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REVIEW ARTICLE

Ligninolytic and cellulolytic enzymes — biocatalysts for green agenda

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Abstract

Human activities have contributed immensely to the large amount of lignocellulose waste globally and are poorly utilized for their economic importance. Lignocellulolytic enzymes provides a sustainable and green solution to the valorisation of these lignocellulosic biomass, yielding products of high economic value while also playing an important part in environmental decontamination and detoxification. Lignocellulose biomass is abundant in nature and gives better choices to environmentally friendly resources for biofuel production, and biotechnology utilization. Although lignocellulose waste degradation poses great challenges to the microbial communities, white rot fungi have been harnessed efficiently in biological degradation and biomass valorisation due to their ability to produce ligninolytic enzymes. This review focused on the different characteristics, features, and properties of lignocellulolytic enzymes and their biotechnological applications in waste management, and wastewater decontamination for a green ecosystem. Additionally, the application of lignocellulolytic enzymes in bioethanol, biofuel, and animal feed productions was reviewed and analyzed. The properties of some fungal and bacterial lignocellulolytic enzymes were critically compared so as to identify the microbes with optimum efficiency. This paper provides a comprehensive and up-to-date review of the different characteristics and properties of lignocellulolytic enzymes and their applications in a green ecosystem. Finally, this review describes the limitations and challenges associated with lignocellulolytic enzymes application and its future prospects for a sustainable green ecosystem.

Keywords Lignocellulose · Green agenda · Lignocellulolytic enzymes · Biomass · Waste management · Environmental pollutant · Degradation and detoxification

Statement of novelty

This paper evaluates the important features of ligninolytic and cellulolytic enzymes for bioconversion of readily available and renewable lignocellulosic biomass into profitable and sustainable value-added products in a zero-waste approach. It also compares and validates the biotechnological potentials of these enzyme systems derived from various sources in bioethanol production, animal feed formulation, waste detoxification, and degradation of emerging environmental pollutants such as pharmaceutical active compounds and bio-composite materials, for a clean and green ecosystem. Furthermore, this paper provides an up-to-date overview of the challenges associated with these bioprocesses as well as their future prospects, which could set a new stage in this field of study.

1 Introduction

Industrialization, urbanization, and global population boom have increased the use of fossil fuels. However, large demand and use of these fossil resources as sources of energy causes environmental hazards via climate changes and global warming [1]. There is a need to search for a better eco-friendly resource that can surpass the much dependent fossil fuels. Lignocellulose biomass which is bio-renewable and abundant in nature gives a better chance

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to environmentally friendly resources for biofuel production and polymers with economic benefits [2]. Lignocellulose waste (industrial waste) degradation poses a great task in environmental sustainability due to its complex/recalcitrant nature, slow decomposition, and inability to bind ionic compounds constitutes environmental pollutants [3]. Literatures have reported that aerobic bacteria belonging to Actinobacteria, Proteobacteria, and Firmicutes degrade lignin; white rot fungi likewise secrete ligninolytic enzymes to degrade waste via biological degradation and decolorization mechanisms [4, 5]. Major lignocellulose waste can be sourced from agricultural, municipal, and industrial activities which constitute affordable and renewable biomass available for biotechnology utilization and wealth creation [6–8].

Lignocellulose waste is the major constituent of renewable biomass in the ecosystem and consists of cellulose (45–51%), hemicelluloses (24–29%), and lignin (16–20%). Cellulose is the major backbone of lignocellulosic molecules and contains thousands of β-1, 4 bonded to D-glucose units in an unbranched linear microfibrils and also bonded by the sides via hydrogen bonding and van der Waals interactions [9, 10]. Lignocellulose is a polysaccharide composed of cellulose, hemicellulose, and lignin. Lignin and cellulose are the major constituents of plant cells which form the major natural biomass in the world [9]. Lignin is widely distributed in plant species and the major natural constituents of organic polymer in the ecosystems. It has a complex aromatic molecule composed of three main lignin precursors which are linked by C-C or C-O bonds and can undergo transamination to form phenylalanine and tyrosine [11]. Lignin is predominant in woody plants and constitutes 25–33% dry mass in softwoods and 21–26% in hard wood. Microorganisms degrade dead cells of plant lignocellulose and this contributes immensely to carbon recycling in the ecosystem. The lignin constituents of these biomasses play a crucial role in carbon fixation in the terrestrial environments [1, 12]. Pectinases, xylanases, and cellulases play crucial functions in the degradation of plant cell walls. Of most significance is the hydrolysing actions of cellulases on the β-1,4 glycosidic linkage of cellulose. Cellulases are synthesized by bacteria and fungi during their growth phase on the cellulose matrix [13]. Due to the inability of some microorganisms to degrade lignin, white rot fungi have been harnessed in the degrading of these molecules via the secretion of specific enzymes [8]. Lignin peroxidase breaks down the hydroxyl-containing aromatic ring in the lignin while manganese peroxidase eliminates the methoxy group on the ring and therefore progresses the degradation phase [2].

Although recent literatures have reported the vast utilization of lignocellulolytic enzymes from microbes, this paper provides a comprehensive and up-to-date review of the different characteristics and properties of lignocellulolytic enzymes and their applications in a green ecosystem. However, a comparative study and properties of lignocellulolytic enzymes from fungi and bacteria, their biological pre-treatment for bioethanol production, have not been critically documented. This review aims at addressing these issues and likewise provides solutions to optimizing the cost of the enzyme production, its limitations, challenges, and future prospects for industries and the environment.

1.1 Ligninolytic and Cellulolytic Enzymes

Ligninolytic and cellulolytic enzymes are macromolecules responsible for the biocatalytic decompositions of lignocelluloses into their various monomeric units that are further bioconverted into value-added products. Often called lignocellulases, they are complex extracellular enzyme systems produced by soil microorganisms and constitute hydrolytic enzymes involved in the breakdown of the cellulosic and lignin components of plant biomass. Lignocellulolytic enzyme systems have been shown to be composed of mainly extracellular polypeptides of lignin-degrading enzymes (oxidases and peroxidases) and hydrolytic enzymes (cellulases, pectinases, amylases, hemicellulases, mannanases, esterases, and proteases) [14]. Enzymes are macromolecular biocatalysts produced by living organisms to speed up the rate of biological and/or biochemical reactions. Under appropriate reaction conditions, enzymes accelerate the formation of useful products from their substrates, resulting in numerous useful biotechnology applications. Based on the type of reactions catalyzed, enzymes are generally grouped into six classes: oxidoreductases, transferases, hydrolases, lyases, isomerases, and ligases [15]. Lignin degraders are oxidoreductases, while hydrolytic enzymes are hydrolases [16, 17].

Enzymes used in the breakdown of lignocellulolytic biomass into its three major constituent polymers are produced mainly by fungi. Both the bacterial and fungal enzymes act extracellularly due to the poor solubility of the substrates. Studies have been done on a number of ligninolytic and cellulolytic fungi such as, Penicillium, Aspergillus, Schizophyllum, Phanerochaete, Trichoderma, and Sclerotium, which are reportedly good producers of extracellular enzymes [18]. On the other hand, production of lignocellulolytic enzymes from bacteria offers rapid culture growth and multi-enzyme complexes' secretion with potent functionality and specificity than those of fungi. As such, bacterial enzyme systems from the phyla Proteobacteria, Firmicutes, and Actinobacteria, and multiple strains of Aquitalea, Bacillus, Burkholderia, Cupriavidus, Gordonia, and Paenibacillus are more stable and could withstand environmental stress more than the fungal counterparts [19]. As a result, bacteria are regarded as sources of essential metabolites and enzymes, having great genetic flexibility. There are still interesting areas of exploration on Actinomycetes genera, particularly the thermophilic actinomycetes, for their potential industrial and

biotechnological applications owing to their ability to withstand harsh environmental conditions. A number of actinomyetes, including *Streptomyces* sp. H1, *Micromonospora* sp. G7, *Mycobacterium* sp. G1, and *Saccharomonospora* sp. T9, have been reported to enhance the breakdown of lignocellulosic biomass via increase in key lignocellulases' activities [20]. Recently, appreciable number of carbohydrate-active enzymes (CAZymes) was found encoded on the genome of the aerobic and filamentous bacterial lineage, *Ktedonobacteria* of the Phylum *Chloroflexi*, revealing yet to be discovered potentials of the *Ktedonobacteria* class for the production of bacterial-derived cellulases, chitinases, xylanases, amylases, and lignin-degrading enzymes [21]. Accordingly, future optimization of ecological/environmental conditions for culture growth could lead to discovery of novel colonies with unique abilities to produce metabolites relevant for future green technology [22]. Two categories of extracellular lignocellulolytic enzyme systems exist among microorganisms as shown in Fig. 1. There exists the oxidative lignin-degrading enzyme system responsible for depolymerization of lignin, and the hydrolytic enzyme system that breakdown cellulose and hemicellulose through the production of hydrolases [23]. The synergistic actions of the lignocellulolytic enzymes are capable of transforming lignocellulose biomass via composting, into value-added products such as stable humic substances (HSs), which are part of the soil's brownish-black organic matter. The HSs are gotten through rapid fermentation during composting of lignocellulose biomass, including microbial mineralization primary and secondary metabolisms, and humification. Humic substances, basically composed of acid-soluble/base-soluble fulvic acid, acid-soluble/base-soluble humic acid, and insoluble humin, possess positive environmental impacts, some of which include reduction in heavy metals and polar aromatic compounds via the formation of HS-heavy metal and HS-polar aromatic compounds complexes, thereby improving the stability, fertility, and productivity of the soil [24, 25]. Table 1 shows the classification of major lignocellulolytic enzymes and their biotechnological applications

1.2 Ligninolytic (lignin-degrading) enzymes

Lignin is an aromatic polymer composed of phenolic and non-phenolic parts. Being polymeric and hydrophobic, Lignin is an aromatic polymer composed of phenolic and non-phenolic parts. Being polymeric and hydrophobic, lignin exhibits structural complexity resulting in its high resistance to degradation by most microorganisms. The monomeric units, known as monolignols, are linked differently among different species and as a result of these heterogeneous linkages, the polymer poses difficulties to the actions of hydrolases unlike other constituents of lignocellulolytic biomass [44]. The challenges of lignin breakdown by microorganisms arise from the extracellular nature and oxidative mechanism of the degrading enzymes due to the presence of ether and carbon-carbon bonds in the polymer, and less specificity of the enzymes unlike the hydrolytic enzymes owing to the uneven spatial arrangement of atoms in the polymeric chains [45]. The oxidative and unspecific nature of lignin-degrading extracellular enzyme systems brings about depolymerization of lignin leading to the release of products requiring several oxidative reactions due to their less stability. Such oxidative reactions, however, are necessary steps required to initiate lignin depolymerization [46]. A number of bacteria, fungi, and some insects such as *Nephotettix cincticeps*, *Manduca sexta*, *Reticulitermes flavipes*, and

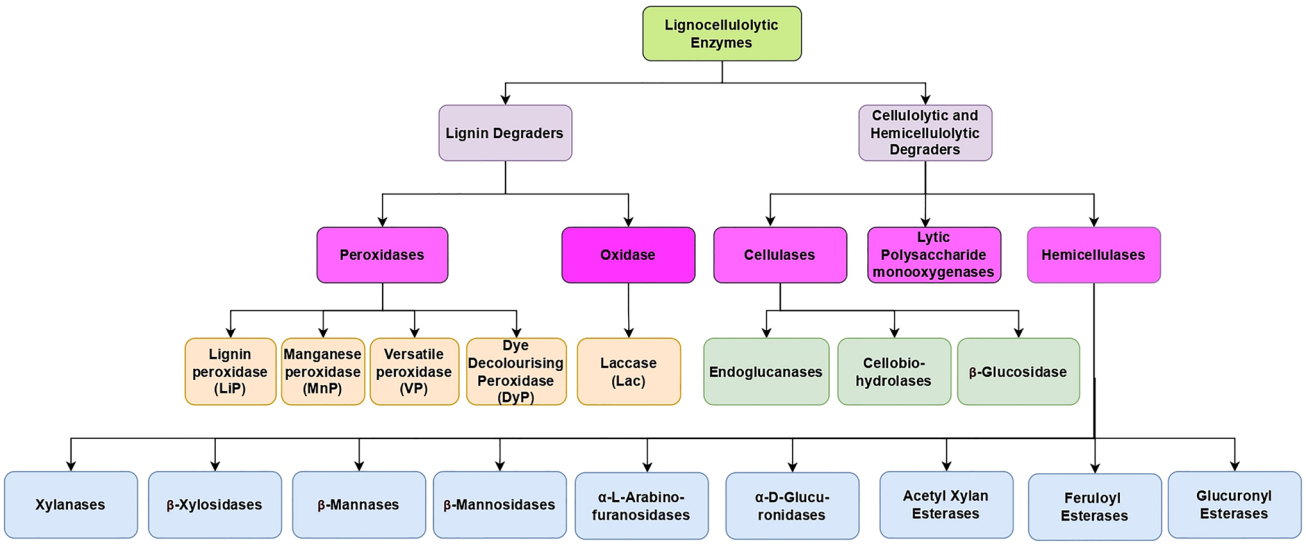

Fig. 1 Categorization of lignocellulolytic enzyme systems

Table 1 Classification of major lignocellulolytic enzymes and their biotechnological applications

Enzyme	EC. number	Mechanism of action	Organism	Biotechnological application	References
Ligninolytic enzymes					
Manganese peroxidase (MnP)	1.11.1.13	Oxidize Mn^{2+} to Mn^{3+} in the presence of H_2O_2, which oxidizes the phenolic substrate, including lignin model compounds and some organic pollutants	*Trametes villosa* *Cerrena unicolor* BBP6	Delignification of agricultural wastes for bioethanol production Dye decolourisation and denim bleaching	[26, 27]
Lignin peroxidase (LiP)	1.11.1.14	Catalyzes H_2O_2-dependent oxidative depolymerisation of lignin and lignin related compounds	*Pseustes sulfurous* *Phanerochaete sordida* YK-624	Degradation of polycyclic aromatic hydrocarbons (PAHs) Removal of endocrine disrupting compounds (EDC)	[28, 29]
Versatile peroxidase (VP)	1.11.1.16	Exhibit catalytic activities of both MnP and LiP	*Pleurotus eryngii*, *Pleurotus ostreatus*, *Pleurotus pulmonarius* and *Pleurotus sajor-caju*	Degradation of phenolic and non-phenolic compounds.	[30]
Dye decolouring peroxidase (DyP)	1.11.1.19	Catalyzes H_2O_2-dependent oxidation of anthraquinone dyes and other lignin derived compounds	*Irpex lacteus* *Vibrio cholerae*	Enzymatic hydrolysis of wheat straw Degradation of anthroquinone dye	[31, 32]
Laccase	1.10.3.2	Uses O_2 to catalyze four-electron oxidation of phenolic components of lignin and lignin related structure in the	*Trametes polyzona* WRF03 *Trametes hirsute* *Paraconiothyrium variabile* (*Pv*L)	Decolourisation of synthetic dyes Pharmaceutical active Compounds (PhACs) removal. Phenol and bisphenol-A removal	[33–35]
Cellulolytic enzymes					
Endo-β-1,4-glucanase	3.2.1.4	Cleaves internal β-1,4 -glycosydic bonds in cellulose	*Trichoderma atroviride*	Treatment of denim fabric and pretreatment of lignocellulosic waste.	[36]
Cellobiohydrolases (CBH1 & CBHII)	3.2.1.91	CBHI hydrolyses β-1,4 -glucosidic bonds in cellulose from the reducing ends. CBHII is specific to the non-reducing end	*Saccharomyces cerevisiae* *Trichoderma reesei* (*Hypocrea jecorina*)	Cellulose hydrolysis Biomass conversion	[37, 38]
β-glucosidase	3.2.1.21	Cleaves β(1-4) bond linking two glucose residues (cellobiose) or glucose-substituted molecules	*Saccharomyces cerevisiae*	Cellulosic bioethanol production	[39]
Hemicellulases					
Endo-β-1,4-xylanase	3.2.1.8	hydrolyses the internal β-(1,4) linkages of the xylan backbone producing short xylooligosaccharides	*Bacillus subtilis*	Biobleaching of nonwoody plant pulps	[40]
β-Xylosidases	3.2.1.37	Removes xylose units from the non-reducing termini of xylooligosaccharides	*Selenomonas ruminantium*	Saccharification of lignocellulosic biomass for producing biofuels	[41]
β-Mannases	3.2.1.78	Hydrolyse the internal mannosidic bonds of mannan based polysaccharides	*Dictyoglomus thermophilum*	Oil drilling operations	[42]
β-Mannosidases	3.2.1.25	Removes mannose units from the non-reducing termini of these mannooligosaccharides	*Paenibacillus polymyxa A-8*	Animal feed formulation	[43]

Tribolium castaneum have the ability to produce enzymes that can break down lignin [12]. These enzymes could be either peroxidases or oxidases.

Peroxidases are glycoproteins with heme prosthetic groups that require the oxidant properties of hydrogen peroxide for the initiation and facilitation of lignin's oxidation. In the presence of a mediator, they also play a role in the oxidation of other phenolic compounds employing H_2O_2 as co-substrate [47] and possess affinity for several substrates, including inorganic and organic compounds. Peroxidases initiate lignin depolymerization by accelerating oxidations that potentially result in free radical formations (e.g., aryl cation and phenoxyl radicals), anions (e.g., OCl^-). These radicals initiate lignin degradation thereby releasing humic substances and monolignols, also oxidation of toxic substances and a number of nonspecific defense reactions [48], making peroxidases suitable for wide industrial usage.

Four classes of peroxidases are found to breakdown lignin: manganese peroxidase (MnP), lignin peroxidase (LiP), dye-decolourising peroxidase (DyP), and versatile peroxidase (VP) [2, 49]. MnP, LiP, and VP belong to the superfamily of microbial and plant peroxidases. They are mainly secreted as secondary metabolites by white-rot fungus and thus are categorized as class II extracellular peroxidases. Lignin peroxidases, central in lignin depolymerization, bring about lignin and other phenolic compounds' degradation in the presence of H_2O_2 as co-substrate and veratryl alcohol as mediators [50]. They also play a role in the breakdown of numerous non-phenolic lignin derivatives to aldehydes and ketones [2] via the withdrawal of an electron from the aromatic ring. This process leads to the release of cation radicals, which undergo several reactions including the oxidation of benzylic alcohol, severance of aryl ether linkages and aliphatic side chains, opening of rings, and degradation into smaller compounds [51].

Manganese peroxidases (MnP) are heme-containing extracellular enzymes secreted as secondary metabolites by the fungus, basidiomycetes. They require the presence of Mn for the oxidation of a variety of non-phenolic and phenolic substrates. MnP works by oxidizing Mn^{2+} to Mn^{3+}, which in turn, oxidizes benzyl-alcohol rings to radicals of phenol thereby bringing about lignin degradation [52].

On the other hand, VPs are capable of carrying out catalytic reactions of both MnP and LiP as they are capable of oxidizing a number of substrates including Mn^{2+} and methoxybenzenes. Unlike other peroxidases, VPs can oxidize substrates in the presence of Mn and possess extensively wide substrate specificity, including both phenolic and non-phenolic dimers. As a result, the enzymes have considerable potential for utilization in bioremediation of a wide range of pollutants and applications in industrial biotechnology [53]. The last class of lignin-degrading peroxidases is the DyPs. They are secreted as secondary metabolites by bacteria and fungi and are genetically unrelated to other lignin-degrading peroxidases — MnP, LiP, and VP. Due to their wide substrate specificity and ability to function in acidic pH, they possess unique capacity of oxidizing anthraquinone dyes with high-redox potentials, and models of lignin compounds [44].

The second group of ligninolytic enzymes is the oxidases, majorly represented by the copper-containing enzymes, the laccases, which occur in fungi, plants, bacteria, and insects. The enzymes function by four-electron oxidation of its substrates followed by the reduction of molecular oxygen to water. Laccases are obtained in high yield as secondary metabolites by fungi through either solid-state or submerged fermentation processes using agro-industrial wastes as carbon sources [54]. They are involved in the degradation of a variety of compounds including lignins and their derivatives through the oxidation of β-O-4 lignin dimers and non-phenolic substances using a mediator [2]. The breakdown of β-O-4 lignin model compounds using molecular oxygen as co-factor results in the release of different phenols, which serve as carbon sources to the fermenting microorganisms.

1.3 Cellulolytic and hemicellulolytic enzymes

Cellulolytic and hemicellulolytic enzymes are a class of hydrolases consisting of a cocktail of enzymes involved in hydrolysis of cellulose and hemicellulose, respectively. The ability of cellulases to convert cellulosic waste materials into value-added products has spurred a lot of research interests in the scientific community, all towards improving the catalytic efficiencies of the enzymes for maximum industrial/biotechnological benefits [55, 56]. Cellulases constitute majorly of three enzymes β-1,4-endoglucanase (EG), β-1,4 Grac-exoglucanase (a.k.a exo-cellobiohydrolase, CBH), and β-1,4-glucosidase (BG) [57].

Endoglucanases on the other hand catalyze the random breaking of β-1, 4 glycosidic bonds within the amorphous regions of cellulose chains, releasing short-chain polysaccharides thereby creating new chain ends for cellobiohydrolases (CBHs) [58] to break off cellobiose units from the non-reducing chain end. As a result, elevated EG activities are necessary conditions for efficient hydrolysis and conversion of lignocellulose [59]. Exoglucanases (CBHs) cleave off β-1,4 glycosidic bonds at the reducing and non-reducing ends of cellulose chain or cellodextrin, releasing cellobiose or glucose units. There are two subtypes of CBHs secreted by fungi — CBH 1 and CBH 2, the former being active on the reducing ends while the latter acts on the non-reducing ends of cellulose chain. The BGs, on their part, break down the cellobiose units into glucose monomers. Both the EGs and CBHs work in tandem to fragment cellulose into short-chain cello-saccharides composed mainly of cellobiose units, which are subsequently hydrolyzed by

β-1,4-glucosidase to glucose units. Thus, microorganisms capable of hydrolyzing cellulose must produce these cocktail of enzymes that function synergistically for efficient cellulose hydrolysis. The synergistic actions of the cellulases begin with the exoglucanases acting on the reducing and non-reducing ends, sandwiching the actions of CBHs and BGs. This is followed by the actions of endoglucanases locating the surface sites along the cellodextrin unit in a random manner, inserting a molecule of water in the β-1,4 bond, thereby causing the existence of a new non-reducing and reducing chain end pair. The glucosidases then break the cellobiose units produced through cellulase action thereby preventing possible end-product inhibition [1]. Furthermore, in addition to cellulases, the complete breakdown of cellulose also involves a copper-ion-dependent oxidase in the form of lytic polysaccharide monooxygenases (LPMOs). The LPMOs nonhydrolases capable of cleaving cellulose chains and breaking β-1,4-glycosidic bonds via the oxidation of a single oxygen atom on C1 or C4 glucose units, thereby, breaking down short- and long-chain polysaccharides based on the breakdown of cellulose [60]. The actions of the above enzymes lead to complete hydrolysis of cellulose into glucose units which are in turn used as source of carbon and energy by microorganisms to release value-added products.

The breakdown of hemicellulose into its simple monomers involves the synergistic actions of a cocktail of enzymes collectively known as hemicellulases. Structurally, the enzymes possess one or few crystalline domains and several other support domains with non-catalytic functions. Hemicellulases function by breaking down glycosidic bonds existing in carbohydrates and those between carbohydrates and noncarbohydrates or support the actions of glycoside hydrolases on the surface of hemicellulose through the removal of methyl groups, phenol esters acetyl groups [61]. The crystalline domain of hemicellulose is a class of 29 glycoside hydrolases or carbohydrate esterases that severs the side-groups' ferulic acid or acetate ester bonds and contains 37 carbohydrate-binding modules (CBMs). The CBMs help in attaching the enzymes to the substrate, thereby favoring the crystalline domains to perform the catalytic functions [62]. Hemicellulose has a more diverse composition than cellulose and hence requires a greater number of enzymes to hydrolyze properly [63]. Hemicellulases are categorized into two classes — the depolymerizing enzymes that hydrolyze the bonds in the main chain (examples: endo/exoxylanases, glucanases, and mannanases) and the ancillary enzymes, which breakdown the ester bonds and glycosidic bonds in the side chains and branches (such as α-L-arabinofuranosidase, acetylxylan esterase, β-glucuronidase, glucuronyl esterase, ferulic acid esterase) [64, 65].

The most important enzymes in the breakdown of hemicellulose are the xylanases, which possess the ability to hydrolyse the β-1,4-glycosidic bonds, requiring the synergistic actions of a series of enzymes. The components of xylanases include β-d-xylosidase, endo-1,4- β-d-xylanases, ferulic acid esterase, and *p*-coumaric esterase. These enzymes break down xylan to xylose and are components of the families of glycoside hydrolases (GH) 5, 8, 10, 11, 30, 43, and 51 [65]. Among the families of xylanases, the GH10 and GH11 are the most studied for hemicellulose breakdown, and they possess varied 3-dimensional structures and mechanistic functions. While H11 xylanase has about seven subsites, those of the GH10 xylanase are about four to five [66] and, as a result, possess different substrate specificities — G10 xylanase breakdown xylan into shorter oligosaccharides in the main chain unlike the GH11 xylanase. On the other hand, the β-1,4-glycosidic bonds linking mannans are hydrolyzed by endo-mannanases (GHs 5, 26, 113, and 134 families), producing manno-oligomers, which are further broken down to mannose by endo-1,4-mannosiddase. In addition, the β-1,4-linked glucan is hydrolyzed to release glucose by glucanase, belonging to the GHs 5, 6, 7, 8, 9, 12, 44, 48, 51, 74, and 124 families [67]. The Arabian side chain chains linked to the xylan backbone are jointly hydrolyzed to arabinose by α-arabinofuranosidase (GHs 23, 43, 51, 54, and 62 families) and α-L-arabinases [62]. Enzymatic breakdown of the xyloglucan polymer by xyloglucanase (GHs 6 families) occurs with higher specificity which could potentially improve the overall hydrolysis of lignocellulosic substrates [65]. All these hemicellulases act in tandem to bring about complete hydrolysis of hemicellulose.

The classes of micobes capable of producing hemicellulases include fungi (*Aspergillus*, *Trichoderma*, *Penicillium*, *and Talaromyces*), aerobic, and anaerobic bacteria. While fungi can secrete all hemicellulases once [64, 68], which act synergistically to hydrolyze hemicellulose completely, aerobic bacteria secrete a small amount of hemicellulases, that degrade hemicellulose, first into large oligomers that are further broken down into monomers by intracellular enzymes [69]. On the other hand, anaerobic possesses cellulosome-like construct of hemicellulase to degrade hemicellulose [62]. Among the bacteria capable of producing and secreting hemicellulases include *Thermomonospora*, *Streptomyces*, *Bacteroides*, *Cellulomonas*, *Pseudomonas*, *Bacillus*, *Chainia*, *Clostridium*, *Butyrivibrio*, *Ruminococcus*, *Aeromonas*, *Thermotoga, Cellvibrio*, and *Cytophaga* [66]. Despite the fact that these lignocellulolytic enzymes perform various functions in the bioconversion of lignocellulosic materials, they have been shown to work in synergy for complete biomass hydrolysis. A thorough examination of the synergistic interactions between these enzymes, as well as their ideal conditions for bioconversion, has been published [63].

1.4 Green biotechnological application of lignocellulolytic enzymes

The urgent demand for green technology has stimulated the search for efficient organic catalysts for applications in many biotechnological processes. These catalysts serve as alternatives to the chemical methods, which are relatively expensive and not eco-friendly. Recently, lignocellulolytic enzymes have found great applications in myriads of biotechnological processes such as in bioremediation, biodegradation, compostage of lignocellulosic materials, bioethanol and biofuel production, animal feed production, and green ecosystem (Fig. 2) [1].

1.5 Bioremediation

The continuous use and discharge of chemicals into wastewaters by many industries is of global concern. Many municipal and industrial wastewater contains varieties of pollutants including synthetic estrogens, polycyclic aromatic hydrocarbon (PAHs), pentachlorophenols (PCP), antibiotics, synthetic dyes, dioxins, polychlorinated biphenyls (PCB), and nitro-aromatic compounds [70]. Most of these pollutants are recalcitrant in nature and as such accumulate in the environment where they pose serious considerable toxic effects on the ecosystem [71]. It is also alarming that most of them are carcinogenic, mutagenic, and endocrine disruptors [72]. Ligninolytic enzymes have the great potential to degrade these pollutants into a nontoxic or less toxic state and are considered to be effective green degrading catalysts [73]. Hence, recent scientific investigations and applications have focused on the utilization of Ligninolytic in wastewater detoxification and decontamination, degradation of PAHs, and decolourisation of textile effluents.

1.5.1 Wastewater detoxification and decontamination

Ligninolytic enzymes have been used effectively to detoxify wastewaters containing contaminants such as phenols, cresols, chlorinated phenols, and the removal of peroxide and pesticides from industrial wastes [74]. Phenols and other aromatic compounds constitute the majority of the pollutants released into the environment as by-products predominantly from industries involved in refining petroleum, mining, metal coating, wood preservation, chemical synthesis, and textile dyeing [75, 76]. Phenols are often very toxic and carcinogenic when exposed to high concentrations [73]. Thus, wastewaters polluted by phenols and their chlorinated forms, cresols, and peroxides are often purified using peroxidases [74]. For instance, a peroxidase extract from a turnip root in the presence of H_2O_2 was used to treat phenol at a laboratory scale; it resulted in a less soluble polymer which was easily separated upon centrifugation and filtration [77]. Laccase isolated from *Trametes villosa* showed great efficiency (95%) in the treatment of buffered synthetic wastewater containing phenols and benzediol [78]. In addition, purified laccase from *Paraconiothyrium variabile* (*Pv*L) applied to phenolic pollutant treatment showed 80% phenol removal after 30 min [35].

Lignocellulosic wastes emanating from various agro-based industries such as pulp and paper mill effluents, agricultural waste effluents, sugarcane molasses–based distilleries effluents, and the food industry also pose a reasonable threat of environmental pollution [79–82]. The toxic effect of effluents from paper pulp mills on the aquatic habitat has been clearly elucidated [83]. Distillery effluents high levels of soluble organic matter resulting in a very dark brown colouration which greatly affects the quality of the receiving water bodies [84]. Owing to their slow rate of degradation and reactivity towards cationic molecules, they could produce complex compounds that pose a serious threat to the environment [85]. It has been observed that ligninolytic enzymes are very good in the removal of these industrial wastes and other toxic substances by degradation and decolourisation [86]. A ligninolytic enzyme producing strain of *Paenibacillus* sp. effectively reduced pollution parameters such as BOD by 83%, COD by 78%, lignin by 54%, color by 68%, and phenol by 86%. Zainith et al. [87] applied manganese peroxidase extracted from *Bacillus aryabhattai* to degrade pollutants from pulp and paper mill waste.

In addition, pesticides have been found in relatively high quantities in many water bodies due to their consistent use in agriculture. Pesticides form stable structures and may remain in the environment for an extended time where they poses serious deleterious effects to both fauna and flora [88]. Pesticide exposure can induce genotoxicity or mutagenicity which may result in adverse health conditions that could affect the endocrine, immune, nervous, and reproductive systems [89]. Research has provided evidence that ligninolytic enzymes have the ability to decompose and remove pesticides from the environment. Zhao et al. [90] used laccase from white-rot fungi to eliminate dichlorodiphenyltrichloroethane (DDT) from the soil. Their results showed that laccase could effectively degrade DDT within 25 days of incubation. Many industries are already applying ligninolytic enzymes for both wastewater treatment and degradation of pesticides [91].

1.5.2 Degradation of PAHs and related compounds

PAHs are made up of two or more coupled aromatic rings and are derivatives from crude oil, creosote, and coal. The excessive use of fossil fuels often leads to contamination by PAHs since there are processes inherent to the production, refining, storage, and transport of oil that can cause

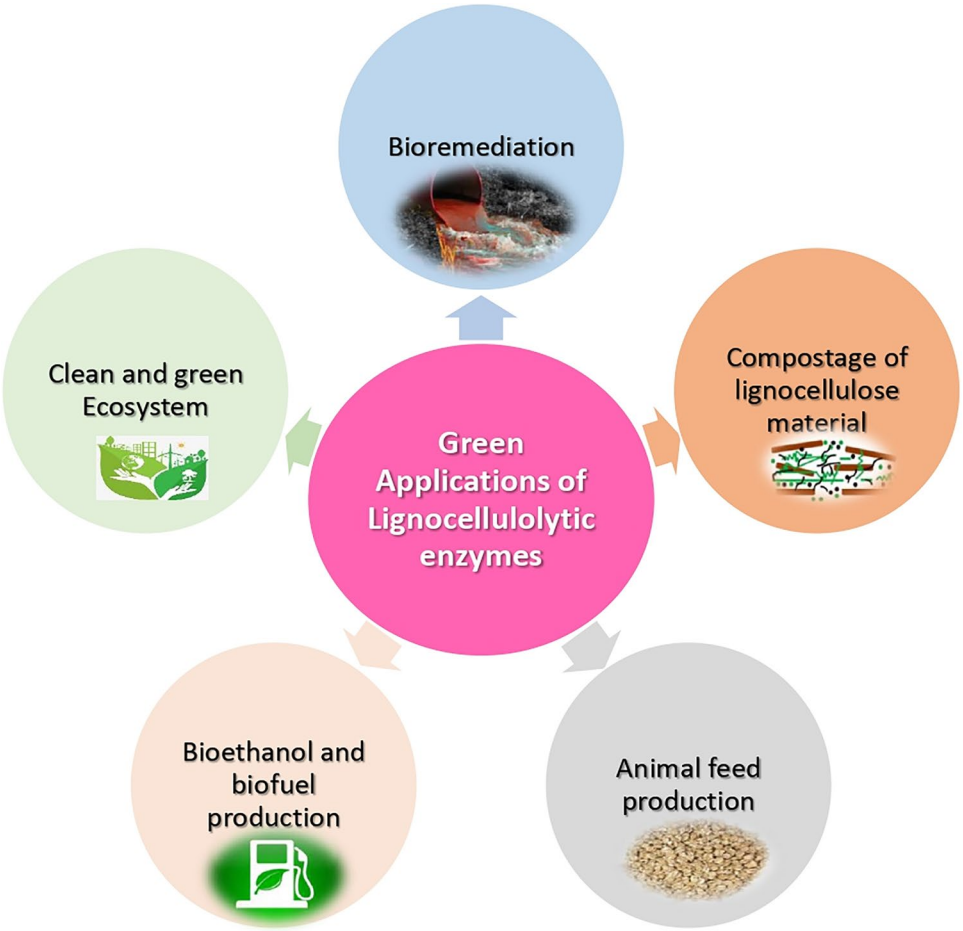

Fig. 2 Green biotechnological application of lignocellulolytic enzymes

spills [92]. Ligninolytic enzymes (phenol oxidases and peroxidases) can act on some particular PAHs by turning them into less harmful products or products that can be easily degraded. Peroxidases such as lignin peroxidase and manganese peroxidase oxidize PAHs. Despite the effectiveness of these peroxidases in bioremediation, they are not yet used on large scales due to the setbacks such as its redox potential and stability; large production should be addressed so as to increase its application in bioremediation [93].

Lee et al. [94] revealed that *Passiflora incarnata* strongly breaks down PAHs by extracellularly produced laccase and peroxidase that is manganese-dependent. The enzyme system displayed high efficiency in percentage breakdown of phenanthrene, pyrene, and fluoranthene by 86.5%, 82.6%, and 77.4% respectively. Agrawal et al. [95] reported that *Ganoderma lucidum* had the ability to degrade phenanthrene (99.65%) and pyrene (99.58%) after 30 days, due to the production of extracellular Ligninolytic enzymes, laccase, LiP, and MnP from the fungus. In another study, laccase from *Aureobasidium pullulans* var. *melanogenum* degraded a mixture of PAHs such as anthracene, naphthalene benzo[a]pyrene, and pyrene with degradation efficiency of 38.16, 24.35, 45.33, and 25.38%, respectively, after incubating for 48 h. Laccase from the same organism degraded anthracene and naphthalene in soil samples by 85.06 and 51.34%, respectively, after 9 days [96].

1.5.3 Degradation of endocrine disrupting compounds

Different ligninolytic enzymes have yielded good results in the removal of endocrine-disrupting compounds (EDC) that resisted conventional wastewater treatment. EDC functions by engaging in a competitive binding with hormone receptors. Their mode of action includes imitating the activity of physiologic hormones, initiating indistinguishable physiologic effects, and coupling to the hormone receptors in a highly competitive manner, hindering the normal hormones from coupling with receptors consequently, leading to interruption in hormone synthesis, transport, metabolism, and their supposed endocrine purpose [97]. Many studies have been reported on the elevated levels of EDC such as androsterone, nonylphenols (NP), trenbolone, hexestrol (HEX), diethylstilbestrol (DES), dienestrol, *trans*-dehydrotestosterone (DEHA), estrone (E1), 17β-estradiol (E2), 19-norethindrone, 4,5-α-dihydrotestosterone (DHT),

17α-ethinylestradiol (EE2), and bisphenols detected in some industrial wastewaters that end up in many rivers [98–100].

The ability of ligninolytic enzymes such as laccase, MnP, and VP to effectively remove EDC from wastewater streams has been demonstrated [101]. Cajthaml [73] revealed that ligninolytic fungi were effective in breaking down a number of EDC by activities of the ligninolytic enzymes. The extracellular ligninolytic enzymes can either polymerize the micropollutants or break down the initial structure [102]. Several have reported the oxidation of EDC by laccase. Eldridge et al. [103] have ascribed the effective breakdown of EE2 by *Lentinula edodes* (Shiitake) to laccase because inducing laccase production in the organism raised the purification of pollutants from 50 to 80%. In addition, Zdarta et al. [104] reported an absolute removal of Bisphenol A (BPA) and bisphenol F (BPF) by laccase isolated from *Trametes versicolor*. However, the same enzyme achieved only about 40% removal of bisphenol S (BPS).

1.5.4 Dye decolourisation

Synthetic dyes are commonly utilized in food, cosmetics, textile, leather, and paper printing industries [105]. About 10–50% of the initial dye used is lost after the dyeing process resulting in high-colored effluents [106]. These dyes pose serious environmental problems because they are resistant to degradation [107]. Thus, effective treatment of dye(s) containing effluents is very crucial prior to its discharge. In recent times, environmental regulatory bodies in some countries insisted that wastewater must be decolourised prior to its discharge in order to minimize environmental risks associated with the effluents. Different physicochemical methods have been put in place for the treatment of wastewaters that contain dyes [107]. However, they are often very expensive, ineffective, and environmentally unsafe due to the chemical nature, molecular size, and structure of these reactive dyes. Recently, enzymatic treatment has proven to be more efficient, less expensive, and environmentally friendly [108].

Ligninolytic enzyme application has proven to be a valuable treatment alternative for the effective removal of recalcitrant dyes from wastewaters. For instance, Eichlerová and Baldrian [109] conducted an extensive screening on synthetic dye decolourisation using different fungal strains. The result showed that the dye decolourization was significantly related to the production of ligninolytic enzymes. In another study, laccase and MnP produced by a fungus, *Perreniporia tephropora*, were responsible for the decolourisation of two synthetic dyes, reactive Blue 4 and methyl orange [110]. Sing et al. [111] applied *Marasmius cladophyllus* that produces laccase and lip for the decolourization of Remazol Brilliant Blue R. A number of ligninolytic enzymes are currently in use in the textile industries for wastewater treatment [91].

1.5.5 Pharmaceutically active compound (PhACs) and bio-composites removal by ligninolytic enzymes

Pharmaceutically active compounds (PhACs) are a growing topic of concern due to the potential risks they pose to the environmental and human health on exposure. The increased consumption of these bioactive compounds such antibiotics (sulfamethoxazole), antiepileptics (carbamazepine), anti-inflammatory drugs (diclofenac), and estrogen hormones have resulted in their gradual accumulation and pseudo-persistence in a number of environmental matrices including rivers, lakes, groundwater, wastewater effluents, and sludge [112–114]. Several novel strategies have been developed to effectively remove these emerging recalcitrant pollutants from the environments. One of such green technical methods include the application of ligninolytic enzymes in the biotransformation and biodegradation of these PhACs [115].

Ligninolytic enzymes present an attractive features as biological catalysts because of their high redox potentials, wide substrate specificity, and environmental friendliness. These enzymes have been reported to remove PhACs from the environment by biotransformation or biodegradation, which is a developing technique with enormous potential. Ligninolytic enzymes are non-specific and oxidize PhACs by electron transfer to molecular oxygen, which is abundant in nature (laccases). It could also be by oxidation-reduction reactions with H_2O_2 as an electron accepting co-substrate (class II peroxidases). Other proposed mechanism of biotransformation include epoxidation, aromatic peroxygenation, hydroxylation, dealkylation, and sulfoxidation [115].

The crude extract of *Phanerochaete chrysosporium* containing manganese peroxidase substantially removed tetracycline and oxytetracycline with average degaradation rates of 72.5 and 84.3%, respectively, after 4 h [116]. Ligninolytic enzyme cocktail from *Irpex lacteus* was investigated for their degradative ability towards some emerging PhACs. The enzymes were able to completely remove hormones (estrone, 17b-estradiol, and 17a-ethinylestradiol) and bisphenol A in less than 1 h while 30% degradation of carbamazepine was observed after 24 h [117]. According to Rodriguez-Rodriguez et al. [118], *Trametes versicolor* was able to colonize and degrade naproxen (NPX) and carbamazepine (CBZ) in sewage sludges using bio-slurry and solid-phase systems. Degradation rate of 47% of NPX and 57% of CBZ was observed after 24 h in the bioslurry cultures. Whereas, complete depletion of NPX and roughly 48% of CBZ were observed after 72 h in the solid sludge cultures.

One of the major challenges associated with the use of ligninolytic enzymes in pollutants removal is the loss of enzyme activity during the treatment process as well as the need for recoverability and resuse. These major hurdles

have been overcome through genetic engineering to increase enzyme stability and immobilization, allowing for easier enzyme recovery and reuse. Laccase immobilized on a polyvinylidene fluoride nanocomposite with multi-walled carbon nanotubes removed two model pharmaceuticals, carbamazepine and diclofenac, with high efficiency (27 and 95%, respectively) in 48 and 4 h [34]. Immobilized laccases from *Pleurotus ostreatus* were evaluated against multiple PhACs, with significant clearance rates ranging from 60 to 100% [119]. The removal of PhACs was studied using pure and mixed free cross-linked enzyme aggregates constituted of laccase from *Trametes versicolor*, versatile peroxidase from *Bjerkandera adusta*, and glucose oxidase from *Aspergillus niger*. The cross-linked mix demonstrated stability in the elimination of acetaminophen, naproxen, mefenamic acid, indometacin, and diclofenac, among others, under environmental and denaturing conditions, with elimination rates more than 80% [120]. After 48-h treatment using fungal cultures of T. versicolor, a total elimination of diclofenac (DCF), naproxen (NPX), indomethacin (IDM), ibuprofen (IBP), and fenoprofen (FEP) and partial degradation of ketoprofen (KEP), clofibric acid (CA), CBZ, propyphenazone (PPZ), and gemfibrozil (GFZ) were observed. Furthermore, in vitro experiments revealed that the laccase preferentially eliminated DCF, NPX, and IDM, implying that intracellular enzymes may also be involved in the degradation of KEP, CA, CBZ, PPZ, FEP, and GFZ [121].

Furthermore, the increased use of bio-composite materials owing to their demands has stirred a growing concerns with respect to their degradation and removal from the environment [113]. Biocomposites are created by combining natural fibers with petroleum-derived biodegradable and non-biodegradable polymers such as Green Polyethylene (GP), polylactic acid (PLA), kenaf bio-composites, and oil palm fiber composites [122]. Their discharge into the environment may have a negative impact on both flora and fauna. Despite the fact that numerous treatment strategies have been tried, the use of white-rot fungi was highly suggested due to their ability to create ligninolytic enzymes capable of oxidative breakdown of these compounds. *Pleurotus ostreatus*, a ligninolytic fungus, degraded polylactic acid (PLA)-reinforced kenaf bio-composites resulting in 48% degradation after 6-month incubation as compared to the control. The degradation also shortened the fiber and reduced the mechanical properties of the bio-composite by 84% [123]. In another study, *Pleurotus ostreatus* degraded GP and altered both its physical and chemical structures [124].

1.6 Compostage of lignocellulosic materials

Lignocellulosic materials (LCMs), composed mainly of polysaccharides (cellulose and hemicelluloses) and an aromatic polymer (lignin), form bulk part of agro-wastes. Though the major feedstock for several biotechnological processes, LCMs are not easily accessible to chemicals because of their structures. Composting is an early key step employed in bioconversion of LCMs but it is not without its challenges [125, 126]. Composting is the biodegradation of a mixture of substrates by a microbial community (mixed microbial populations) in warm, moist, and aerobic conditions and in the solid state. The success of a microbial population in composting a lignocellulosic biomass depends on the lignocellulolytic enzymes it can produce. Different strategies of composting have been developed to overcome the difficulties posed by the recalcitrant nature of lignin [127]. A number of factors that affect the success of composting have been documented in the literature.

The structure of the microbiota involved in composting can determine the rate and quality of the process. This microbiota structure is itself dependent on other factors like pH, temperature, and stage of the composting process. Juan et al. [128] established links between specific species or groups of fungi and phases in composting. The species *Gibellulopsis nigrescens* and *Microascus brevicaulis*, though not the most represented, were detected at all the composting stages and showed the highest relative abundances. Investigation of why some species are available at all stages of composting will be appreciated. Carbon: nitrogen ratio (C:N ratio) is one of the major factors that affects composting of lignocellulosics (the optimum range being between 25 and 30). Too high C:N ratio slows down the initiation of composting, whereas low C:N ratio leads to too high emission of NH_3. This challenge is also complicated by the fact that the optimal C:N ratios vary with the nature or source of the LCMs in question [129, 130].

Other parameters worth optimizing during composting include particle size (optimum values: 10 mm for agitated systems, 50 mm for naturally aerated systems), moisture content (optimum values: 50–75%), temperature (optimum range: 45 to 60 °C), pH (optimum values: 6.5–8.5), and oxygen/aeration (0.6–1.8 m^3 air/day/kg of substrate). Depending on the composting processes, e.g., the composting of sewage sludge, bacteria may be more important than fungi from the beginning and vice versa [131, 132]. To regulate temperature in some cases, the composting pile will be turned to maintain different temperatures at different phases (mesophile, thermophile, cooling, and maturation) of the composting process, and this determines the nature of the final product. Aeration supplies oxygen to the involved microbiota, expels CO_2, and regulates temperature. Attendant to inadequate aeration is manifestation of anaerobic zones followed by release of foul-smelling metabolic products, whereas excessive aeration hampers microbial activity by impacting a cooling effect that attenuates moisture [129]. The number of glucose units in cellulose (i.e., degree of polymerization of cellulose) contributes to the recalcitrance of LCMs, though it is yet to

be lucidly illustrated and difficult to investigate individually with the current knowledge. Notwithstanding, varying the degree of polymerization of cellulose also alters the physical properties of LCMs such as crystallinity and porosity [130].

One of the strategies adopted to improve the efficiency or quality of composting of LCMs is inoculation with some special microbial species and addition of urea as a source of nitrogen. Wu et al. [133] demonstrated higher degradation of LCMs based on Fenton pretreatment of rice straw. The choice of carbon source for the composting microbial consortium is also crucial. For instance, the high electrical conductivity of cotton fiber renders it unsuitable for use as a carbon source [134]. Inoculation of different types of LCMs with thermophilic actinomycetes has been shown to improve the structure of the bacterial community and the activity of lignocellulolytic enzymes, thereby increasing the degree of degradation of LCMs during composting [20]. Sometimes, co-substrates may be added to the LCMs to improve some physical parameters like porosity. If the particle size of the LCMs is too small, this will hinder adequate aeration and as such, a bulking material may be added as a co-substrate to improve the porosity and hence aeration of the system. Examples of such co-substrate include fly ash, phosphorus rock, jaggery, and wood chips. It is also possible to enhance the porosity of the feedstock by separating particular components from the feedstock. Woody components may be removed from a LCM feedstock if the woods are so large as to make the overall particle size unsuitable for build-up of temperature during composting [135]. There is limited information regarding the use of obligate anaerobes in composting. Also, there is a dearth of information pertaining to the genetic manipulation of microorganisms for better composting. Given that some of the disadvantages of composting LCMs are consumption of longer periods, release of malodorous gases, and toxic metals like arsenic, it is paramount to develop recombinant degraders of LCMs that will avert such challenges as mentioned.

Lignocellulolytic enzymes are the essential molecular tools that compostage microbiota employ to degrade the LCMs. For example, laccases depolymerize lignin by breaking phenolic bonds whereas lignin peroxidase and versatile peroxidases cleave the non-phenolic bond in lignin [136]. In lignocellulosic bioethanol production, cellulases enhance the yield by degrading cellulose which increase the concentration of glucose in the fermenter. During compostage of LCMs, the microbes perform their essential secreting lignocellulolytic enzymes (cellulases, hemicellulases, and ligninases) [137]. Lytic polysaccharide monooxygenases are a group of enzymes recently reported to, in synergy with cellulases, partake in the degradation of cellulose by cleaving the glycosidic linkages at C-1 and C-4 positions [138]. The activity of lignocellulolytic enzymes in a compost is also enhanced by expansin-like proteins such as loosenin and swollenin. Microbial communities in compost secret a wide number of lignocellulolytic enzymes like acetyl xylanoesterases, glyoxal oxidase, manganese peroxidases, cellobiose dehydrogenase, α-l-arabinofuranosidases, and 1,4-β-xylosidases, to mention but few, yet no single microorganism produces all the enzymes required for efficient compotage of LCMs [14, 15].

Various factors affect the activity of a lignocellulolytic enzymes. These include incubation periods/stages of compostage, the concentration of enzymes, pH and temperature of the medium, nature of the microbial community in compost, and the presence of activators (co-factors, inhibitor), and sometimes these enzymes have concerted effects; they act synergistically [139–141]. To overcome some of these challenges, compost conditions have been optimized with respect to pH and temperature [142]. Being that the rate of biodegradation during composting is generally slow, the microbial cells may be engineered genetically to improve the rate of secretion of the lignocellulolytic enzymes and accessory enzymes such as aryl-alcohol oxidases and glyoxal oxidase. It is noteworthy, however, to mention that fungi are less amenable to genetic manipulation than bacteria [136, 139]. Moreover, enzyme engineering approaches may be employed to increase key properties of enzymes such as substrate specificity, tolerance to high substrate concentration, thermostability, and tolerance to wide range of pH and hence ultimately achieve more rapid biodegradation of LCMs [138, 141]. Generally, heavy metals inhibit lignocellulolytic enzymes during composting [141]. Nanozymes may also be considered in compostage of LCMs. Deeper and wide knowledge of the mechanisms by which all lignocellulosic enzymes and their accessory/helper proteins act will help improve enzymatic compostage of LCMs.

1.7 Bioethanol and biofuel production

The dawn of the twenty-first century came with increasing demand for biofuels owing to the fact that they are not only renewable but also ecofriendly and that fossil-based fuels are environmentally hazardous. This increasing demand has propelled scientists to embark on research aimed at investigating the production, process improvement for higher yields with less costs, up-scaling, and the challenges associated with biofuel production [143, 144]. Hence, a number of strategies have been adopted to produce biofuels from a myriad of feedstock. Notwithstanding, there still remain some obstacles that need to be overcome for the highest yield of biofuels. There are different types of biofuels such as biogas, biodiesel, and bioethanol [145, 146].

Bioethanol is one of the major biofuels being produced in large quantities and it shares the general properties of biofuels. Bioethanol is produced from a wide variety of lignocellulosic materials and other feedstocks like sorghum, whey,

molasses, sugarcane, cassava, rice straw, agricultural wastes [147–149]. Cutzu and Bardi [150] reported substantial yield of bioethanol from some agro-wastes: apple, kiwifruit, and peaches wastes; and corn threshing residue, using *Saccharomyces bayanus* as starter yeast. They also successfully scaled up the process. Bioethanol has also been produced from microalgae, which have cell walls rich in cellulose Iα (triclinic crystalline form) as opposed to cellulose Iβ (monoclinic crystalline form) of plant cell wall. Microalgae have an advantage over plant-based lignocellulosics in that the Iα cellulose has weaker hydrogen bonds and so renders ease of access to cellulose by the cellulolytic enzymes during hydrolysis. Notwithstanding, the cost of production of the involved hydrolytic enzymes (cellulases) is high [151]. Though there may be slight variations in the production processes adopted by many researchers, there are common steps that are consistent in the literature. Generally, the biomass is first subjected to pretreatment, followed by hydrolysis and the fermentation, which gives rise to the final product, bioethanol. The pretreatment may be physical, physicochemical, chemical, or biological [152]. For instance, in the production of bioethanol from rice straw, Wi et al. [153] used a popping method of pretreatment to improve yield. The pretreatment step is crucial. For example, pretreatment of lignocellulosic biomass frees the cellulose from by disrupting the native structure. This increases the reactivity of cellulose by giving enzymes easy access to cellulase, thereby heightening the yield of sugars released, and ultimately high yield of bioethanol [154]. In the hydrolytic step, acids or enzymes may be used but the downside of using chemical methods is the harmful nature of concentrated acids and the difficulty of recovering them. The chart below (Fig. 3) shows the general procedure for the production of bioethanol from lignocellulosic biomass. Metabolic and enzyme engineering is a key approach being employed in boosting the yield of bioethanol. However, genetic manipulation of non-producers has been shown to yield poorer results than when wild-type producers are modified genetically [146].

Some of the challenges facing bioethanol production from lignocellulosics are optimizing the conditions for both enzymes (cellulolytic and lignocellulolytic enzymes) and the microorganism required for the fermentation. This is because both enzymes and microorganisms have their optimal conditions of pH, temperature, ionic strength, substrate concentration, substrate specificity, etc. Genetic engineering has been used to handle some of these problems. *Saccharomyces cerevisiae* is the common candidate used for fermentation after hydrolysis of microalgal biomass for bioethanol production. However, the pretreatment step releases mixed sugars including the pentose xylose, which is not amenable to rapid fermentation by yeast and fungi. In this instance, bacteria have been preferred for fermentation [151]. Recycling of yeast used in alcoholic fermentation is of interest because it saves resources. However, there is always concomitant contamination by other microorganisms like gram-positive bacteria and some of which are recalcitrant even at treatment with the so-called broad-spectrum antibiotics [155]. In sub-Saharan Africa, the use of some crops as feedstock for bioethanol production is hotly debated due to the fact that they are common staples and committing such them to bioethanol production will culminate in food scarcity [152]. Though yeasts have been genetically modified to improve the production of bioethanol, some key setbacks relating to metabolism of xylose or pentoses by yeasts are difficulty in transporting pentoses, cofactor imbalances, and unsuitability of real biomass for genetically modified yeasts [156]. Silencing *pyc* gene in *Myceliophthora thermophila*, Li et al [157] witnessed 23% increase in ethanol production, reaching up to 11.3 g/L on cellobiose, by the modified strain. Bacteria are also amenable to genetic engineering for the purpose of bioethanol production [158]. Thapa et al. [159] succeeded in increasing the yield of ethanol from *Enterobacter aerogenes* ATCC 29007 1.5 times greater than obtained from the wild type. This was achieved by deleting the D-lactate dehydrogenase (ldhA) gene to block the production of lactic acid.

Non-conventional lignocellulosic materials may be used in the generation of biofuels so as to curtail the scarcity posed on agricultural produce when crops are used rather. Water hyacinth, straw, grasses, crop stubble, palm oil waste, switchgrass, *Chromolaena odorata*, *Sphagneticola trilobalata*, and *Tridax procumbens* are some of the non-conventional lignocellulosic biomasses [160–162]. Water hyacinth, being an invasive and rapidly-growing weed, is being exploited for bioethanol production. It is low in lignin but rich in cellulose and hemicellulose and this gives it an edge over other conventional LCMs in terms of ease of pretreatment [160]. Matutes and Besagas [161] reported up to 12.217% bioethanol yield from three invasive weeds of the *Astera* plant family using chemical pretreatment and commercial enzymes for fermentation. Nano-catalysts have been used to enhance the yield of biofuel from mixed weed biomass [162]. Trejo et al. [163] produced a significant amount of bioethanol from elephant ear plant weed using only mild physical pretreatment and enzymatic hydrolysis and *S. cerevisiae* for fermentation. These weeds are cheap, amenable to mild pretreatments, of low recalcitrance than woody LCMs, and their usage does not pose threat to the availability of agricultural food produce but is rather an approach to weed control. Plant cell wall engineering has been used to reengineer second-generation LCMs [163] and it may be extended to these weeds (non-conventional LCMs). One potential challenge to metabolic engineering is the lack of genomic information about the target plants.

Biological pretreatment of LCMs for bioethanol production depolymerizes the complex structure of lignocellulose to expose cellulose hemicellulose, thus improving the yield

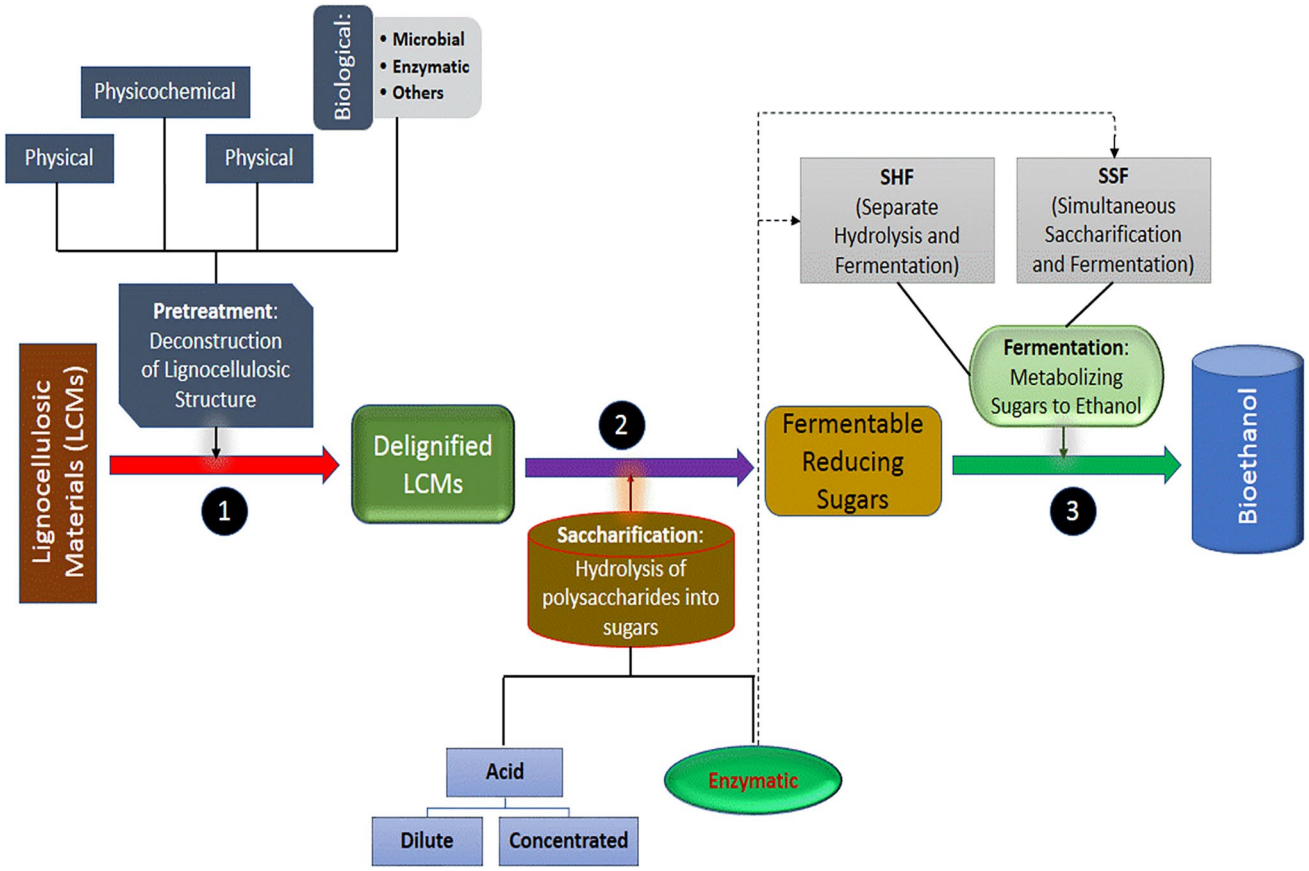

Fig. 3 Flow chart for bioethanol production from lignocellulosic materials

of reducing sugars during saccharification and, ultimately, increasing bioethanol yield. This approach uses microorganisms, ligninolytic enzymes, or both [163]. Fungi are major microbes employed in biological pretreatment of LCMs. Some commonly reported fungi are the white rot (e.g., *P. ostreatus*, *P.* chrysosporium, *T. versicolor*) brown rot, and soft rot fungi with as high as 70% delignification [164, 165]. These fungi achieve perform their role by secreting lignocellulolytic enzymes and their accessory enzymes/proteins such as lignin peroxidases (LiP), manganese peroxidases, laccases, mannanases, pectinases, xylanases, expansin-like proteins, swollenins, and the like, which aid in delignification [166, 167]. Bacteria have also been used for deconstruction of lignocellulose structure. Examples of bacteria used in pretreatment of LCMs are *A. lipoferum P. campinasensis*, *B. subtilis T. fusca*, and *C. fimi*. Though bacteria generally secrete lesser quantities of lignocellulolytic enzymes than fungi, they have shorter reproduction time and are more amenable to genetic manipulations than fungi [166]. Enzymatic pretreatments, which are more rapid than whole cell (fungal and bacterial) approaches, have been used to successfully delignify microalgae [168]. Biological pretreatment methods allow for better sugar yield during saccharification as they do not release enzyme inhibitors in the process [166]. Despite the eco-friendly and less energy-demanding nature of microbial pretreatments, they are non-specific (i.e., they target both lignin and cellulose) and generally slow [167]. The use of microbial consortia, bioaugmentation, metabolic engineering of lignocellulosic bio-degraders, rational design and directed evolution of lignocellulolytic enzymes, and control of culture parameters are key approaches that may be imbibed to overcome some of the challenges inherent in biological pretreatment of LCMs.

1.8 Enzymatic improvement of lignocellulosic biomass for animal feed

The limiting factor in the use of substrates, such as refined hemicellulose, cellulose, pectin, and starch in formulation of animal feeds is the high cost of these refined polysaccharides. In order to produce cost-efficient animal feeds and to alleviate the competition of food and feed for limited resources, animals should be encouraged to feed on non-edible, renewable, and cheap lignocellulosic biomass (LCB) such as rice straw, nutshells, peels, wheat bran, sugarcane bagasse, forest residues, corn straw, wheat straw, grasses

forest crops (softwood and hardwood), and energy crops, (salix and switchgrass) [169–172]. These alternative substrates are renewable sources of animal feed due to their abundance availability, low price, and high sugar content [170, 173–176]. However, non-hydrolyzed lignocellulosic biomasses are not nutritious, provide little protein, high amounts of fiber, and low digestibility and contain anti-nutrients [169, 177] when consumed by animals. Recently, there have been many studies published on valorization of agro-industrial wastes, but this study concentrated on how enzymes could be used to improve nutritional value of lignocellulose biomasses in animal feed production, while maintaining a green and sustainable agenda.

The major polymer compounds in LCB are hemicellulose (20 to 40%), cellulose (30 to 60%), pectin (2–35%), and lignin (15–25%) and their interlinkages make the energy in the LCB less extractable by the animal's digestive system [169, 178, 179]. The recalcitrance (high-lignified) nature of lignocellulosic biomasses' cell walls limits their utilization as feed for animals [169, 172]. The removal of lignin, the increase of fiber porosity, and the reduction of cellulose crystallinity are key in improving the enzymatic hydrolysis of plant biomass [127, 180]. The nutritional value of LCB can be improved using physical, chemical, and biological processing approaches [169–171, 180, 181]. The end product of chemical pretreatment may not be safe for animal feed as some toxic substances such as furfural may be produced [182]. Steam explosion pretreatment of LCB was reported to improve the digestibility of wheat straw [183]. Supercritical fluid, organosolv, ionic liquid, and deep eutectic pretreatment are green solvent–based pretreatment methods due to their operation under milder reaction conditions, producing fewer waste materials, using less poisonous chemicals, and energy [184]. However, organosolv pretreatment has major setbacks that involve loss of hemicellulose in the lignin stream, which is difficult to recover sugars due to the presence of other inhibitory compounds such as phenolics [185].

Enzymatic improvement of lignocellulosic biomass for animal feed involves the use of enzyme consortium [186]. This is highly commendable due to the following advantages: greater catalytic performance, milder processing conditions, and higher reaction specificity [187]. Delignification of LCB requires manganese peroxidase, versatile peroxidase, lignin peroxidase, and laccase [2, 187]. These enzymes remove lignin via oxidation and reduction reactions utilizing molecular oxygen as the ultimate electron acceptor. The optimal conditions for enzymatic delignification of different lignocellulosic biomass have been reported [187]. Pretreatment of wheat straw using ligninolytic enzyme consortium (LiP, MnP, and laccase) at pH 4.5 resulted in a 58.5% reduction in lignin. Enzymatic pretreatment of corn stover and sorghum stover using ligninolytic enzymes immobilized on alginate chitosan beads resulted in 50.25 and 63.01% delignification [187]. Sugarcane bagasse (30g) pretreated with a crude cocktail of laccase, manganese peroxidase, and lignin peroxidase from *Pleurotus ostreatus* IBL-02 at temperature and pH of 35 °C and 4.5, respectively, for 48 h resulted in 33.6% delignification [180]. Delignification (58.5%) was obtained using an enzyme consortium of laccase, MnP, and LiP [187]. A total of 48% delignification was achieved when wheat straw was pretreated with *Picnoporus cinnabarinus* laccase (65 U g^{-1}) in the presence of 20% 1-hydroxybenzotriazole (HBT) as a mediator, whereas 18% was obtained without a mediator [188].

Another set of enzymes such as xylanases, pectinases, cellulases, α-amylase, β-mannanase, α-galactosidase, proteases, and phytase is required for animal feed production [177, 189]. These enzymes eliminate some anti-nutrients and increase the bioavailability of nutrients and digestibility. The carbohydrases (xylanases, pectinases, cellulases, α-amylase, β-mannanase, α-galactosidase) act on the fiber or starch, improving the digestibility of the LCB, thus increasing energy for animal production [182]. The cellulose component of biomass is hydrolyzed by exo-β 1, 4-glucanase (EC 3.2.1.91), endo-β 1, 4-glucanase (EC 3.2.1.4), and β-glucosidase (EC3.2.2.21). Endoglucanase hydrolyses the interior cellulose fibers by cleaving the β-(1,4) glycosidic linkages between β-D glucose units in cellulose, creating free ends which are acted upon by the exo-β 1, 4-glucanases to produce units of cellobiose. These cellobiose units are hydrolyzed by β-glucosidase into glucose units [182, 190]. Cellulases improve animal feed by increasing digestibility thereby releasing reducing sugars for energy [190, 191]. Hydrolysis of hemicellulose is carried out by a group of enzymes such as glucomannanase, xylanases, β-xylosidase, galactomannanase, glucuronidase, and acetylesterase [182, 192]. Amylases are used as digestive tools to increase the digestibility of animal feed ingredients [193]. Proteases improve protein digestibility through solubilization and hydrolysis of the protein content of LCB. Phytase degrades phytate bonds releasing trapped nutrients, improves the use of phosphorus, and reduces the need to supplement the feed with inorganic phosphorus [193]. Hydrolysis of laccase pretreated samples resulted in a 40 and 47% increase in glucose and xylose yield [188]. Rice bran and wheat bran are excellent sources of protein, and glucose content [194, 195]. Therefore, enzyme hydrolysis of these biomass in animal feed improves its nutritional composition.

1.9 Lignocellulolytic enzymes for clean and green ecosystem

The world production of lignocellulosic biomass from corn stover, rice straw, wheat straw, and other agro wastes is about 181.5 billion tons per year [182]. Some lignocellulosic biomasses produced from agriculture sectors are not

fully utilized but are burnt or left to decay naturally, which may take years [1]. Accumulation of lignocellulosic biomass poses serious environmental problems due to inadequate biomass waste management concerns [196, 197]. Currently, the use of non-renewable fossil resources is discouraged whereas renewable sources are encouraged in the production of chemicals and materials. This awareness has globally spread via various industries. This paradigm shift has made the use of lignocellulosic biomass as feedstock in fuel and chemical production to be perceived as a way of achieving a green and sustainable agenda. Citric acid, succinic acid, lactic acid, ethanol, acetone, and butanol are examples of bio-based chemical products with many applications. The use of lactic acid is tremendously growing in polyacetate production used as bioplastic [198, 199]. More so, bioethanol production (which is a renewable and sustainable biofuel) from biomass is presently the interest of the world due to issues on climate change. Bioethanol production from renewable lignocellulosic biomass (LCB) and its use in the transportation sector can reduce greenhouse gas emissions significantly as well as excess dependence on fossil fuels. These provide opportunities for carbon-neutral fuel, cleaner, sustainable, environmentally safe, and green alternatives for fossil fuel [200]. Also, some chemical products which are complex and recalcitrant are emptied into the water bodies without treatment. These toxic contaminants are of great concern, due to their adverse effects on aquatic lives [201]. Glucose production from lignocellulosic biomass generally relies on extreme conditions of temperature and pH. These produce chemical contaminants that confound downstream processing [201, 202].

To ensure a clean environment while utilizing biomasses as sustainable feedstock, it is pertinent to develop new technologies that aim at eliminating the use and generation of environmentally noxious chemicals, production of green and sustainable products with minimized energy requirements, environmentally friendly, non-toxic, can degrade to safe chemicals, recyclable, or have minimum waste during production [199, 203].

A promising green approach is the use of enzymes obtained from microorganisms [187, 201]. The lignin modifying enzymes (LMEs), laccase (phenol oxidase), lignin peroxidase, manganese peroxidase, and versatile peroxidase, are easily produced from renewable and biodegradable resources, making them a valuable means for environmentally friendly technologies. Microorganisms are biodegradable, non-hazardous, biocompatible, produced via green and sustainable means [201], suitable for the production of lignocellulolytic enzymes.

Lignocellulose biomasses are very difficult to break open due to their recalcitrant structure and require some form of chemical pretreatment to render the glycosidic and ester bonds accessible for hydrolytic enzymes [182]. Hydrolysis of lignocellulosic biomass gives a mixture of cellulose, hemicellulose, and lignin. The cellulose and hemicellulose are further hydrolyzed by cellulase, xylanase, and amylase into fermentable sugar monosaccharides for ethanol production. The lignin components of the lignocellulose are then transformed by laccases, lignin peroxidase, and manganese peroxidase into other value-added and environmentally friendly compounds.

Enzyme-based treatment is promising due to some benefits such as higher catalytic efficiency, higher reaction specificity, milder processing condition, generating less waste than other chemical reaction routes, and energy efficiency [187, 204, 205]. Improved cost efficiency in the use of lignocellulosic enzymes can be achieved by optimizing the production and application conditions as well as immobilization of the enzymes.

Lignin degrading enzymes are divided into lignin modifying enzymes (LMEs) and enzymes that are auxiliary to the degradation of lignin. The former can degrade and mineralize some recalcitrant majorly aromatic compounds owing to their specific characteristics, and high catalytic potential, suggesting that they can act with low energy consumption and under mild conditions [201]. The biotechnological potential of these enzymes can increase production, reduce process cost or the cost of treatment steps, and reduce the number of wastes released to the environment [12, 187, 201].

To maintain the green policy, there is the need to remediate effluents generated from industries before emptying them into the environment [201]. Therefore, these enzymes can be used to reduce the recalcitrant pollutants present in the biomass hydrolysate after chemical and physicochemical treatment before release to the environment [12]. LMEs play important roles in the oxidation of many types of pollutants that are structurally similar to lignin and possibly enhance the biotechnological applications of these compounds [201]. Under optimized conditions of temperature, pH, enzyme concentration, and mediators, phenolic compounds in rice straw hydrolysate were reduced by 92% and furan derivatives such as polyunsaturated alcohols and 5-hydroxymethylfurfural were detoxified using ligninolytic enzymes [187]. Lignin degrading auxiliary enzymes cannot alone break down lignin but are needed to completely degrade the poly-aromatic polymer. These enzymes include methanol oxidase, glucose oxidase, aromatic peroxygenases, pyranose-2-oxidase, chloroperoxidase, aryl alcohol oxidase, glyoxal oxidase, and cellobiose dehydrogenase [201]. Simultaneous enzymatic saccharification and communition (SESC) of lignocellulosic biomass have been reported to improve saccharification efficiencies of 60 and 80% at an optimum pH of 6.0 under laboratory and large scale processes. This process provided a mild and clean approach for bioconversion of biomass into glucose on a large scale, preventing the generation of unwanted chemical inhibitors

[202]. A comparative study on the evaluation of a bacterial laccase from *Streptomyces ipomoeae* and *Trametes villosa* in delignification and detoxifcation of steam-exploded wheat straw showed a reduction in the phenol content by 35 and 71% with respect to bacterial and fungal laccases, respectively [206]. Thermostable xylanases and cellulases from *Pseudomonas fluorescens* are used in animal feed production due to their ability to enhance digestibility and quality of animal feed [207]. Expression of thermostable β-1, 4-glucanase, endocellulase, and cellobiohydrolases in corn for easy inclusion in animal feed has been reported. Properties of some fungal and bacterial lignocellulolytic enzymes are summarized in Table 2.

2 Limitations and challenges in the application of lignocellulosic enzymes

The huge quantity of wastes generated annually around the globe poses a great risk to the environment and the entire ecosystem if not properly managed. Despite recent attempts, the annual generation of tons of waste continues to rise thereby placing a significant financial burden for governments of various nations to dispose of and manage. There is an extremely high cost involved in the collection and processing of environmental/agricultural wastes from the generation point to the point of disposal, as it necessitates a considerable workforce [220]. This is one of the limitations in the application of lignocelluloses-based waste in industrial processes as raw materials. While using enzymes to unlock the utilization of lignocellulosic biomass is a potential alternative, without pretreatment, lignin remains as a barrier, making it difficult to access cellulose, which would then undergo further enzymatic action and be transformed to fermentable sugar [167]. The most expensive processing step in the conversion of lignocellulosic biomass to fermentable sugars is pretreatment [220]. It is considered a significant barrier to the widespread use of lignocellulose-based processes. The five major steps of pretreatment process have a number of limitations and advantages. For instance, the biological pretreatment process which utilizes microorganisms and enzymes during its procedure to generate biofuels such as hydrogen, methane, ethanol, and other biomaterial is advantageous in that it is cost-effective due to the fact that it utilizes low energy, mild operating conditions, environmentally friendly, and no chemical is used.

Despite these advantages, the biological process is time-consuming, experiences difficulty to scale-up for the industrial processes, and requires close monitoring, slow reaction rate low efficiency, and also leads to considerable loss of carbohydrates [8, 221]. The physical pretreatment method carried out through milling, microwave, extrusion, grinding, freezing leads to the generation of bioethanol and biogas. The physical method is very easy to operate and can be used together with other methods for maximum efficiency. The physical method faces a lot of challenges such as high operation and energy cost, system complexity, and inadequate delignification [221]. Similarly, the chemical method has high delignification rate, good yield, ease of adoption on an industrial scale, least selective with regard to the substrate, effective lignin removal. Like other methods, the chemical method has some drawbacks such as generation of toxic by-products, high cost, corrosive in nature as acids, alkaline, oxidative, carbon-dioxide ionic-liquid, and metal salts are used in this procedure [222, 223]. Lastly, the physicochemical method is effective in reducing cellulose crystallinity, high retention of hemicellulose and cellulose, and efficient lignin removal leading to the generation of bioethanol and other useful product like heat and energy but its major challenge is the high cost of equipment, higher power consumption, and low yield [167, 224].

Because the use of water or organic solvents produces wastewater as a by-product, toxicity and waste are also important considerations when choosing a pretreatment method. This adds another handling stage to the process that must be taken into account in order to avoid environmental pollution. The viability of lignocellulosic biofuels is still debatable, as some studies have indicated that the energy consumed during biomass conversion may be greater than the energy generated from the process [225]. Additionally, enzymes are employed in the entire process of conversion of lignocellulosic waste to valuable products. It is also worthy to note that these enzymes are also utilized in other steps such as enzymatic hydrolysis which relies on pH, time, substrate, and temperature. Aside from these general effects, many compounds produced during the pretreatment and saccharification of biomass can inhibit or inactivate lignocellulolytic enzymes. Sugars, sugar derivatives, and phenolic compounds are among the inhibitors [200]. The main issue with cellulase is its inefficiency in acting on natural crystalline cellulose [201].Despite numerous studies on the molecular mechanisms of substrate binding and catalysis, little information has been used to guide cellulolytic enzyme engineering.

Lignocellulolytic enzymes can be made more viable and cost-effective by using genetically modified species for simultaneous saccharification and fermentation. The enzymes employed for the degradation of hemicellulose and cellulose are added in the same tank in a process called SSF (simultaneous saccharification and fermentation) and SSCF (simultaneous saccharification and co-fermentation) which are more preferably to the conventional method of SHF (separate hydrolysis and fermentation) where enzymatic saccharification and fermentation are performed separately thereby the cost and the risk of contamination [12, 225, 226]. Recent

Table 2 Properties of some fungal and bacterial lignocellulolytic enzymes

Microorganisms	Lignocellulolytic enzymes	Optimum temperature (°C)	Optimum pH	Level of activity obtained	Substrate (biomass)	References
Fungi						
Cadophora malorum	Xylanase CMCase	30 70	8 6	16 U/mg 5 U/mg	Xylan CMC	[208]
Pseudogymnoascus destructants	Xylanase CMCase	50 60	6 6	13 to 15 (U/mg protein) 9 to 10 (U/mg protein)	"	[208]
Emericellopsis maritima	Xylanase CMCase	50 60	6 6	18 to 21 (U/mg protein) 8 (U/mg protein)	"	[208]
Pleurotus ostreatus	Laccase	50-55	3.0 – 4.5	286 to 548 U/L	Corn cob and sawdust	[209, 210]
	CMCase			24 to 45 U/L	Sawdust and corn cob	[210]
	Xylanase				Corn cob, sawdust	[210]
Pleurotus sajor-caju	Laccase	37-50	3.0 to 4.0	1850.7 U/L	molasses	[209, 211]
Pleurotus citrinopileatus	Laccase	55	4-5	1000 U/L	Olive mill wastewater (OMWW)	[212]
Microsporum distortum)	Lignin peroxidase	40	5	-	-	[213]
Trametes polyzona WRF03 (*Tp*WRF03)	Laccase	55	4.5	21,523 U/mg	Wheat bran	[33]
Bacteria-						
Bacillus subtilis	Lignin peroxidase	35	6.5	-	-	[213]
Bacillus sp. MABINYA-1	Lignin peroxidase	30	5	21–47 U	Saw dust, maize stover, wheat straw	[214]
Ensifer adhaerens NWODO-2	Lignin peroxidase	30	7	3.76–37.5 U	Saw dust, wheat straw, corn stover	[214]
Bacillus mycoides AR20-61	CMCase	40-50	5	Relative activity was 100%	CMC	[215]
Pseudomonas species	Laccase	20-80	3-8			[216]
Alcaligenes faecalis	Laccase	80	5-8	-	Guaiacol	[217]
Anoxybacillus ayderensis SK3-4	Laccase	75	7	Relative activity was 100%	Syringaldazine	[218]
Streptomyces thermocarboxydus	Xylanase	40-70	4-8	Relative activity was 100%	Wheat bran	[219]
Dictyoglomus turgidum	β-glucosidase	80	4.5	160 U/mg	-	[207]

study shows and demonstrated that a modified Bacillus strain outperformed the widely used industrial strain in terms of yield and was a good option for industrial-scale applications [227]. Similarly, the use of engineered xylose-fermenting strain was shown to improve yield [228]. Currently, more technological advancements are needed to make the usage of lignocellulosic materials more viable, cost-effective, and suitable in real-world applications.

3 Conclusion and future perspectives

Enzymes are important in many biological processes. The involvement of lignocellulolytic enzymes in converting waste of lignocellulolytic origin into beneficial products has gained a lot of attention globally. The green technological process not only is eco-friendly but also leads to the generation of value-added products of high economic value and zero negative impact on public life and health. They have already proven to be successful as energy crops in the biorefinery process of making ethanol, with countries like Brazil and the USA producing large amounts for general use. Given the exhaustive nature of fossils and their detrimental impact on the environment, lignocellulose is a better alternative, as human activities, primarily agricultural and food waste, can produce enough raw materials needed for the powering of biorefineries and the consequent production of green products to meet people's needs.

With the ever-growing world population, the fear of food crises continues to rise; it is more important than ever to look into the waste stream for lignocellulose raw materials to ensure that food meant for human consumption is

not channelled to energy production. To avert this problem, an urgent study is needed to ensure that the benefits of green energy and products made from lignocellulosic sources are not overlooked and that the cautions about food availability and security are addressed. Finding viable applications for agricultural and food waste in line with Sustainable Development Goal (SDG) 12, conscientious consumption and production, and environmentally friendly waste management during their life cycle will all be part of the solution. Finding viable, cost-effective pretreatment, and green solutions is critical to overcoming the problems associated with the application of lignocellulose, and lignocellulolytic enzymes can play a key role in this after the limitations and challenges are addressed. The discovery of new microbial interactions could lead to the simultaneous development of lignocellulolytic enzymes, which could assist in overcoming the challenges of adoption and cost. Additionally, the adoption of novel pretreatment methods such as hydrothermal pretreatment and ionic liquid pretreatment can also help to avert the challenges experienced in biological, chemical, physical, and physicochemical pretreatment methods.

Peroxidase, cellulase, and laccase are currently receiving a lot of attention. More research on other enzymes identified is needed to investigate if optimization, enzyme cocktails or combinations, and genetic manipulation can help separate lignocellulose into its major components for further processing into usable and viable products. Furthermore, the potentials of bacteria for lignocellulolytic action are still in its early stages, and many novel enzymes with intriguing properties may eventually be discovered. Best waste management strategies are critical as we seek sustainability in our processes, and finding beneficial uses for lignocellulose biomass will help to limit the amount of waste that ends up in landfills and provide the necessary re-use and recycling frameworks for our ever-increasing waste pool. Understanding the enzymes involved in the disintegration of lignocellulose will go a long way towards solving the problem. More research is needed to identify undiscovered microbial communities with the potential for lignin degradation and cellulolysis. Following their discovery, technological advancements can aid in replicating the optimal environmental conditions for their growth in the laboratory and studied further and consequent utilization in biotechnology advancements. As more information on lignocellulolytic enzymes becomes available, new applications are expected to emerge.

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Data availability Data sharing not applicable to this article as no datasets were generated or analyzed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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