groups [99]: (i) type 1—blue copper centre; (ii) type 2—normal copper; and (iii) type 3—coupled binuclear copper centres. LaC can oxidize aromatic phenols and amines, destroying the stability of the aromatic ring. Thus, laccases demethylate, decarboxylate, and demethoxylate phenolic and methoxyphenolic acids [5], since all four atoms of copper are fully oxidized (Cu^{2+}) in the native laccase form [4]. LaC can efficiently degrade G-lignin. Peroxidases and laccases degrade lignin by using low molecular weight free radicals, such as hydroxyls, which depolymerize lignin polymers that contain non-phenolic and phenolic groups, and mineralize insoluble lignin [39]. These enzymes are not specific and oxidize various phenolic aromatic compounds and non-phenolic lignin compounds [9]. Laccases have a broad substrate specificity and can use atmospheric oxygen as an electron donor instead of hydrogen peroxide used by peroxidases. Laccase mediators are sometimes used for more efficient lignin degradation [4]. A mediator, a small chemical compound, is constantly oxidized by laccase and reduced by the substrate. Since the substrate is too large for the active site of laccase, the role of the mediator is the transfer of electrons between the enzyme and the substrate, thus solving the steric problem between them [100]. Examples of mediators are: 3-hydroxyanthranilic acid, 4-hydroxybenzoic acid, phenolsulfonphthalein, acetosyringone, syringaldehyde, vanillin, and methyl syringate [4]. The examples of bacteria that produce laccases are *Ecsherichia coli*, *Streptomyces cinnamoneus* [39], and *Brevibacillus thermoruber* [8].

LiPs are relatively non-specific to their substrates [101]. LiPs can oxidize sites of especially high redox potential involving the moderately activated aromatic rings of non-phenolic model lignin compounds that can constitute up to 90% of the polymer [102]. LiPs contain ferrous ions. The lignin substrates size influences the LiP catalytic efficiency, because smaller lignin substrates can be degraded more easily. LiPs mediate the degradation of phenolic hydroxyl [8]. For LiPs, veratryl alcohol can be a diffusible mediator, in spite of a very short half-life of the veratryl alcohol cation radical [103]. LiPs have the ability to oxidize the substrates that are not oxidized by other peroxidases because of the high potential of LiPs [13]. Some of the bacteria that produce LiPs are *Pseudomonas fluorescens*, *Streptomyces cinnamoneus* [39], *Arthrobacter* sp. C2 [27], and *Brevibacillus thermoruber* [8].

MnP can reduce phenolic lignin model compounds, dyes, and amines, but cannot oxidize non-phenolic lignin model compounds. MnP is characterized by the ability of Mn^{3+} generation as a diffusible charge-transfer mediator that has the ability to oxidize targets distanced from the active site of the enzyme [104]. The range of the MnP oxidative activity can be extended by the secretion of organic acids, such as oxalic acid, that chelate Mn^{3+} in stable complexes [15]. It also contains ferrous ions. MnP can remove methyl groups on phenolic hydroxyl groups and contributes to the subsequent degradation steps to form small molecules [8]. The examples of the bacteria that produce MnP are *Pseudomonas putida* [39], *Streptomyces* sp. and *Microbacterium* sp. [6], *Arthrobacter* sp. C2 [27], and *Brevibacillus thermoruber* [8].

VP has the properties of MnP and LiP catalytic activity, and can cleave non-phenolics of high redox potential, and aromatic compounds and amines of lower potential [105]. VP oxidizes Mn^{2+} as well as usual substrates of LiP, methoxybenzenes, veratryl alcohol, and non-phenolic model lignin compounds [106,107]. VP has the ability to oxidize azo-dyes and other non-phenolic compounds of high-redox potential in the mediators' absence [106].

DyPs are not related phylogenetically to VP, LiP, and MnP, and belong to a new heme peroxidases family [108]. DyP, a heme peroxidase, has a different structure and characteristics that are associated with plant and microbial peroxidases [109]. There are four (A, B, C, and D) subfamilies of DyPs, with fungal and bacterial enzymes phylogenetically [110,111]. DyP peroxidase possibly performs the degradation of the lignin. It has the ability to oxidize β-O-4 bonds, dyes, and non-phenolic lignin compounds such as veratryl alcohol [112]. Lignin degradation by brown-rot fungi involves oxidation reactions using non-enzymatic methods that produce –OH radicals using Fenton chemistry. DyPs are suggested to be the bacterial equivalent of the fungal lignin-degrading peroxidases [113]. The examples of the bacteria that produce DyP are *Pseudomonas putida* and *Enterobacter lignolyticus* [39].

White-rot fungi secrete auxiliary enzymes such as aryl-alcohol oxidase (veratryl alcohol oxidase) from *Pleurotus eryngii*, and glyoxal oxidase from *Phanerochaete chrysosporium* that produce hydrogen peroxide needed by the peroxidases. Numerous fungi secrete oxidoreductases such as quinone oxidoreductase and cellobiose dehydrogenase that can reduce the radical methoxy groups of compounds derived from lignin [5].

Sphingobacterium from Bacteroides phylum has manganese superoxide dismutase, an enzyme that oxidizes lignin via a mechanism of a hydroxyl radical [45].

7. Degradation of Lignin from Pulp and Paper Manufacturing Industry

The lignin degradation and decolourization can be performed by biosorption [114] or by the means of microorganisms/enzymes [14]. For the removal of lignin from paper mill wastewater, different biological approaches have been investigated with bacteria [10,115,116], fungi [10,116,117], and numerous microorganisms in biological wastewater treatment processes having been proven to be able to remove the lignin and colour from paper and pulp industry effluent [10,115,117–119]. Regarding fungi, crude ligninolytic and purified enzymes [120], as well as fungal strains [117], have been tested. For the treatment of real wastewater, in comparison with fungi, bacteria can tolerate a wider range of pH values, temperature, and oxygen availability, and bacteria are easier to manage in comparison with fungus [8], and therefore for the paper and pulp industry effluents the fungal ligninolytic system are not as successful as the bacterial one [121]. Moreover, a high proportion of lignin-degrading genes have been found in some bacteria [15], which implies potential novel enzymes and pathways [5].

The role of fungi in lignin degradation is described more in detail in the chapter on Biological lignin degradation. Among fungi, Basidimycotina and Ascomycotina (white-rot fungi) are the most commonly used microbes [83]. Regarding degradation of lignin from paper and pulp mill effluent, the fungi *Schizophyllum commune*, *Tinctoria borbonica*, and *Phanerochaete chrysosporium* [20,122] have been reported. Moreover, for the lignin degradation and decrease of the colour from the hardwood pulp bleach effluent the fungi *Trametes versicolor* [20,122], *Trichoderma* spp. [122], and *Aspergillus niger* [20] were recorded, and

Aspergillus flavus for the lignin degradation and chemical oxygen demand reduction [123]. Costa et al. [117] reported up to 97% and 74% of lignin degradation by *Bjerkandera adusta* and *Phanerochaete crysosporium*, respectiveliy, and during 8–10 days 100% delignification of industrial pulp and paper mill wastewater by both fungal strain, with substantial total organic carbon reduction. Furthermore, for the colour removal the fungi *Gliocladium virens* from the paper mill effluent [20] and *Phanerochaete chrysosporium* for the reduction in chemical oxygen demand, phenol, and lignin from paper industry effluent [124] have been successful. A lignin degradation of 79% from paper and pulp mill effluent was achieved with *Merulius aureus* syn *Phlebia* sp. and *Fusarium* sambucinum Fuckel MTC3788 [125]. *Emericella nidulans* var. *nidulans* achieved a 37% lignin degradation from pulp and paper mill effluent [21] and 35–40% with *Cryptococcus* sp. [126]. The lignin degradation of 66% of alkyl lignin by *Trabulsiella guamensis* [127], and 19–41.6% by *Aspergillus flavus* and *Emericella nidulans* was achieved [128].

The conventional wastewater treatment methods for the treatment of paper mill wastewater are not efficient [76,129], but there are bacteria that have the ability of lignin degradation (Table 1). The role of bacteria in lignin degradation is described in Sections 3–5.

Protozoa and bacterial consortia present in sediment that receives the effluent from paper mill has the ability of lignin degradation [130]. The bioremediation of paper and pulp effluent was reported with *Paenibacillus* sp. [76] and *Serratia liquefaciens* [83,129]. The lignin degradation from paper industry wastewater is more efficient with the microbial consortium, *Bacillus* sp., *Bacillus endophyticus*, and *Bacillus subtilis*, than with individual bacterial strains separately [48]. The strains *Bacillus* sp. [37], *Bacillus subtilis* [37,131], *Bacillus megaterium* [37], and *Pseudomonas aeruginosa* [63] were also effective for the degradation of lignin and the colour decrease from paper and pulp mill wastewater. Yeber and Silva [115] reported that with the bacterial strain RGM2262 in the form of biofilm and in suspended form, at pH value 8 and 9, on the second day of the treatment, 100% removal of colour and phenolic structure was achieved, and simultaneously, 70% total organic carbon and 80% chemical oxygen demand was reduced. Lignin degradation of 53% with *Bacillus* sp. [37]; 54% with *Paenibacillus* sp. strain LD1 [76]; 58% with *Serratia liquefaciens* [83]; 40.19% with *Bacillus subtilis*, *Bacillus endophyticus*, and *Bacillus* sp. [48]; and 44% with *Bacillus altitudinis* SL7 [51] was achieved from paper and pulp mill effluent. Furthermore, the degradation of lignin of 85% by *Bacillus flexus* RMWW II from alkali lignin [52] and 38.9% by *Bacillus ligniniphilus* L1 from alkaline lignin [12] was reported. A 74% of lignin degradation by *Planococcus* sp. TRC1 [58], and a 54% of lignin degradation by *Serratia marcescens* NITDPER1 [132] were obtained from paper mill sludge. Lignin degradation of 82% by *Bacillus magnetrium* and *Pseudomonas plecoglossicida* from black liquor [50], and lignin degradation of 58% from kraft lignin by *Bacillus subtilis* and *Klebsiella pneumonia* were also recorded [57].

8. Conclusions

Lignin, a recalcitrant and abundant material in nature, requires special attention for its degradation/delignification/decomposition. Due to structural rigidity, the degradation/delignification/decomposition of lignin is complicated. Lignin degradation by microorganisms/enzymes is an economically and environmentally friendly alternative. Numerous bacteria and their enzymes have been described regarding the degradation of lignin, decolourization, and toxicity reduction; however, the bacterial strains for efficient pulp and paper mill wastewater treatment must be investigated. The lignin degraders' bacterial community belongs to α-proteobacteria, γ-proteobacteria, some Firmicutes, and actinomycetes. The group of ligninolytic enzymes, i.e., laccases, lignin peroxidase, manganese-dependent peroxidase, versatile peroxidase, and dye-decolourizing peroxidase, are involved in sequential degradation and transformation of lignin. The high proportion of lignin-degrading genes detected in actinobacteria and proteobacteria classes points to the probability of undiscovered pathways and enzymes, which opens the door for future research of lignin degradation.

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