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Use of Basidiomycetes in Industrial Waste Processing and Utilization Technologies: Fundamental and Applied Aspects (Review)

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Abstract—This review provides an analysis of recent data on the mechanisms of degradation of lignocellulosic materials and xenobiotics by basidiomycetes. Special attention is given to the analysis of the current state of research of ligninolytic enzymes and their involvement in the degradation of xenobiotics. Data on the practical use of basidiomycetes for bioconversion of industrial wastes are systematized. The most promising areas of bioconversion technologies are considered, such as contaminated water purification (including wastewater), cleanup of soils contaminated with heavy metals and xenobiotics, and degradation of difficult-to-degrade substrates (lignin and lignocellulose wastes, low-energy coal, and synthetic polymers).

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INTRODUCTION

Basidiomycetes are higher fungi with multicellular mycelium numbering approximately 30 thousand species of both microscopic fungi and fungi with large fruiting bodies. Although basidiomycetes are found in various ecosystems including meadows, steppes, and deserts, they are most diverse and common in forest ecosystems. The main function of basidiomycetes in nature is to decompose lignin and cellulose. This ability attracts the attention of researchers both in terms of elucidation of mechanisms underlying this process and in order to develop procedures for biotechnological utilization of wood and plant waste [1–5].

A unique feature of basidiomycetes is the ability to synthesize extracellular enzymes lignin peroxidases, Mn-peroxidase, versatile peroxidases, and laccases with a broad substrate specificity [6, 7], which allows them to decompose organic matter not only of natural origin but also various xenobiotics. The most dangerous organic pollutants whose degradation can be accelerated by basidiomycetes are polycyclic aromatic hydrocarbons, chlorophenols, polychlorinated biphenyls, pesticides, and municipal wastes. To date, the main mechanisms of decomposition of xenobiotics by basidiomycetes are studied sufficiently well, and the use of basidiomycetes as biological agents for processing and utilization of industrial waste has been considered in several reviews [8, 9]. However, new data are constantly being accumulated that clarify the mechanisms of degradation of xenobiotics by basidiomycetes and describe examples of using basidiomycetes and their ligninolytic enzymes for detoxification and degradation of pollutants in various industries.

The purpose of this review was to analyze the current state of technology of bioconversion of lignocellulosic materials and xenobiotics by basidiomycetes.

Main pathways of transformation of lignocellulosic materials and xenobiotics by basidiomycetes. Investigation of decomposition of lignocellulosic materials and xenobiotics by white rot fungi demonstrated the possibility of their use in technologies of processing and utilization of poorly degradable anthropogenic waste. Recent experimental data obtained in this field are summarized in several reviews [2, 6–10]. It was established that degradation of xenobiotics and lignocellulosic materials by white rot fungi includes the action of a multienzyme complex, whose synthesis depends on the substrate on which the fungus grows, its physiological and biochemical characteristics, and genomic organization. The efficiency of degradation is ensured by a combination of extracellular ligninolytic enzymes, organic acids, mediators, and related enzymes. According to the modern notion, there are three main pathways of decomposition of natural polymers and xenobiotics by basidiomycetes: direct enzymatic degradation, indirect enzymatic degradation, and nonenzymatic degradation (Fig. 1).

Each of these pathways is characterized by specific mechanism of decomposition of poorly degradable compounds. The enzymatic pathway includes molecular transformation of the substrate with alteration of its properties and ultimate complete degradation, which are accompanied by de novo synthesis of compounds. Indirect enzymatic degradation is based on the formation of radicals in the main products and by-products of enzymatic reactions, with subsequent trigger of radical processes. Nonenzymatic degradation is

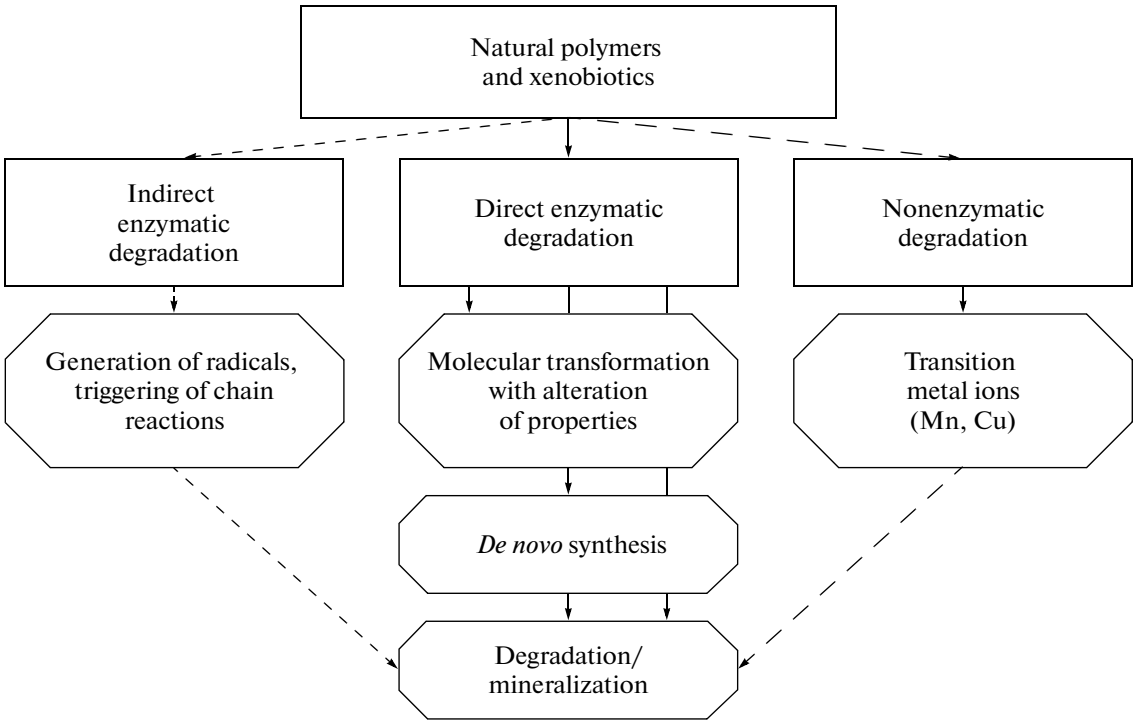

Fig. 1. Main pathways of degradation of natural polymers and xenobiotics by basidiomycetes.

performed at the expense of reactive radicals and ions of transition metals. Under natural conditions, basidiomycete degradation processes are multi-stage and, as a rule, include all the above mechanisms. However, both direct and indirect types of enzymatic degradation are performed with the participation of oxidoreductases and hydrolases, which determines the significance of these enzymes in the degradation of xenobiotics and biopolymers. In our opinion, the enzymatic decomposition is of greatest practical importance. Examples to support this assumption will be discussed below.

Characteristics of ligninolytic enzymes of basidiomycetes. Basidiomycetes are able to synthesize many extracellular enzymes involved in modification and degradation of lignin. Currently, the common name of these enzymes is ligninases [2, 12], although some authors assign this term to lignin peroxidase [10, 11]. Ligninases can be divided into two groups: phenoloxidases (laccases (**LAC**, EC 1.10.3.2)) and heme-containing peroxidases, namely lignin peroxidase (**LP**, EC 1.11.1.14), manganese peroxidase (**MP**, EC 1.11.1.13), and multifunctional (versatile) peroxidase (**VP**, EC 1.11.1.16) [11, 12]. These two groups of enzymes have different electron acceptors: molecular oxygen for laccase and hydrogen peroxide for heme-containing peroxidases (Table 1).

Lignin peroxidase (LP). LP is a glycoprotein containing 1 mol of ferriprotoporphyrin IX per 1 mol of the enzyme and 6 to 20% of carbohydrates (Table 1). The molecular weight (**MW**) of LP ranges from 39 to 43 kDa, and isoelectric points of isozymes range from 3.0 to 4.5 [13, 14]. Lignin peroxidase was first detected in *Phanerochaete chrysosporium* in 1983 [15, 16]. Later, the presence of LP was established in various strains of *P. chrysosporium* and *Trametes versicolor* [17]. Screening of basidiomycetes revealed the presence of LP genes in *Panus* sp., *P. coccineus, P. sanguineus*, and *Perenniporia medulla-panis* [18]. LP is nonspecific with respect to substrates: it oxidizes a wide range of aromatic substrates of phenolic nature and nonphenolic components of lignin with a redox potential less than 1.4 V (relative to the normal hydrogen electrode) in the presence of hydrogen peroxide. The catalytic cycle of LP is similar to the catalytic cycles of other heme peroxidases (Fig. 2).

A unique feature of LP, which distinguishes it from other peroxidases, is the ability to oxidize methoxylated lignin substructures with high redox potentials. For phenolic substrates, the oxidation rate is higher than for nonphenolic substrates; as a result of oxidation, phenoxyl radicals are formed. In the presence of oxygen, phenoxyl radicals can interact with various compounds, leading to rupture of the aromatic ring and/or polymerization.

Veratryl alcohol (VA), which is produced by ligninolytic fungi as a secondary metabolite, is of particular importance for the functioning of ligninases. This compound protects ligninase from inactivation by hydrogen peroxide. It can also induce the synthesis of ligninase in culture medium and serves as a redox mediator during the oxidation of various substrates,

Table 1. General characteristics of ligninolytic enzymes

Enzyme	Active site structure	Localization	Catalyzed reaction	MW, kDa	Glycosylation	pH optimum	Mediators	References []
Lac	Ensemble of four copper ions: T1 copper center and the copper cluster consisting of T2 copper ion and T3 antiferromagnetic pair	Intracellular and/or extracellular enzyme	4 benzenediol + O_2 = = 4 benzene semiquinone + $2H_2O$	50–70	*N*-glycosylation	2–10	ABTS, GBT, TMPO, transition metal complexes	[2], [21], [28], [31], [45]
LP	Ferriporphyrin IX	Extracellular enzyme	1. LP[Fe(III)] + H_2O_2 $\longrightarrow$ LP*-I[Fe(IV) = O^{*+}] + H_2O 2. LP-I+AH $\longrightarrow$ LP-II[Fe(IV) = O^{*+}] + A^{*+} LP-II+AH $\longrightarrow$ LP + A^{*+}	39–43	*N*-glycosylation	1–5	Veratryl alcohol	[8], [10], [11], [20], [21]
MP	Ferriporphyrin IX	Extracellular enzyme	MP + H_2O_2 = MP-I + H_2O MP -I + Mn^{2+} = MP -II + Mn^{3+} MP-II + Mn^{2+} = MP + Mn^{3+} + H_2O	38–62.5	*N*-glycosylation	2.5–6.5	Organic acids as chelators, toles, unsaturated fatty acids	[2], [8], [10], [21]
VP	Heme	Extracellular enzyme	Donor + H_2O_2 = Donor (oxidized) + $2H_2O$	42–45	Glycosylation type not determined	3–5	Same compounds that for LP and MP	[2], [8], [11], [29]

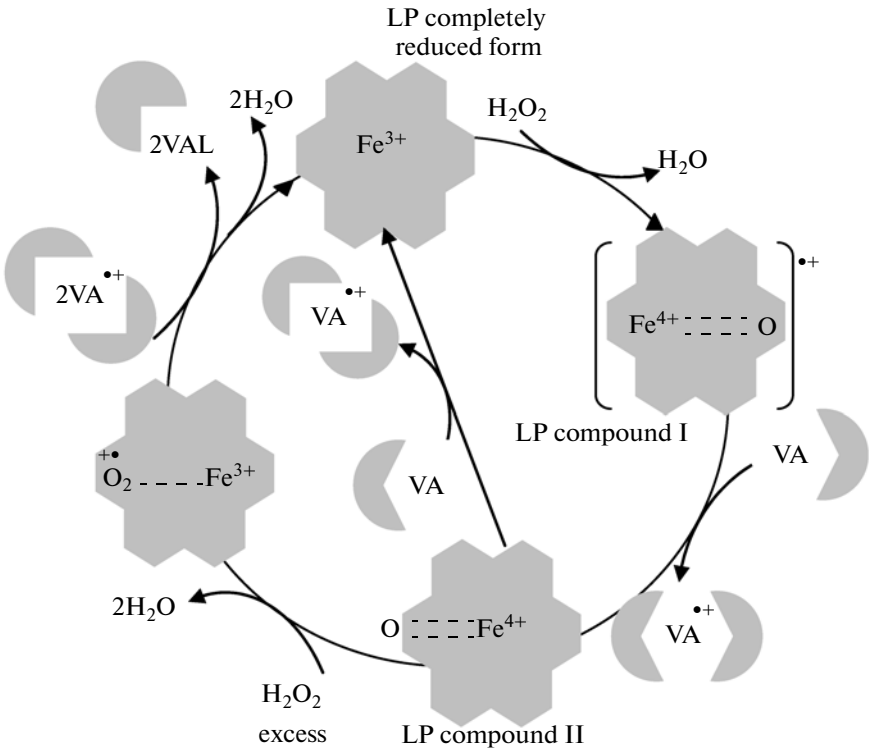

Fig. 2. Catalytic cycle of lignin peroxidase (LP).

including the lignin polymer [19]. During catalysis, cation radicals of veratryl alcohol are formed, which are highly reactive and enter nonenzymatic reactions.

Currently, the ability of ligninases to catalyze the following reactions has been established [10–12]:

(1) Cleavage of C–C-bonds in dimeric lignin models

(2) Oxidation of benzyl alcohol.

(3) Oxid ation of methyl substituents in benzyl compounds.

(4) Hydroxylation of benzyl methyl groups.

(5) Hydroxylation of olefinic bonds.

(6) Decarboxylation of phenylacetic acid.

(7) Cleavage of ester bonds

(8) Opening of aromatic rings.

(9) Polymerization of phenols.

The crystalline structure of LP shows that the heme group is located inside the structure and is bound to the surface through a channel whose diameter is too small for penetration of large polymeric structures of lignin but quite sufficient for penetration of small molecules and their subsequent binding [20].

Manganese peroxidase (MP). Manganese peroxidase, similarly to LP, is a glycoprotein containing protoheme IX (ferriprotoporphyrin IX), which is easily separated from the apoenzyme during electrophoresis even under nondenaturing conditions. The molecular weight of MP ranges from 38 to 62.5 kDa; the majority of purified enzymes have an MW of ~45 kDa [21]. Basidiomycetes produce a large number of MP isoforms. For example, 11 isoforms were described for *Ceriporiopsis subvermispora* [22]. The isoelectric point values of MP vary from 2.5 to 6.8 [23].

Manganese peroxidases are produced by the majority of white rot fungi (families *Polyporaceae*, *Meruliaceae*, and *Coriolaceae*) and certain fungi that inhabit the soil litter (families *Strophariaceae* and *Tricholomataceae*). Today, as many as 56 fungi producing MP are known [23].

MP catalyzes the oxidation of Mn^{2+} to Mn^{3+} in the presence of hydrogen peroxide. The catalytic cycle of MP in the presence of a chelating agent (oxalate, malonate, malate, tartrate, and lactate) leads to the formation of highly reactive Mn^{3+}–chelator complex, which can oxidize many phenolic substrates by the one-electron mechanism, including phenolic compounds with the formation of lignin phenoxyl radicals (Fig. 3) .

The reaction is initiated by the binding of H_2O_2 to the native enzyme and formation of an iron–peroxide complex. Subsequent break of the -O–O- bond leads to the transfer of two electrons and formation of compound MP I, which is an Fe^{4+}-oxo-porphyrin–radical complex. Then, after the bond is broken, one water molecule forms. Further reaction involves the formation of compound MP II (Fe^{4+}-oxo-porphyrin complex). The monochelated Mn^{2+} ion functions as a one-electron donor for this porphyrin complex and is oxidized to Mn^{3+}. The reduction of compound II proceeds similarly, and another Mn^{3+} ion forms from the

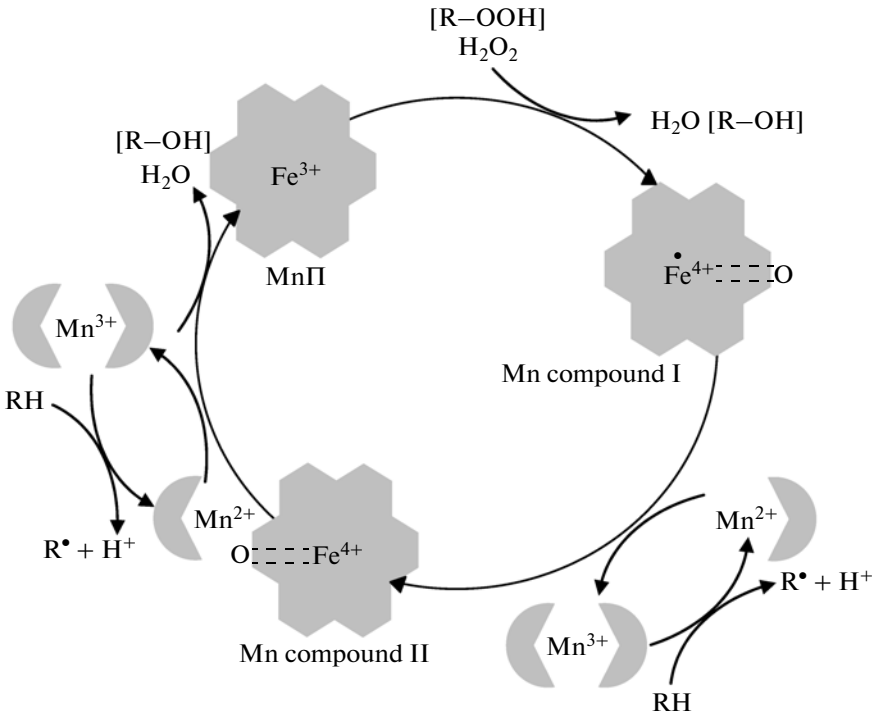

Fig. 3. Catalytic cycle of manganese peroxidase (MP).

Mn^{2+}, leading to the formation of the native form of the enzyme and release of a second water molecule. Mn^{3+} ion is stabilized by organic acids, such as oxalate, and functions as a low-molecular-weight redox mediator that nonspecifically attacks the substrate with cleavage of the hydrogen ion and one electron. Phenolic and aminoaromatic compounds are oxidized with the formation of phenoxyl and amino radicals, respectively [23]. The oxidation potential of the Mn^{3+}–chelator complex is insufficient for oxidation of lignin structures of phenol. Nonphenolic substrates can be oxidized by MP only in the presence of a second redox mediator with the formation of reactive radicals. Organic acids, such as oxalate and malonate, function as such redox mediators. In the absence of enzymatic system that generates H_2O_2, the formed radicals can be used as by MP a source of hydrogen peroxide and increase the efficiency of lignin degradation by the fungus.

MP can catalyze bond breaking in nonphenolic lignin structures at C_α–C_β bonds and alkyl–aryl and participate in C_α-oxidation of model lignin structures of the syringyl type β–1. In addition, it is believed that MP oxidizes nonphenolic lignin structures by producing highly active radicals from unsaturated fatty acids and thiols [24]. The authors of some studies assumed that nonphenolic lignin structures can be oxidized by MP after preliminary removal of methanol from aromatic rings of lignin molecules with the participation of cellobiose dehydrogenase [25].

The crystal structure of MP and the structure of its active center (heme) are largely similar to LP. The main difference of the classical peroxidases from LP is the presence of a manganese-binding site. The bound Mn^{2+} ion is coordinated by three amino acid residues, the propionate residue at position 6 of heme and oxygen atoms of two water molecules. The binding site is located on the surface of the enzyme and is readily accessible [26].

Laccase. Lac is a glycoprotein containing 10 to 45% of carbohydrates per enzyme molecule [27]. Many researchers believe that the carbohydrate moiety of the molecule provides the conformational stability of the protein globule. Fungal laccases have an MW of 50–70 kDa [28] and isoelectric points at pH 3–5 [23, 30, 31]. Laccases were found in fungi, bacteria, and insects [31]. Today, the main source of the enzyme, including the enzyme used for industrial purposes, are fungi. A large number of fungi that produce this enzyme are known. The most comprehensively laccase producers are *Podospora anserina, Agaricus bisporus, Rhizoctonia practicola, Pholiota aegerita, Trametes versicolor, Pleurotus ostreatus* [32], *Coriolus hirsutus* [33, 34], and *Neurospora crassa* [35, 36]. All fungal laccases are monomers or dimers, except for isoform 1 of *Podospora anserine*, which is apparently a tetramer. The majority of fungi produce both intracellular and extracellular enzyme.

The family of laccases that were discovered more than a century ago remains a subject of basic research primarily because the detailed mechanism of action of

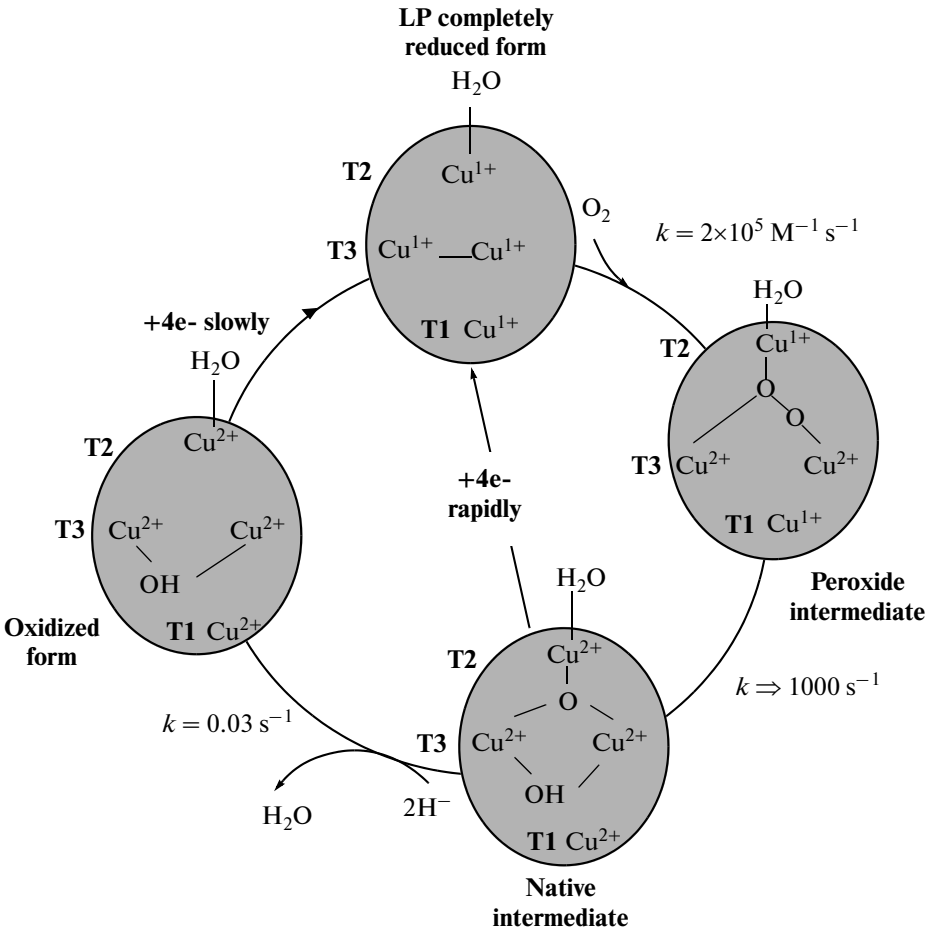

Fig. 4. Catalytic cycle of laccase (Lac) [28].

the enzyme is still obscure. The catalytic cycle include the oxidation of the substrate (an electron donor) and electron transfer to the T1 center of the enzyme. The transfer of four electrons from the copper ion in the T1 cluster to the T2/T3 cluster is followed by sequential recovery of all three copper ions in the cluster; the copper ion T3α, which has the highest electron affinity, is reduced first. The reduction of T3α is accompanied by protonation of the μ3-oxo center and μOH-ligand, with protons dissociating from the reduced T3α center. The next stage is the reduction of the T2 center. The key step in this process is the formation of a "bridge" hydroxyl between T2 and T3β, through which electrons can be rapidly transferred to the T2 center. Therefore, this model suggests the formation of a pair of copper ions of a mixed valence. Further reduction of the T3β copper ion is postulated as a rapid process of electron transfer along the cysteine–histidine dipeptide between T1 and T3, which is accompanied by protonation of the bridge hydroxyl followed by dissociation of two water molecules from the cluster [28].

Laccases have a broad substrate specificity and catalyze oxidation of various compounds, including *o*,*p*-diphenols, aminophenols, polyphenols, polyamines, lignin, certain inorganic ions, and aryl diamines, with concomitant reduction of molecular oxygen to water [37, 38]. Laccases are capable of direct bioelectrocatalysis, that is, direct electron transfer from the electrode to the active site.

It is assumed that laccase oxidizes phenol hydroxyl of substrates to form a phenoxyl radical, which enters the nonenzymatic reactions of demethoxylation of lignin and methoxyphenolic acids, as well as the reaction of quinone formation and oxidative elimination of carboxyl groups.

The structures of laccases isolated from different sources are very similar [39–41]. Molecules of laccases are usually monomers consisting of three sequentially linked cupredoxin-like domains folded into a dense globule. The T1 copper center is located in the third domain and is coordinated by two imidazoles of histidine and the sulfhydryl group of cysteine, which form a trigonal structure. It is a component of the substrate-binding "pocket" and is located at a distance of 6.5 Å from the protein surface. Usually the T1 center is located at a distance of 12 Å from the T2/T3 cluster and is linked with it through the His–Cys–His tripeptide, which is highly conserved among laccases. Trinu-

Table 2. Possibility of degradation of natural compounds and xenobiotics by LP, MP, and laccase during (1) direct and (2) indirect oxidation

Compound	LP		MP		Laccase	
	1	2	1	2	1	2
Lignin and its model components	+	+	+	+	+	+
Phenolic lignin components	+	+	+	+	+	+
Nonphenolic lignin components (aromatic alcohols)	+	+	+	+		+
Alcohols	+					
Amino acids, proteins	+				+	+
Aromatic amines	+					
Hydroxyphenylacetic acid and its derivative		+			+	+
Unsaturated fatty acids		+		+		
Cinnamic acids		+		+	+	+
Carbohydrates and their derivatives						+
Humic substances		+		+	+	+
Inorganic ions	+		+		+	+
Xenobiotics						
PAHs	+	+	+	+	+	+
PCBs	+				+	+
Pesticides	+	+	+	+		+
Dyes	+	+		+		+
Halogenated phenols	+	+	+	+	+	+
Azo compounds, aniline, acrylamide, hydrazine, benzotriazoles	+		+	+	+	+
Amines (aryldiamines, hydroxylamine)					+	+
Naphthols					+	+
Benzene homologues						+

clear T2/T3 cluster is located between the first and third domains and has amino acid ligands in each of them. The three copper ions of oxygen-reducing T2/T3 cluster form an almost equilateral triangle with distances 3.7 to 5.1 Å. The T2 copper ion has two Nε2 ligands from two histidine residues and one oxygen ligand O_2, which form a trigonal planar configuration. Water molecule or the OH group may serve as oxygen ligands. Each copper ion of the T3 pair is coordinated by three histidine residues and an oxygen ligand, which is located between two T3 ions. The coordination of each of them can be described as a distorted tetrahedron.

Versatile peroxidase (VP). Polyfunctional peroxidase is a glycoprotein exhibiting hybrid properties of LP and MP. There is still confusion about the definition of these enzymes: sometimes they are called hybrid peroxidases and sometimes they are abbreviated. Currently, the group of VP includes enzymes that catalyze the oxidation of typical peroxidase substrates including Mn^{2+} and veratryl alcohol. Versatile peroxidases were isolated from *Bjerkandera adusta, Bjerkandera* sp. (BOS55), *Bjerkandera* sp. (B33/3), *B. fumosa, Pleurotus eryngii, P. ostreatus*, and *P. pulmonarius* [42, 43]. This group of enzymes is very attractive in terms of practical use because of their ability to oxidize Mn^{2+} as well as phenolic and nonphenolic aromatic compounds. It is assumed that VP can oxidize a wide range of substrates with different potentials—from low to high, comparable to those for LP. Versatile peroxidases are more effective than LP and MP, which are not able to effectively oxidize phenolic components in the absence of veratryl alcohol and to oxidize phenols in the absence of Mn^{2+}, respectively. This substrate specificity is determined to their hybrid molecular structure. The catalytic cycles of MPs are similar to those of VP and LP [29].

As in other heme-containing peroxidases, heme in VP is located within the globule and is connected with the surface by two channels. The function of the first channel, which is highly conserved in heme peroxidases, is similar to that of LP, and the second channel is characteristic of VP, and MP and serves for the oxidation of Mn^{2+} to Mn^{3+}.

Biodegradation of biopolymers and xenobiotics with participation of enzymes of the ligninolytic complex. Degradation of biopolymers and xenobiotics in nature under the influence of ligninolytic enzymes produced

by basidiomycetes is a process whose intensive study is primarily determined by the need to design environmentally friendly biotechnology. As a result, ample factual material on biodegradation with LP, MP, and laccase by both direct and indirect oxidation pathways has been accumulated to date. The list of compounds degraded by direct and indirect oxidation by lignin peroxidase, MP, and laccase is presented in Table 2.

Analysis of published data led us to conclude that a compound can be directly oxidized by a ligninolytic enzyme only if it can be a substrate of this enzyme (judging by its chemical structure) and if its redox potential is below the redox potential of the enzyme [11]. For example, the comparison of the effectiveness of oxidation of a homologous series of methoxybenzenes with different redox potentials (from 0.81 to 1.76 V at pH 3.0) by horseradish peroxidase, LP, MP, and laccase showed that, out of the 12 compounds tested, ten are oxidized by LP, four (redox potentials, 0.81–1.12 V) are oxidized by horseradish peroxidase and MP, and only one compound (1,2,4,5-tetramethoxybenzene; redox potential, 0.81 V) is oxidized by laccase [44]. Thus, LP oxidizes a wide range of aromatic compounds with redox potentials less than 1.4. By the increase in the efficiency of substrate oxidation, ligninolytic enzymes can be arranged in the following order: laccase, MP, and LP. However, the situation changes when the possibility of using the enzyme–redox-mediator system for degradation and/or detoxification of biopolymers and xenobiotics is considered. The effectiveness of such a system is determined by the stability of the enzyme during catalysis and by the redox properties of the mediator, including the stability, lifetime, and reactivity of generated free radicals. The most effective enzyme–redox-mediator system is the laccase–redox-mediator system [45]. This is primarily due to the fact that hydrogen peroxide inactivates all heme peroxidases after several catalytic cycles are completed. Laccase that uses molecular oxygen as a cosubstrate is quite stable. In addition, the pH and thermal inactivation of ligninolytic peroxidases, which is associated with the release of two Ca^{2+} ions from the enzyme molecule, also reduces the effectiveness of such a system.

Versatile peroxidase is of special interest because of catalytic multifunctionality—the ability to degrade a wide range of compounds in reactions of direct oxidation that cannot be oxidized by LP and VP. Recently, it was demonstrated that VP effectively degrades polycyclic aromatic hydrocarbons [42]; pollutants of phenolic and nonphenolic nature [46]; pesticides [47]; industrial dyes [48]; Active Blue 38 and other azo dyes; Active Black 5 and other phthalocyanine pigments; anthracene and its derivatives; benzopyrene; pyrene; 2,4-dichlorophenol; and pentachlorophenol. However, all limitations on the use of peroxidases in xenobiotic degradation technologies also apply to VP. Thus, currently, the most promising system to be used in detoxification and degradation technologies is the laccase–redox-mediator system.

Nonenzymatic degradation of lignocellulosic materials and xenobiotics by basidiomycetes. The nonenzymatic pathways of degradation of polysaccharides, lignin, and xenobiotics has been attracting the attention of researchers for decades. All mechanisms of nonenzymatic degradation are based on radical processes [1, 11, 12]. Similarly to the processes of degradation of lignocellulosic materials, the first stage of degradation of xenobiotics by basidiomycete may include the production of highly reactive low-molecular-weight compounds that function as oxidants. Such compounds are involved in the "treatment" of wood and ensure the availability of wood lignin for enzyme attack. The main radicals involved in these processes are hydroxyl radicals (OH*).

The main pathways of generating OH* by basidiomycetes are the reactions catalyzed by cellobiose dehydrogenase (**CDG**), low-molecular-weight peptides/quinone redox cycle, and redox reactions catalyzed by glycopeptides (Fenton reaction catalyzed by glycopeptides). In addition, almost all basidiomycetes have systems generating hydrogen peroxide, which not only is used by enzymes as a cosubstrate but also enters the Fenton reaction to form OH* radicals. The latter attacks lignocellulosic material and/or polysaccharides of the cell wall and leads to cleavage of biopolymers and facilitates penetration of ligninases. It can be assumed that xenobiotics are degraded by a similar mechanism.

Main directions of use of basidiomycetes in technologies of utilization and processing of anthropogenic structures and waste. Currently, basidiomycetes are of most demand in technologies that require decomposition of lignin and its modifications. Lignin and lignocellulosic waste is produced mainly during agricultural activity (straw) and constitutes a considerable part of household as well as wood processing and pulp and paper industry waste [49].

Decomposition of lignin and lignocellulosic agricultural waste. The most common agricultural waste containing lignin and lignocellulose is straw. Straw is a valuable organic fertilizer [50]; however, if left in the field and plowed on the spot, it is degraded too long because of the low content of the carbon source and the high content of fiber and organosilicon compounds. In the arable soil horizon, its residues remain for three to five years. In view of this, to improve utilization of straw, it was suggested to perform its inoculation with an association of nitrogen-fixing and polysaccharide-producing bacteria and basidiomycetes with a high cellulolytic activity.

In addition, agricultural lignocellulosic waste is poorly assimilated when fed to cattle [49, 51]. The presence of lignin impedes the access of hydrolytic enzymes—cellulase and hemicellulose—to their substrates. Preliminary biodelignification of plant feeds is the most promising way to improve their quality. Justi-

Table 3. Patented methods of pulp and paper mill wastewater treatment using basidiomycetes

Fungal species	Degraded compound	Source
Alternaria alternata	Water-soluble lignin sulfate	[66]
Phlebia tremellosa	Lignin and lignin-containing resins in paper pulp	[69]
Scytinostroma galactinum	Degradation of lignin-containing wastes, cellulose, and chlorine aromatics	[70]
Scytinostroma galactinum strain F361	Degradation of lignin, cellulose, and chlorine aromatics	[71]
Schizophyllum commune, Trichaptum biforme, Phanerochaete gigantea	Lignin and lignin-containing resins in paper pulp	[72]
White and brown rot fungi	Degradation of lignin in paper pulp	[73]

fication for such an approach was shown in numerous studies with rice and wheat straw, cotton stalks, and cardboard [52]. The method of producing feed product based on straw delignified by *Panus tigrinus* [53] and *Pleurotus ostreatus* [54] is described in patents [53, 54].

Recycling wastes of wood and wood-processing industry. Chips, sawdust, and other wood processing wastes, as a rule, are never used or used only slightly. Large amounts of these raw materials are accumulated over years near wood-processing enterprises. A common practice for disposal of waste wood using basidiomycetes is to grow edible mushrooms on them. The most widely spread is the Oyster mushroom *Pleurotus ostreatus*, a delicious and nutritious mushroom, which has earned worldwide recognition due to the relatively simple farming techniques of its cultivation and resistance to pests and diseases.

Among wood wastes, wooden railroad ties pose a particular problem. Their life varies from 6 to 40 years depending on the type of wood of which ties are made, the climatic conditions in the area where the railway line is located, and the extent of the workload of paths. A characteristic feature of this type of wood waste is that they are saturated with the antiseptic creosote, which prevents rotting and, therefore, decreases the possibility of biological degradation. Several methods of decomposition of creosote-containing wood wastes were patented abroad. It was suggested to use a range of basidiomycetes, such as *Antrodia radiculosa, Meruliparia incrassata, Neolentinus lepideus, Melanoporia niger, Polyporus* sp., *Crustoderma dryinum, Gloeophyllum subferrugineum, Phanerochaete sordida, Peniphora pseudopini*, and *Ceriporia spissa* as biological agents [55–57].

Of other lignocellulosic wastes that can be degraded by basidiomycetes, we should mention the utilization of coconut fibers with *P. ostreatus* [58]; degradation of park waste using *Coriolus versicolor, P. ostreatus*, and *Ganoderma applanatum* [59]; and degradation of coconut fibers and mulching materials using a consortium of basidiomycetes including *P. ostreatus, P. pulmonarius, P. dryinus, P. tuberregium, Piptoporus betulinus, Fomitopsis pinicola, F. officinalis, Trametes versicolor, Hypsizygus ulmarius, Ganoderma lucidum, G. applanatum, G.curtisii, G. oregonense*, and *G. tsugae* [60].

In conclusion, it should be mentioned that progress in studying the degradation of lignocellulosic waste has made it possible to develop their future application in space flights [49]. It is possible that, in the near future, lignocellulosic waste transportation to the space station will lead to significant cost savings. Lignocellulose can become a raw material for obtaining everything necessary: fuel, energy, chemical raw materials, food, and water. Experiments conducted within the framework of the program "Closed Ecological Life Support System" (CELSS) showed that the treatment of plant wastes with the white rot fungus *P. ostreatus* for this purpose is a promising approach [61].

Treatment of pulp and paper mill (PPM) wastewater. Enterprises that use molecular chlorine for cellulose bleaching produce polychlorinated dibenzo-*n*-dioxins (**PCDDs**) and polychlorinated dibenzofurans (**PCDFs**)—highly toxic carcinogenic compounds that are chlorinated cyclic aromatic esters [62]. The ability to detoxify pulp produced by PPM was shown for a number of basidiomycetes, including *Phanerochaete chrysosporium, T. versicolor, Fomes lividus*, and *Thelephora* sp. [63, 64]. In our country, it was also recommended to use the method of sludge lignin utilization using a wood-decomposing basidiomycete *Trametes pubescens* strain as a biological method of utilization of solid PPM wastes containing chlorinated aromatic compounds [65]. The calculations of the authors of [66] showed that the efficiency of degradation of phenols and chlorinated compounds contained in the Baikal Pulp and Paper Mill waste by *T. pubescens* was 100%. In addition to *T. pubescens*, the method of biological purification of pulp and paper industry wastewater from water-soluble lignin sulfate by *Alternaria alternata* was patented in the Russian Federation [66].

In most cases, fungal laccase plays the key role in the detoxification of PPM wastewater [62, 67]; the key role of MP was shown only for certain strains (e.g., *T. versicolor*) [68]. Basidiomycetes belonging to genera *Alternaria, Phanerochaete, Phlebia, Scytinostroma*,

and *Trichaptum* are used in technologies of biological treatment of PPM wastewater (Table 3).

Purification of wastewater from textile dyes. The ability of basidiomycetes to decolorize various dyes that are present in textile industry effluent was studied sufficiently well [43, 48, 74–83]. Analysis of available data showed that discoloration of dyes was demonstrated for 31 species of basidiomycetes and 77 dyes and mixtures thereof. Among the basidiomycetes studied, genera *Phanerochaete* and *Trametes* were described in the most detail as capable of degradation of a wide range of dyes. However, the preparation based on *Flavodon flavus* is the only preparation patented to date [84], which indicates the necessity of further study of basidiomycetes of genera *Phanerochaete* and *Trametes*, which can be used for bioremediation of textile industry wastewater.

Purification of wastewater containing heavy metals and radionuclides. Biological treatment of water from heavy metals and radionuclides by using basidiomycetes is based on their ability to rapidly absorb toxicants. The absorption of metals by fungi can occur not only due to adsorption processes, as in the case of bacteria, but also due to active transport of metals into cells [85, 86]. This unique feature makes basidiomycetes, in some cases, the best agents for biological purification of water from metals and radionuclides.

In our country, the trend to use fungi in bioremediation rapidly developed at the end of XX century, as evidenced from patents that now have ceased to have effect [87, 88]. Ascomycetes (*Aspergillus, Penicillium*, and *Phizopus*) were recommended to be used for this purpose as fungi capable of intensive absorption of radionuclides and heavy metals. In recent years, however, increasing attention is being paid to studying basidiomycetes as potential biosorbents, apparently due to their lower pathogenicity. The authors of [89] demonstrated that *Schizophyllum commune* is promising for removal of uranium, and the possibility of using *Phanerochaete chrysosporium* for removal of cadmium was shown in [90]. Since high concentrations of heavy metals in the environment are toxic to basidiomycetes, when selecting a strain for bioremediation, its sensitivity to heavy metals should be studied. According to data obtained in [91], high resistance to metals is characteristic of *P. ostreatus, P. cystidosus, Stereum hirsutum* (resistant to Cd and Hg), and *T. versicolor* (resistant to Cd, Zn, Ni, Co, Cr, Mo, Pb, Hg, and Sn). The list of basidiomycetes that are able to accumulate different metals is given in Table. 4. The ability to accumulate the most broad range of heavy metals is characteristic of fungi belonging to genera *Pleurotus, Trametes*, and *Phanerochaete*, which makes the representatives of these genera the most promising tools in terms of using in technologies of biological treatment of wastewater from heavy metals.

Cleanup of environment contaminated with oil hydrocarbons. In the classical scheme of purification from crude oil and petroleum, biological methods are used only at the final stages of treatment; however, today there is a tendency to replace the multistep purification schemes with one-step schemes. The developed approaches are based on the use of microbial consortia, which include representatives of filamentous fungi, yeasts, and bacteria, which effectively transform oil components into nontoxic and low-toxic substances. At the same time, purification of contaminated media in situ can be performed by maintaining and stimulating the natural oil-oxidizing microorganisms by creating optimal conditions for their development (aeration and introduction of nitrogen and phosphorus fertilizers to the contaminated focus) and by introducing an active strain of the destructor to the contaminated site.

To clean the water surface from oil spills, a complex mycosorbent containing strains of ascomycete fungi *Fusarium solani, F. moniliforme, Trichoderma harzianum*, and *Cladosporium resinae* was developed in Russia. These fungi are immobilized on hydrophobic carriers and are used as oil sorbents and destructors [113]. To clean soil and water surfaces from crude oil and oil products, a complex product containing ascomycetes (*Aspergillus niger*) and basidiomycetes (*Phanerochaete chrysosporium*) was developed and is currently used. This preparation is sprayed over the water surface in a mixture with detergents and sorbents [114]. Similar preparations containing *Phanerochaete chrysosporium* strain and designed to clean up environment contaminated with petroleum hydrocarbons was registered in the United States [115].

To clean up soil from oil pollution, biological preparations containing mostly bacteria, such as *Pseudomonas, Rhodococcus, Bacillus, Arthrobacter, Acinetobacter, Azotobacter, Alkaligenes*, and *Mycobacterium*, as well as *Candida* yeast and filamentous actinomycetes *Streptomyces*, are used. In preparations of fungal origin, primarily ascomycetes of the genera *Aspergillus* and *Penicillium* are used [116]. Among the higher basidiomycetes, a high oil-degrading ability was shown only for genera *Phanerochaete, Pleurotus*, and *Trametes*. According to [117], the amount of petroleum hydrocarbons in the presence of *P. chrysosporium, P. ostreatus*, and *T.* (*Coriolus*) *versicolor* decreased 12 months after inoculation by 68.7, 53.1, and 78.1%, respectively. A characteristic feature of biodegradation of petroleum hydrocarbons by basidiomycetes is the ability of the latter to metabolize the aromatic fraction of aromatic hydrocarbons, whereas bacteria degrade primarily paraffin-naphthenic hydrocarbons [118]. Patents containing the description of preparations based on basidiomycetes, which are intended to clean up soils contaminated with oil, are absent in the Russian Federation. In the United States, the only patent containing a description of purification of oil-contaminated environment by using *P. chrysosporium* was registered [115].

Cleanup of contaminated soils. To date, approaches to remediation of soils contaminated with various

Table 4. Basidiomycete species and metals accumulated by them

Fungus	Metal	Source
Phanerochaete chrysosporium, Phellinus sanguineus, Pleurotus ostreiformis, Pleurotus sajor-caju, Pycnoporus sanguineus, Trametes versicolor, Volvariella volvacea	Cd	[90], [92–103]
BDT-14 (DSM 15396), *Phanerochaete chrysosporium, Pleurotus ostreiformis, Pleurotus sajor-caju, Trametes versicolor, Volvariella volvacea*	Cr	[92], [93], [104]
Coriolopsis strumosa, Daedalea tenuis, Ganoderma lucidum, Lentinus strigosus, Lenzites malaccenis, Lepista nuda, Oudemansiella mucida, Phanerochaete chrysosporium, Phellinus sanguineus, Phellinus xeranticus, Pycnoporus cinnabarinus, Pycnoporus sanguineus, Rigidoporus lineatus, Rigidoporus microporus, Trametes lactenia, Trametes versicolor	Cu	[86], [93– 95], [97], [103], [105], [106]
Phanerochaete chrysosporium	Hg	[108, 109]
Phanerochaete chrysosporium, Pleurotus sajor-caju, Pleurotus ostreiformis, Trametes versicolor, Volvariella volvacea	Ni	[92], [93], [110], [111]
Phanerochaete chrysosporium, Phellinus badius, Phellinus sanguineus, Pleurotus ostreiformis, Pleurotus sajor-caju, Pycnoporus sanguineus, Trametes versicolor, Volvariella volvacea	Pb	[92–97], [103], [107]
Innonotus mikadoi, Tricholoma conglobatum	U, Th	[112]

Table 5. Patented methods of degradation of various xenobiotics using basidiomycetes

Fungus species	Degraded compound	Source
Antrodia radiculosa *Meruliporia incrassata*	Pentachlorophenols (in wood)	[119]
Marasmiellus troyanus	Benzo(a)pyrene	[120]
Phanerochaeta chrysosporium *Gloeophyllum striatum*	Antibiotics and quinolone naftiridon	[121]
Phanerochaete chrysosporium	Halogenated hydrocarbons, DDT	[122]
	Dioxin, heptachlor, DDT, dieldrin, toksofen	[123]
	PAHs	[124]
	PCBs	[125]
	Halogenated hydrocarbons, pentachlorophenol	[126]
Phanerochaete gigantea *Resiniciun bicolor* *Pleurotus ostreatus*	Dioxins, polihlorfenily, biphenyls	[127]

xenobiotics, including PAHs, polychlorinated biphenyls (PCBs), nitroaromatic compounds, and pesticides by basidiomycetes have been developed. The most comprehensively studied basidiomycete genera capable of degradation of xenobiotics of different nature are *Phanerochaete, Trametes*, and *Pleurotus*. The list of basidiomycetes used in patented preparations for decomposition of various xenobiotics is shown in Table 5. Fungus *P. chrysosporium* is the most widely used for degradation of various xenobiotics.

Degradation of low-energy coals. Basidiomycete species that can degrade coal wastes and humates extracted from them were isolated primarily from wood (tree trunks, logs, branches, and stumps) and, therefore, cannot be competitive under conditions of soil [128]. In other words, the problem of assessing the possibility of depolymerization of coal wastes in situ remains to be solved [129]. The currently existing patented methods of coal biosolubilization are based on the use of *P. chrysoporium* [130, 131] and *Polyporus versicolor* [132] and imply coal processing ex situ.

Another urgent problem is the search for basidiomycetes that can not only degrade coal wastes but also actively participate in degradation processes in soils.

Currently, only one fungal species (*Collybia dryophila*) meeting these requirements is known [133]. During the screening, the ability of the fungus to synthesize and release extracellular enzymes should be taken into account, because these enzymes are responsible for coal degradation.

Decomposition of synthetic polymers. Along with degradation of natural polymers (lignin, cellulose, and humic substances), published data describe the ability of basidiomycetes to degrade synthetic polymers.

Synthetic polymers (plastics) are widely used in today's world. Because of their extreme stability and steady accumulation in the environment, it is important to find methods for their biodegradation. The possibility of using basidiomycetes for this purpose has been little studied, but there are several studies in this field. In particular, seven species of white rot fungi were shown to be able to degrade polyvinyl chloride (PVC), a widespread synthetic fabric [134]. Marked depolymerization recorded by reducing the number of CH bonds was demonstrated for *P. chrysosporium, P. sajor caju*, and *Polyporus versicolor*; the least depolymerization potential was observed for species belonging to the genus *Pleurotus*. According to [135], fungus *Pycnoporus cinnabarinus* can degrade polyvinyl alcohol, another synthetic polymer that is used as an adhesive. The authors of [135] showed the relationship between the polymer degradation and laccase production. Fungi *P. chrysosporium* and *Trametes versicolor* were demonstrated to be able to degrade the polymer nylon (nylon-66), which is widely used in textile industry [136]. Later, isolation and characterization of the enzyme responsible for the degradation of this polymer showed its similarity to the MP [137].

The authors of [138] demonstrated the ability of basidiomycetes to degrade remains of rubber tires. It was found that the most effective is, apparently, *Resinicium bicolor*. The treatment of aromatics, which are used as additives to rubber, with *Resinicium bicolor* showed an increase in the growth of bacteria *Thiobacillus ferrooxidans* on rubber as well as acceleration of devulcanization. Based on these results, the authors of [138] concluded that cocultivation basidiomycetes and bacteria for biodegradation of waste rubber is a promising approach for purposes of resin waste biodegradation.

Despite the demonstrated principal possibility of using basidiomycetes for the degradation of synthetic polymers, this direction of using basidiomycetes in technologies of processing and utilization of industrial wastes has not yet found practical application.

Thus, in recent years, the interest in using basidiomycetes for degrading lignocellulosic materials and xenobiotics has significantly increased. Numerous studies are still devoted to ligninolytic enzymes, with the majority of works describing the development of approaches to the degradation of xenobiotics and lignocellulosic materials, obtaining recombinant strains producing these enzymes, and increasing the efficiency of catalysis, pH, and thermal stability.

The analysis revealed that, at present, basidiomycetes can be used in technologies of processing and utilization of anthropogenic structures and wastes in the following directions:

(1) Purification of contaminated water (including sewage water of textile industry pulp and paper mills, water contaminated with petroleum hydrocarbons, sewage water formed during production of olive oil and sugar from sugar beets or sugar cane, water suspension remaining after coagulation of latex in rubber industry, and waste water containing heavy metals and radionuclides).

(2) Cleanup of contaminated soil (including contamination with xenobiotics and heavy metals).

(3) Degradation of difficult-to-degrade substrates (including lignin and lignocellulosic waste, low-energy coal, and synthetic polymers).

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