ABSTRACT

Background: The genus Pleurotus is most exploitable xylotrophic fungi, with valuable biotechnological, medical, and nutritional properties. The relevant features of the representatives of this genus to provide attractive low-cost industrial tools have been reported in numerous studies to resolve the pressure of ecological issues. Additionally, a number of Pleurotus species are highly adaptive, do not require any special conditions for growth, and possess specific resistance to contaminating diseases and pests. The unique properties of Pleurotus species widely used in many environmental technologies, such as organic solid waste recycling, chemical pollutant degradation, and bioethanol production.

Methodology: The literature study encompasses peer-reviewed journals identified by systematic searches of electronic databases such as Google Scholar, NCBI, Springer, ResearchGate, ScienceDirect, and ISI Web of Knowledge. The search scheme was divided into several steps, as described below.

Results: In this review, we describe studies examining the biotechnological feasibility of Pleurotus spp. to elucidate the importance of this genus for use in green technology. Here, we review areas of application of the genus Pleurotus as a prospective biotechnological tool.

Conclusion: The incomplete description of some fungal biochemical pathways emphasises the future research goals for this fungal culture.

INTRODUCTION

The large-scale commercial production of edible mushrooms derived from the successful implementation of microbial technology owing to their nutritional, economic, and ecological value and medicinal properties. Notably, the genus Pleurotus (Jacq.: Fr.) Kumm. (Pleurotaceae, higher Basidiomycetes) is the second most distributed edible mushroom worldwide and has unique high nutritional value and therapeutic properties. The culture of growing oyster mushrooms was introduced to the West from China and during World
War I. Germany successfully developed cultivation methods for the production of *Pleurotus ostreatus* as a new and valuable food source to defeat hunger (*Piska, Ziaja & Muszynska, 2016*). At present, several species of the genus *Pleurotus* have high commercial value in the global market of edible cultivated mushrooms (*Pawlik et al., 2012*). The presence of essential amino acids, such as arginine, glutamine, and glutamic acid, as well as vitamins and minerals, is characteristic of *Pleurotus* species (*Da Silva et al., 2012*). The most popular among them, *Pleurotus ostreatus*, also known as hiratake, is a traditional edible, highly nutritious mushroom with a nutrient-rich dietary composition (*Gregori, Svacelj & Pohleven, 2007*). This mushroom has high nutritional value due to its high protein, fiber, and carbohydrate contents. Beside obvious importance in the worldwide agriculture and food industry, oyster mushrooms also were considered as an important object for the medical purpose (*Moussa, 2009*). Secondary metabolites isolated from *Pleurotus* fruiting body and mycelia show strong, versatile health-promoting and therapeutic effects. Valuable bioactive compounds from oyster mushrooms can be divided into two groups with high and low molecular weight (*Morris et al., 2017; Golak-Siwulska et al., 2018*). A bundle of reports concerning oyster mushrooms brings to light the new substances with such properties as an antibiotic, antitumor, antiviral, and anticholesterolic activities (*Selegean, Putz & Rugea, 2009*). The radioprotective effects of an extract from *Pleurotus ostreatus* mycelium have been studied by *Lauradó et al. (2015)* and administered in a prophylactic schedule to Balb/c mice. In general, compounds with pharmacological activities that identified in fungi, stimulate different cell populations of the immune system, such as macrophages, natural killer cells, T-cells, and modulate cytokine system as well (*Oloke & Adebayo, 2015*).

Additionally, oyster mushrooms are low-calorie and exhibit low fat and sodium contents (*Patiil et al., 2010*). Because of low lipid concentration and sugars, *Pleurotus* species are classified as low-energy food products (*Kalać, 2016*). According to the *Pleurotus* species mineral composition analysis, the most evaluated elements are Cd, Hg, As, and Pb (*Deepalakshmi & Mirunalini, 2014*). Mostly, fruit body nutritional content depends on what kind of substrate and pollutants concentration is represented. Standard content for mushrooms from unpolluted fields reach on such elements as Al, Zn, Mn, Cd, and others, either (*Gucia et al., 2012*). On another hand, heavy metals for white-rot fungi, in general, are the critical factor for synthesis of cellulolytic and hemicellolytic enzymes during the biodegradation process. Thereby, the increased attention should be paid to the accumulation of heavy metals in *Pleurotus* mushrooms as a food source (*Bellettini et al., in press*). However, the ability of *Pleurotus* species to absorb heavy metals from the environment can be helpful in recovery strategies, such as mycoremediation (*Alves et al., 2017*).

*Pleurotus eryngii* also has established economic importance among the species in this genus. The fruiting bodies of *Pleurotus eryngii* are comparable to those of cultivated oyster mushrooms but possess a distinctly pronounced aroma and superior nutritional quality (*Stamets, 2011; Mau et al., 1998*) studied the flavor compounds of *Pleurotus eryngii* and found them to consist of mostly volatiles and taste components. *Mohamed & Farghaly (2014)* described the difference in chemical composition between fresh and dried
Pleurotus ostreatus and their bioactive secondary metabolites. Among the studied substances, the authors found 107 different metabolites and recommended fresh mushroom fruit bodies as a source of aromatic compounds and dried mushrooms as a source of antioxidants. Ahmed et al. (2008) described the cultivation of Pleurotus floridanus (Singer, 1948) on different straw wastes, such as soybean, paddies, and wheat straws, and their combinations to determine the effects of the straw substrate additives on yield, moisture content, and crude protein. In perspective, usage of those substrate formulas could be considered as a basis for the cultivation of Pleurotus florida regarding raw material abundance for large-scale production. Cultivation of those species is basically an adaptation of their mycelial growth and fruiting to existing raw materials as the development of substrate-processing technologies.

In contrast, the regulation of fruit body nutritional content can be acquired via the application of different agricultural wastes with different chemical compositions and supplements. Additionally, the selective properties of Pleurotus enzymatic systems are desirable for applications in biomass degradation and the production of derivatives for green chemicals and biofuel. The principal moments of Pleurotus application and emphasise some informational gaps that define “critical” areas of research and their relevance to the industrial sector investigated in this study.

SURVEY METHODOLOGY

The literature study encompasses peer-reviewed journals identified by systematic searches of electronic databases such as Google Scholar, NCBI, Springer, ResearchGate, ScienceDirect, and ISI Web of Knowledge. The search scheme was divided into several steps, as described below.

First, we focused on technological and nutritional fungal properties, the primary fungal enzymes, and examples of biotechnological applications, while collecting the primary information. Thus, every selected category was used in combination with a comparable keyword reflecting the review questions. Papers with a high citation rate in Google Scholar (180 peer-reviewed articles) were collected in an initial database to gain an overview of the general research interest in that area. The dates were identified as the timeframe for the analysis.

Categorization and research relevance, number of subsequent citations, and journal impact factor were then used to verify and compare the content from research databases such as NCBI, Springer, ResearchGate, ScienceDirect, and ISI Web of Knowledge. An expert analysis was applied to validate the competence of the selected articles and optimize the structure. A total of 121 articles were chosen and organized into the list by Zotero (http://www.zotero.org/) to obtain the file extension .ris for applications using the software for further analysis.

Finally, we conducted and visualized the bibliometric map using the software VOSviewer (http://www.vosviewer.com/) to cluster related and frequently occurring keywords and terms. According to the co-cited terms, the visualization density map for collected articles lists most of the frequently observed keywords, such as phylogeny, genetic variability, environmental microbiology, mushroom cultures, lignin oxidation,
mushrooms’ bioactive proteins, straw pretreatment, and mycelium assessment. In order to do that, the main article was developed to elucidate current knowledge gaps and further identify research applications for the genus Pleurotus in biotechnology.

RESULTS

Taxonomic identification of Pleurotus spp.

The “life story” of Pleurotus spp. is an excellent example of the domestication of a common fungal saprotrophs from forest ecosystems (Pathak, Joshi & Dwivedi, 2009), (Vilgalys & Sun, 1994). Pleurotus spp. belong to the family Pleurotaceae, which contains six genera with a total of 94 species (Hawksworth et al., 1996). The genus Pleurotus contains 30 species and subspecific taxa of Pleurotus ostreatus (Venturella, Gargano & Compagno, 2015). Some species, such as Pleurotus cystidiosus or Pleurotus dryinus, have been shown to undergo the asexual sporulation during their life cycle, which is uncommon for Pleurotaceae. Therefore, industrial cultivation of such species is considered insufficient (Shnyreva et al., 2017).

Pleurotus mushrooms have enormous potential for the biotechnological degradation of lignocellulosic materials and some organic pollutants (Sánchez, 2010). The most notable feature is an ability to selectively biodegrade lignin by exposes celluloses and hemicelluloses (Kerem, Friesem & Hadar, 1992; Elisashvili et al., 2008; Bánfia et al., 2015). In contrast, many species of the genus Pleurotus have been reported to participate in numerous interactions with microorganisms, plants, or animals (Tsuneda & Thorn, 2011). For example, Pleurotus eryngii can live as a saprobe and a parasite on the roots of umbelliferous plants, for example, family Apiaceae (Hilber, 1982). In the past, fungal population growth on host-plant roots or the lower parts of stems, separately or in small groups arising from the same location, has been complicated by the simultaneous identification of several taxa, leading to ambiguity of the obtained data and challenging interpretations. In the last century, the determination of fungal taxonomic status has been based mainly on the characterization of morphological features.

Pleurotus fruitbodies are identified based on their unique morphological characteristics, such as the shape, color, and size of the hymenophore. However, this strategy can sometimes lead to inaccurate taxonomic conclusions (Vilgalys et al., 1996), (Choi, Ding & Cha, 2007). Hence, the importance of elucidating the Pleurotus taxonomy at the molecular level is evident. Cultivated fungal varieties can lose their genetic diversity through inbreeding events (Urbanelli et al., 2007), which may lead to the loss of valuable biotechnological properties in newly introduced hybrids that lack species-level identification markers. Thus, it is essential to identify Pleurotus cultivars during any period of hyphal development by applying DNA-based analyses of molecular markers, such as simple sequence repeats (Ma et al., 2009), random amplified polymorphic DNA (Yan & Jiang, 2005), and amplified fragment length polymorphism (Urbanelli et al., 2007), and sequence analyses of mitochondrial small subunit ribosomal ribonucleic acid (SSU rRNA) (Gonzalez & Labarère, 2000), cytochrome oxidase genes (cox) (Seifert et al., 2007; Nguyen & Seifert, 2008), and partial Elongation factor 1-alpha (ef1α) and RNA polymerase II (rpb2) genes (Estrada, Jimenez-Gasco & Royse, 2010). Additionally, the
fungal mitochondrial genome (mtDNA) is widely used not only for classification purposes, but also to reveal mitochondrial origination and horizontal gene transfer events (Seif et al., 2005; Seifert et al., 2007; Wang et al., 2008). Morphologically, fungi share typical characteristics, that is, the ability to produce asexual arthrospores on basidiomata or on vegetative mycelium (Zervakis, Moncalvo & Vilgalys, 2004). The original study of the sexuality of Pleurotus fungi was reported by Vandendries (1933). Additionally, a high percentage of polymorphic loci and an increased genetic distance in Pleurotus eryngii relative to other Pleurotus spp. were demonstrated by Zervakis, Sourdis & Balis (1994). Concurrently, the classification of Pleurotus spp. based on phylogenetic analyses of small mitochondrial subunit ribosomal (rns) genes has also been described in several reviews (Garber & Yoder, 1983; Gonzalez & Labarère, 2000). Furthermore, the phylogenetic relationships among closely related species of genus Pleurotus have been investigated through cladistics analysis using the V4 domain of mitochondrial rns (Bao, Aimi & Kitamoto, 2005). Also, the phylogeny of this genus was constructed by rRNA gene cluster analysis based on internal transcribed spacer sequences of rDNA. The phylogenetical tree was designed for 31 Pleurotus strains of different origin and 10 reference sequences from GenBank (Shnyreva & Shnyreva, 2015). A great example of using phylogenetic analyses for Pleurotus ostreatus species complex for the industrial purpose demonstrated on report of Li et al. (2017). Seven different oyster mushroom lineages were identified from a pool of 284 samples with different commercial names gathered from different mushroom spawn preservation centers, companies, and field isolations. For Li et al. (2017), the rpb2 gene is the most useful marker for Pleurotus ostreatus lineage identification among four promising barcode genes they used.

Clustering analysis was performed for two closely related species (17 strains) of Pleurotus ostreatus that show identical restriction polymorphism (RFLP) types. As reported by Wang et al. (2008), the complete mitochondrial genome has a circular shape and a size of 73,242 bp encompassing 44 known genes encoding 18 proteins and 26 RNA genes. According to the complete genome sequence of Pleurotus ostreatus, nine genes from the manganese peroxidase (MnP-) and VP-encoding (versatile peroxidase) gene family were identified to play significant roles in the degradation of some biopolymers like lignin (Salame et al., 2014). Investigation of the expression of certain MnP/VP genes identified the complex work for both of them in the ligninolytic system (Nakazawa et al., 2017). Additionally, mutation in chd1-1 gene and targeted disruption of wtr1 gene leads to the ability of Pleurotus ostreatus to biodegrade wood lignin. These genes are valuable for biotechnological use, such as the processing of agricultural waste.

Lignin degradation by Pleurotus spp.

Lignin is the second most abundant plant biopolymer in world ecosystems after cellulose. It is an aromatic polymer and one of the significant components of plant secondary cell walls, providing plant cells with rigidity, water impermeability, and resistance to microbial attack. The irregular chemical structure of this polymer imposes special restrictions on its ability to undergo biodegradation (Kirk & Farrell, 1987). In general, the worldwide lignocellulosic biomass of different kinds of crops is produced in large
amounts of approximately 73.9 Tg/year and leads to waste utilization problems (Kim & Dale, 2004). In contrast, the waste biomass has a high potential for further production of biotechnological products, such as bioethanol, biogas, and other useful chemicals. One of the main issues is the derivatisation of heterogeneous waste biopolymers, such as lignin, cellulose, and hemicellulose. To date, numerous reports have described different methods of lignocellulosic biomass pretreatment of agricultural wastes using physical, mechanical, and chemical mechanisms. Enzymatic systems from various microorganisms target lignin matrix decomposition and the release of other lignocellulose structure monomers, oligos, and polymers (Guerriero et al., 2016). Applications of white-rot fungi are the most popular because their pure cultures can mineralize lignin fibers from a substrate into CO₂ and water (Hatakka, 1983; Hatakka & Hammel, 2011; Isroi et al., 2011). However, lignin is not a target source of energy or a substrate of primary metabolism for white-rot fungi. The decomposition of lignin is aimed at the gain of cellulose and hemicellulose, which are energy-rich substances (Bazanella et al., 2013). Fungal biodegradation of lignin mostly is a result of the oxidation process with peroxidase and laccase. Peroxidase isoenzymes are present in almost all living organisms and catalyze many different important for life reactions. This kind of ferments is also applying for industrial purpose. Recently was identified novel VP from the fruiting bodies of Pleurotus pulmonarius that differs those of mushroom peroxidases (Zou, Wang & Zhang, 2018). The difference of peroxidases from liquid cultures of Pleurotus eryngii was confirmed by comparison for N-terminal sequence and peptide mapping analysis. According to the description, this novel enzyme has a high potential for future application in treatment and utilization of agricultural wastes.

White-rot fungi can quickly and non-specifically degrade lignin polymers in woody tissues (Eriksson, Blanchette & Ander, 1990; Camarero et al., 1999; Wesenberg, Kyriaides & Agathos, 2003). Pleurotus species produce MnP and VP enzymes that provide high adaptability for growth and fruiting for a wide variety of agricultural and industrial types of lignocellulosic disposal (Mikiašvili et al., 2006; Fernández-Fueyo et al., 2014). However, successful enzymatic activity and lignin degradation depend on many factors, such as the fungal strain, nutrient composition of the substrate, moisture content, and pH, among others (Snajdr & Baldrian, 2007). A recent investigation of the lignin-degrading capacity for five white-rot fungi, Phanerochaete chrysosporium, Pleurotus ostreatus, Lentinus edodes, Trametes versicolor, and S22 was reported (Wu, Xiao & Yu, 2005). According to the authors, mushrooms were individually used to treat black liquor from a pulp and paper mill. Among all five species, over 71% of lignin and 48% of chemical oxygen demand were removed from the wastewater. Another report described the utility of paper mill as a lignocellulose-based substrate for Pleurotus cultivation and shown the strong dependence between mushroom’s growth and medium composition (Skočaj et al., 2018). The highest peroxidases specific activities were detected at days 34 and 40 of the incubation period. During the fermentation, extracellular enzymes with different activities were extracted. They were determined to four groups: cellulase, xylanase, lipase, and peroxidase. The authors demonstrated the capacity of solid wastes as a good substrate for the production of commercially
interesting enzymes. Moreover, with the strong of worldwide paper waste and the minimization of lignocellulosic volume toward decreasing the ecological pressure, this strategy of *Pleurotus* application is very promising.

*Myronycheva et al. (2017)* has shown that temperature sensitivity, vegetative growth, and the generative response are factors affecting the successful cultivation of several oyster mushroom strains grown under conditions typical of European climate zones, indoors on agricultural waste. According to that report, some *Pleurotus ostreatus* strains exhibited differences in response to variations in climatic and substrate conditions. Hence, flexibility in both vegetative growth and fruit body formation suggests a high potential of the presented *Pleurotus* strains for commercial purposes. Required fungal features can be enhanced through alterations of external and inner conditions.

**Manganese peroxidase**

An important factor affecting biodegradation processes is the presence of metals in the substrate. One report (*Baldrian et al., 2005*) determined the possible effects of some heavy metal ions on the process of wheat straw degradation by *Pleurotus ostreatus*. Moreover, one of the main toxic elements spread into the environment is cadmium because it inhibits many of natural processes (*Bellettini et al., in press*). During biodegradation on the wheat straw substrate, *Pleurotus ostreatus* produces enzymes, such as endo-1,4-β-glucanase, exo-1,4-β glucanase, 1,4-β-glucosidase, endo-1,4-β-xylanase, 1,4-β-xylosidase, endo-1,4-β-mannanase, and 1,4-β-mannosidase, as well as the ligninolytic enzymes MnP and laccase. Additionally, the effect of copper and cadmium with further increases in laccase activity in liquid cultures of *Pleurotus ostreatus* has been described (*Palmieri et al., 2000*). The authors observed a loss of dry mass and reduced rate of extractable phenolic compounds in the presence of Mn, and low hydrogen peroxide concentrations indicated higher consumption of MnP during the catalytic cycle.

Due to the ability of *Pleurotus* species to produce one or several lignin-degrading enzymes, they are efficient in breaking down synthetic dyes. Manganese peroxidase (MnP, EC 1.11.13) can oxidise natural substrates with subsequent depolymerisation of lignin or recalcitrant xenobiotics to produce aromatic radicals (*Van Aken et al., 1999; Camarero et al., 2000*), as well as phenols and other small redox potential compounds (*Hildén et al., 2005*). One study (*Sarkar, Martínez & Martínez, 1997*) described the catalytic properties of MnP isoenzymes extracted from *Pleurotus ostreatus* growing in a liquid medium with peptone. The authors also emphasised the significance of the medium composition because the N-terminal sequence of the *Pleurotus ostreatus* isoenzyme differed from their previously published sequence of MnP extracted from these fungi growing in liquid medium with ammonium tartrate (*Martínez et al., 1996*). Additionally, MnP extracted from *Pleurotus ostreatus* had the same pl (3.75) and N-terminal sequence as MnP1 isolated from *Pleurotus eryngii*.

In addition to the ability to interact with Mn2+ as an ion donor, some MnPs also oxidise phenolic and non-phenolic aromatic compounds (e.g., veratryl alcohol) under certain conditions (*Hofrichter, 2002*). This kind of enzymatic property has been described...
for *Pleurotus eryngii* and a few other white-rot fungi (Böckle et al., 1999). In another review (Giardina et al., 2000), the production of two different MnP isoenzymes—MnP2 and MnP3—by *Pleurotus ostreatus* was examined during the growth cycle on wood sawdust as the solid substrate. Moreover, oyster mushroom growth has been shown to be accelerated on fir sawdust compared with poplar, but with reduced production of MnP. MnP can also be involved in the degradation of bisphenol A (2,2-bis(4-hydroxyphenyl)propane, BPA), an endocrine-disrupting chemical produced by *Pleurotus ostreatus* (Hirano et al., 2000). Over 12 days of mycelial growth, a BPA content of 80% was reduced by MnP. Bisphenol A is metabolised to phenol, 4-isopropenylphenol, 4-isopropylphenol, and hexestrol. Enhanced expression of fungal MnP as an efficient degrader of lignin and different pollutants represents an attractive tool either for bioconversion or waste utilisation (Irie et al., 2001). The recombinant MnP isozyme MnP3 in *Pleurotus ostreatus* was expressed using a DNA-mediated transformation system consisting of a molecular breeding approach. The transformation of oyster mushroom was performed using the PEG/CaCl<sub>2</sub> method (Honda et al., 2000). An MnP-overproducer was isolated from *Pleurotus ostreatus* transformants containing recombinant mnp3 constructs under the control of *sdil* expression signals with a carboxin-resistant vector plasmid pTM1. The transformed fungi showed several times higher levels of MnP activity than the wild-type control strain during the early stage of liquid culture.

**Laccase**

Another type of ligninolytic enzyme produced by *Pleurotus* spp. is represented by the laccases (benzenediol: oxygen oxidoreductases, Lac, EC 1.10.3.2)—copper-containing oxidases that act on phenolic substrates by catalyzing the oxidation their phenolic hydroxyl groups to phenoxy radicals while dioxygen (O<sub>2</sub>) is reduced to water (Bourbonnais et al., 1995; Wong, 2009; Christopher, Yao & Ji, 2014). Laccases are broadly functional enzymes involved in lignin biosynthesis, the process of pigment formation during fungal sporulation, plant pathogenesis, iron metabolism, and kernel-browning processes in plants (Hoopes & Dean, 2004; Higuchi, 2004). Moreover, laccase, as a glycoprotein enzyme that is expressed by white-rot fungi and participates in the carbon cycle, together with other ligninolytic fungal enzymes, can degrade lignin, which is one of the principal components of wood (Leonowicz et al., 2001; Widsten & Kandelbauer, 2008).

Genes for this enzyme have been identified in both ascomycetes and basidiomycetes. Comparison of laccase gene sequences from different fungi has revealed a high degree of identity among them (Thurston, 1994; Soden & Dobson, 2001). The strong oxidative capabilities attract researchers’ attention for these enzymes. The biotechnological potential of those enzymes has thoroughly studied for more than 20 years. A wide range of recent articles described progress in laccase engineering with further application perspectives for numerous issues. Thus, through site-directed mutagenesis, a mutant of *Pleurotus ostreatus* strain was obtained with the most thermostable enzyme among all laccases produced by other known *Pleurotus ostreatus* strains (Autore et al., 2009).

The substrate composition, as a source of carbon and organic nitrogen, plays a vital role in laccase production. Thus, during the cultivation of *Pleurotus sajor-caju* strain PS-2001 in
liquid culture with fructose or glucose as carbon sources, the enzymatic activity was found to be 37 and 36 U·mL$^{-1}$, respectively (Bettin et al., 2009). Furthermore, because of the absence of results with respect to the production of phenoloxidases by Pleurotus in medium containing a low-cost nitrogen source, authors studied the application of casein. Pure casein as a source of organic nitrogen was the most appropriate compound hence, during the cultivation of fungi in medium with sucrose and casein, laccase at 13 U·mL$^{-1}$ was obtained.

Additionally, the presence of silicon-based antifoam and/or Tween 80 at low concentrations had no significant influence on enzyme formation.

On another report, the increasing of Pleurotus ostreatus CP-50 fungal culture growth was related to the influence of the carbon and nitrogen sources in the medium (Tinoco et al., 2011). Implementation of additional carbon and nitrogen amount in malt growth medium showed the decreasing of specific laccase production (U/mg biomass). However, fungal culture growth and laccase volumetric activity were increased in four and six times. It could be explained that the sugars are efficient and fast utilized by fungi substrate that induce the laccase activity for biomass production. Extracellular laccase production and laccase isozyme regulation in Pleurotus sajor-caju studied via modification of physiological conditions, (Soden & Dobson, 2001). The authors identified four unique laccase isozyme genes that showed a high degree of similarity to laccases from other basidiomycetes and average identities with ascomycete laccases (24–62%). The results indicated that Pleurotus sajor-caju laccase isozyme genes differentially regulated at the transcriptional level in response to metals such as copper, manganese, and nutrient nitrogen, among others. As an example, the great laccase producing was found on copper sulphate induced solid-state fermentation medium for Pleurotus ostreatus PH-1 (Patel et al., 2014). The presence of copper was detected as a central ion in the presence of iron, zinc, and copper laccase purification. Also, it has been shown the increasing of laccase and isoenzymes synthesis in the presence of copper (Baldrian & Gabriel, 2002) in another report, the same Pleurotus sajor-caju strain PS2001 was examined for dye-decolorizing ability and polyphenol degradation in liquid culture (Munari, Aparecida Gaio & Dillon, 2009). Pulp and paper mill, as residues of paper manufacturing, were used as substrates with high lignin levels, endowing the effluents with a specific brownish color. The fungal capacity for residue degradation of 90% of the raw effluents from the medium oxygen delignification and bleaching stages were used in the study. The addition to the substrate up to 10% of the mineral solution and different levels of glucose as substrate gives higher yield. The liquid culture of Pleurotus sajor-caju effectively reduced the levels of total polyphenols and amounts of dye in residues from the paper industry. Effluent degradation was obtained in the presence of ligninolytic enzymes such as laccases and peroxidases, but the authors did not detect enzymatic content production by the fungus (Munari, Aparecida Gaio & Dillon, 2009). However, the study of Stajić et al. (2006) clearly demonstrated that laccase and peroxidases production depends on the species and strains of the genus Pleurotus, conditions of cultivation, and carbon sources as well as nitrogen sources and concentrations.

In general, laccases catalyse the oxidation of a range of aromatic compounds, such as acrylamines, aminophenols, or diphenols. Report by Munari et al. (2008)
demonstrated the ability of *Pleurotus sajor-caju* PS2001 to undergo dye decolourisation, which shown for nine anthraquinone-type industrial textile dyes using the agar plate method to achieve a final dye concentration of 100 mg L\(^{-1}\). Additionally, the mushrooms were cultivated under conditions of solid-state fermentation as well as liquid culture separately. The solid-state cultivation substrate contained pine sawdust and wheat bran to obtain the enzymatic extract. Enzymatic extracts from solid-state cultures were used to determine laccase and manganese-peroxidase activities and further test their capacity to degrade the textile dyes. Hence, the *Pleurotus sajor-caju* PS2001 strain was shown to have the potential for use in the degradation of textile dyes in residue manufacturing.

The ability of laccase to degrade some polyaromatic hydrocarbons (PAHs) produced by blue laccase from *Pleurotus ostreatus* D1 (BLPO) in the presence of conventional synthetic mediators has been described by Pozdnyakova et al. (2006). To study PAH-degrading compounds containing three to five aromatic rings in the presence of mediators such as ABTS (2,2-azino-bis-(3-ethylbenzthiazoline-6-sulphonic acid) diammonium salt), syringaldazine (4-hydroxy-3,5-dimethoxybenzaldehyde azine), 2,6-dimethoxyphenol, and catechol were used. According to the results, ABTS was a better mediator of anthracene oxidation by BLPO and HBT (1-hydroxybenzotriazole) and a better mediator of fluorene oxidation. Concurrently, pyrene and anthracene were degraded more rapidly in a mixture than separately. Thus, the degradation ability of BLPO depends on the structure of the PAH molecule, type of organic solvent, presence and type of detergent, enzyme concentration, and duration of the reaction.

**Versatile peroxidase**

Another type of ligninolytic peroxidase called versatile peroxidase (VP, EC 1.11.1.16) is found in some *Pleurotus* and *Bjerkandera* species (Camarero et al., 1996, 1999; Martínez et al., 1996; Mester & Field, 1998; Moreira et al., 2005) and exhibits activity on aromatic substrates. VP oxidises Mn2+, as MnPs, phenolic and non-phenolic substrates that are typical for LiPs, related peroxidases (e.g., horseradish peroxidase), and generic peroxidases (low redox-potential peroxidases of plant and fungal origin). The structure of VP enzymes is closer to LiP than to MnP isozymes. Moreover, VP can directly oxidise high-redox potential compounds like some industrial dyes, while LiP shows catalytic activity only in the presence of redox mediators. According to the study by Morales et al. (2012), two catalytic sites are responsible for low-redox potential dyes and phenol oxidation. High-redox potential substrate oxidation by VP occurs because VP site Trp-164, as well as a low-efficiency site involved in the oxidation of the same phenols, is localized at the entrance of the heme-distal pocket of the VP molecule. However, a natural oxidizing substrate, H\(_2\)O\(_2\), leads to reduced stability of the VP molecule and prevents the broad use of the enzyme in industrial and environmental applications (Martínez et al., 2009). Thus, Sáez-Jiménez et al. (2015) studied different ways to improve VP stability in the presence of H\(_2\)O\(_2\). Primary results were gained by substitution using site-directed mutagenesis of amino acid residues located at specific positions near the heme group affecting the formation, stabilization, and decomposition of Compound III.
Hence, the development of a modified biomolecule made this enzyme an attractive industrial tool for further improvement of the molecular structure in response to changes in temperature and an alkaline pH (Garcia-Ruiz et al., 2012).

Tetraterpenoid compounds, which are derived differently from carotenoids, are synthesized for biotechnological application and have attracted increasing interest in the fragrance industry. A new approach to the introduction of a secreted wild-type VP in submerged cultures of *P. sapidus* for β-carotene degradation proposed by Schüttmann et al. (2014). As nitrogen and carbon sources, residues from biogas plants used.

The enzyme was purified and characterized biochemically with further cloning of the encoded cDNA due to the heterologous expression of VP in yeast *Hansenula polymorpha*. According to bioinformatics analyses of VP sequences, an open reading frame of 1,083 bp found with 90% similarity to VPs from *Pleurotus eryngii*. A heterologous enzyme successfully produced with an activity of 450 ± 20 mU mg⁻¹ by culturing *H. polymorpha*.

Solid-state cultures of *P. eringii* on the banana peel/skin and other lignocellulose residues such as growth medium were used to evaluate the feasibility of agricultural residue remediation by VP (Palma et al., 2016). Glucose-based liquid medium for comparison of the catalytic parameters of the produced enzyme has used as a conventional source of VP production. The enzymatic activity of VP generated by solid-state culture was detected after 18 days of cultivation and determined to be 10,800 U L⁻¹ (36 U g⁻¹ of the substrate), whereas the enzymatic activity of VP from liquid culture was only 1,800 U L⁻¹. The obtained results included the H₂O₂ inhibitory effect and were observed for the enzymes produced in both media. However, the reaction rates for VP synthesized by solid-state cultures showed a reduced impact. VPs were also successfully applied for the degradation of different dyes, both with low-redox and high-redox potential, as a powerful tool in bio-decolourisation. Thus, the ability to decolourise different azo dyes has been shown for VPs isolated from *Pleurotus eryngii* and *Bjerkandera adusta* (Camarero et al., 1999). One report (Pozdnyakova et al., 2015) compared the catalytic properties of VPs produced by *Pleurotus ostreatus* strain D1 and *Bjerkandera fumosa* strain 137. The decolourisation activities of both enzymes were tested on a wide range of dyes containing condensed aromatic rings, such as anthraquinone and anthracene dyes. Both peroxidases rapidly decolourized the anthraquinone dyes with subsequent formation of polymerisation reaction products. In contrast, anthracene-type dyes were degraded very slowly by both tested enzymes. Hence, the differences between dye structures significantly affected the manner of decolourisation, probably due to the different electron distribution, charge densities, or steric factors. In the case of overexpression of the VP, MnP2 may lead to improved enzymatic properties. Thus, enhanced productivity of VP MnP2 was gained by using DNA-transformation technology consisting of a molecular breeding approach for isolated *Pleurotus ostreatus* strains (Tsukihara et al., 2006). The recombinant plasmid was introduced into wild-type oyster mushroom using the PEG/CaCl₂ method, and recombinant strains overexpressing VP MnP successfully obtained. Screening of the obtained recombinants was conducted in the presence of Poly R-478 due to the decolourisation of dye on agar plates in the absence of Mn2+. Additionally, benzo(a)pyrene-removing activity by treatment with recombinant fungal strains...
also analyzed. According to this report and numerous other relevant studies, VP enzymes are highly attractive industrial tools due to their ability to oxidise different substrates under altered environmental conditions (Knop et al., 2016). However, along with the presence of multiple active sites exhibiting a wide range of VP activities, the potential of the enzymes depends on a variety of factors.

**Waste biodegradation**

In the past, mushrooms had not received much attention as a powerful biotechnological tool due to the relatively long duration of biomass pretreatment as well as substantial losses of cellulose and hemicellulose contents during processing (Balan et al., 2008). Despite these deficiencies and after meticulous assessments of fungal enzymatic systems, which have described in many reports, the total duration of biotechnological processes has become much shorter, and sugar loss can be minimized through the use of white rot fungi. Here, *Pleurotus* spp. produced a range of enzymes that are required in biotechnological processes and provide successful applications of fungi for the biodegradation of cellulose-containing substrates: cotton stalks, sugarcane fiber, wheat, or rice straw, among others. This tremendous biotechnological potential was found for the cultivation of the genus *Pleurotus* without requiring the presence of a composting or casing layer and without grinding the substrate and mixing it with water. The substrates used in each region usually depend on locally available agricultural wastes. Since *Pleurotus* spp. can efficiently decompose lignocellulose without chemical or minimal biological pretreatment, a large variety of lignocellulosic wastes can be utilized and recycled (Cohen, Persky & Hadar, 2002).

The preparation of *Pleurotus* substrate from shredded wheat straw has become a routine practice. Wheat straw is the most abundant agricultural residual in the territory of Europe and the second after rice straw on a global scale (Kim & Dale, 2004). In earlier reports (Müller & Trösch, 1986), a range of different basidiomycetes, mostly white-rot fungi, have been studied and tested to identify species that are capable of efficient biogas (methane) production. Hence, Müller and Trösh studied 22 different fungal species grown on wheat straw. Among them, *Pleurotus florianus* showed more rapid delignification of straw waste. The methane yield was twofold higher than the total amount of straw without pretreatment and huge effect on digestibility of pretreated by fungi biomass has a microbial consortia in the process (Zhong et al., 2011). In the next study of biogas production (Vasmara et al., 2015; Marchetti, Vasmara & Florio, 2016), lignolytic white-rot fungi and cellulolytic or xylanolytic fungi were compared regarding biogas production. Pretreated wheat straw with or without pig slurry during the co-digestion process was used as a substrate. The authors reported a maximum gas production with shorter reaction time for co-digestion compared with fermentation during monoculture digestion. It was shown that the efficiency of pig slurry utilization as a hydration medium for anaerobic digestion can be used for higher bioethanol production.

The efficiency of wheat straw polymer decomposition by *Pleurotus* spp. has been reported with use of commercial cellulose as a standard to compare the release of glucose monomers from untreated straw with that from straw pretreated with *Pleurotus* solid-state
fermentation. In that study, lignin content decreased by 51% during the incubation period (90 days) (Kempken, 2013). Also, sugarcane is an excellent substrate for the cultivation of *Pleurotus* species. To date, great attention has focused on this plant as an efficient source of raw material for bioethanol production. The lignocellulosic matrix of sugarcane contains mainly cellulose and hemicellulose as polysaccharides that are suitable for hydrolysis for further production of ethanol and other chemicals. Camassola & Dillon (2009) reported the use of *Pleurotus sajor-caju* PS 2001 in the pretreatment of sugarcane bagasse. The obtained biomass subsequently utilized in the production of cellulases and xylanases by *Penicillium echinulatum*.

Cotton is another biotechnological crop that is distributed worldwide and generates a significant amount of local agricultural waste. Cotton stalks as a substrate have successfully utilized for commercial *Pleurotus* cultivation (Silanikove, Danai & Levanon, 1988). Thus, in the studies of *Pleurotus* growth (Hadar et al., 1992) used cotton stalks because of their fibrous structure, which is similar to hardwood and creates challenges for agrotechnical utilization. During 4 weeks of solid-state fermentation, they detected a significant decrease in lignin content and increased in digestibility in vitro. Ruminants consumed the fermented product at a level of up to 40% of their diet. In another report (Huttermann et al., 2000) described the process for the recycling of agricultural wastes by *Pleurotus* spp., which included the pasteurization of wet straw by solar heat, treatment of wet straw with detergents, and amendment of straw with wastes from the food industry, such as potato pulp and tomato pomace. The methods were suitable for farming applications with low energy consumption. In vitro and in vivo studies reported that the biological treatment with *Pleurotus* species improves the digestibility of roughage for animals because of enzymatic modification effect on cellulose and lignin. In feeding experiments, rams fed with fungus-treated straw exhibited an increase in body weight. The nutritive value of agricultural residues, such as rice straw or corn stalk, was improved by the fungal treatment.

In comparison to chemical approaches like acid hydrolysis, the application of fungal hydrolytic systems is one of the most fruitful and conventional methods in waste utilization technology (Galbe & Zacchi, 2007). Combined technology, in general, includes four steps: pretreatment waste mass for the preparation of cellulose for further enzymatic hydrolysis; enzyme production; enzymatic saccharification of the pretreated waste mass to fermentable sugars; fungal or chemical conversion of the obtained sugars to the final product (e.g., biofuel) (Tian, Fang & Guo, 2012). Rice straw is another agricultural crop that is a vital source of lignocellulose biomass. One report (Balan et al., 2008) described the treatment of rice straw with *Pleurotus ostreatus*, followed by ammonia fibre expansion (AFEX). This pretreatment led to significantly elevated levels of glucan and xylan conversion under less severe AFEX conditions compared with the treatment of rice straw waste directly with AFEX. The main component of rice straw is cellulose, which can be hydrolyzed into glucose with further conversion into bioethanol or biogas.

Mustafa, Poulsen & Sheng (2016) recently described a new approach to methane production by comparing two groups of fungi, ascomycetes (*Trichoderma reesei*) and basidiomycetes (*Pleurotus ostreatus*), to improve the biological degradability of rice straw.
waste and increase methane production via solid-state anaerobic digestion. During the pretreatment period, *Pleurotus ostreatus* caused significant degradation of the lignin component of straw waste. Simultaneously, this fungus had a limited effect on cellulose degradation. However, by comparison, the application of *Trichoderma reesei* provided better results for lignin and hemicellulose removal. Hence, lignin degradation by *Pleurotus ostreatus* was 33.4% with selectivity (lignin/cellulose removal ratio), resulting in a 120% increase in methane yield compared with untreated rice straw. After applying *Trichoderma reesei*, 23.6% lignin removal and a 78.3% increase in methane yield achieved.

Utilization of food residues is a dominant issue for global foodstuff consumption and has great potential for biotechnological retreatment processes. Banana mostly consumed fruits in India and one of the largest commodities worldwide. This crop generates the potential mass of available agricultural waste ([Centre for Monitoring Indian Economy (CMIE), 2001](https://www.cmie.org)), and banana residuals mainly consist of lignocellulose material suitable for the growth of white-rot fungi. Two species, *Pleurotus ostreatus* and *Pleurotus sajor-caju*, were used for the bioconversion of the banana leaf and pseudostem biomass to investigate their ability to produce ligninolytic and cellulolytic enzymes for solid-substrate fermentation ([Reddy et al., 2003](http://www.ncbi.nlm.nih.gov/pubmed/12777654)). Both *Pleurotus* species showed similar levels of enzymatic activities and patterns of production. However, deficient concentrations of cellulolytic enzymatic activities observed during the process. The authors also demonstrated the dynamics of extracellular protein formation produced by both fungi during biomass degradation over a 40-day period. Another *Pleurotus* species, the white-rot fungus *Pleurotus dryinus* IBB 903 isolated and identified in Georgia, has also displayed high activities of all studied lignocellulolytic enzymes. This strain can also produce a range of enzymes for the submerged fermentation of mandarin peels and tree leaves ([Elisashvili et al., 2006](http://www.ncbi.nlm.nih.gov/pubmed/16817985)).

**Organopolutant biodegradation**

Bioremediation is the process of the biological conversion of hazardous wastes to harmless compounds, or to levels that are below dangerous level. Thus, *Pleurotus ostreatus* has been found to degrade and mineralize xenobiotic compounds, such as PAHs, industrial dyes, and other soil pollutants, as described below ([Cohen, Persky & Hadar, 2002](http://www.ncbi.nlm.nih.gov/pubmed/11487668)). PAH substances have potent carcinogenic features and may be metabolized to bay-region diol epoxides, which are their ultimate carcinogenic forms. Unfortunately, currently encountered PAHs are common environmental pollutants that are strongly suspected of functioning as carcinogens to humans and the natural ecosystem ([Rummel et al., 1999](http://www.ncbi.nlm.nih.gov/pubmed/9953378)). Current studies include investigations of the biochemical mechanisms responsible for the degradation of these xenobiotics by different organisms and the enzymatic systems involved in these processes. White-rot fungi are a priority of most research interests for this purpose. Since the discovery that lignin is a natural polyaromatic compound that is degraded by ligninolytic extracellular oxidative enzymes from white-rot fungi, it is logical to hypothesise that these fungi can degrade PAHs using the same enzyme. Ligninolytic enzymes may reduce biotoxicity to the fungi and presumably also increase the availability of PAHs to facilitate degradation processes. During degradation, fungi can
metabolize the initial PAH by cleaving the aromatic ring to form ring fission compounds with subsequent mineralization (Hammel et al., 1992; Nikiforova, Pozdnyakova & Turkovskaya, 2009). Prominent findings for the elimination of PAHs and other pollutants have shown in numerous studies targeting the genus Pleurotus for the biodegradation of PAHs. For example, Bezalel et al. (1996) have demonstrated the ability of Pleurotus ostreatus to degrade pollutants such as pyrene, anthracene, fluorene, and dibenzothiophene. According to their results, metabolites from pyrene, dibenzothiophene, anthracene, and fluorene amount from 45% up to 96% of the total organic-solvent-extractable metabolites, respectively. As a result, the authors concluded that the white-rot fungus Pleurotus ostreatus initially metabolises polycyclic aromatic hydrocarbons via the reactions. However, in contrast to non-ligninolytic fungi, Pleurotus ostreatus can mineralize these polycyclic aromatic hydrocarbons.

Adenipekun et al. (2015) studied the degradation of PAHs in spent and fresh cutting fluids (SCF and FCF) from contaminated soils and demonstrated that Pleurotus ostreatus degraded almost all of the PAH fraction to a greater extent than naphthalene in the fresh cutting fluid-contaminated soil. The degradation of PAHs in liquid cultures of some rot fungi, including Pleurotus ostreatus, has been studied by Schützendübel’s et al. (1999) group. During 7 weeks of mushroom cultivation, all PAHs uniformly removed, and fluorene, as well as anthracene, degraded more rapidly than other PAHs. Another chemical pollutant, chrysene, and its bioconversion by Pleurotus ostreatus D1 by cultivation conditions have been described by Nikiforova et al. (2010).

Recent studies of pollutant biodegradation have demonstrated a high potential capacity for the adsorption of PAH-contaminated water by cork waste (Jové et al., 2016). Following the PAH-adsorption process from water, the remaining cork waste should be treated and utilized. Thereby, according to the ability of some mushrooms to degrade PAHs, a new technology of contaminated cork utilization by some filamentous fungi, including Pleurotus ostreatus, was developed. In another report, Hadibarata & Teh (2014) Pleurotus pulmonarius strain F043 from tropical rainforest was used to degrade pyrene, a four-ring PAH in mineral medium broth. The maximum degradation level (90%) detected at pH 3, and the lowest level of PAH degradation (2%) observed at pH 10. Also, the degradation of pyrene increased from 2% to 96% when the temperature increased from 4 to 25 °C.

Descriptions of the biodegradation pathways of various PAHs have been provided by Cerniglia & Sutherland (2001), who examined the enzymatic mechanisms involved in the degradation of PAHs. Phase I and phase II enzymatic activities found in cell extracts of Pleurotus ostreatus. Cytochrome P-450 monooxygenase and epoxide hydrolase were found to oxidise and further hydrate phenanthrene. The involved enzymes are responsible for the initial attack of the aromatic ring in Pleurotus ostreatus, which leads to the mineralization of organic pollutants. An ortho-ring-cleavage activity of protocatechuate 3,4-dioxygenase was detected in the cytosolic fraction of Pleurotus ostreatus cell-free extracts and considered be responsible for the cleavage of the aromatic ring (Bezalel, Hadar & Cerniglia, 1997). Pleurotus ostreatus has an unusual combination of enzymes that catalyze the metabolism and degradation of PAHs through an initial oxidation mechanism.
similar to non-ligninolytic fungi and further activities of ring cleavage and mineralization similar to ligninolytic fungi. However, laccases of other white-rot fungi may also be involved in PAH oxidation via the mediation of laccase substrates (Johannes & Majcherczyk, 2000). In a study conducted using nutrient-rich liquid medium, the fungi exhibited potential in the decontamination of PAH-polluted soils (Eggen, 1999; Baldrian et al., 2000).

Another group of environmental pollutants is heavy metals from soil, water and different residues. Global ecosystem contamination with metals mostly is a result of progressing anthropogenic activity. Thereby, using mushrooms for mycoremediation of such kind pollutants gives a chance to decrease the anthropogenic pressure onto the environment through the natural sequestration process. Mycoremediation strategies provide suitable and eco-friendly solutions such as complete mineralization of the contaminants (Perelo, 2010). Among others, Pleurotus species can take out heavy metals from soil, such as Cu, Zn, Mn, and Fe, as it described on report (Boamponsem et al., 2013). In another work described the utilization of waste newspaper using a mycelium with Pleurotus ostreatus (Kopiński & Kwiatkowska-Marks, 2012). Newspaper waste and wheat straw mixture were composed for growing substrate. The maximum utilization was observed in the 3:1 mix of waste newspaper and wheat straw, according to the report. Presence of heavy metals in a substrate, such as Pb, also can effect on the mycelia growth and fruiting body production (Dulay et al., 2015). After examining five Pleurotus strains, decreasing of lowest mycelial growth was identified. Mercuri also has a negative influence on growth and fruit body production, as it has described for Pleurotus tuber-regium (Akpaja, Nwogu & Odibo, 2012). In general, mycoremediation baes on biosorption potential of different species. Pleurotus species tend to be a promising candidate as a biosorbent for heavy metals. According to the number of reports, a degree of tolerance varies among Pleurotus species for different heavy metals (Kapahi & Sachdeva, 2017).

CONCLUSIONS

In this review, we have described research concerning the advantages of Pleurotus in industrial applications, ranging from reports about lignin decomposition to straw waste and phenolic compound degradation, dye-decolourising ability, nutritional content values, and other investigations. All the studies suggest the significant potential of the utility and profitability of Pleurotus spp. However, despite extensive research on its biotechnological applications (in agro-business, pollutant biodegradation, and life sciences), a large portion of the biochemical pathways that make the genus Pleurotus an attractive biological target for future research purposes remain undescribed.

Additionally, various highly effective methods for studying fungal genomic variability are applied using various systems of genetic transformation. The modification of genes through their transformation to create fungal mutant lines is an essential step in investigations of gene function and relationships (Poyedinok & Blume, 2018). Such strategies will facilitate analyses of fungal genetic classification and improve the biosynthetic activity of many biotechnologically important Pleurotus strains.
Here we address the economic feasibility of the technologies described above in large scale; only mushroom production could be considered as a successful implementation of agricultural residues biodegradation. In order to realize the full potential and use the circular economy approach, we need to mention the low technology readiness level of the potential of these technologies for biorefinery such as, for example, enzymatic decomposition of lignocellulose to valuable chemicals. Moreover, there are limited market opportunities that do not allow to estimate investment and manufacturing cost. The estimation of the potential of the spent mushroom substrate for biorefinery is only under technological development. In our other study related to shiitake cultivation, we developed an approach where the total mass balance was applied, and the potential for biorefinery was estimated (Xiong et al., 2019).

**ADDITIONAL INFORMATION AND DECLARATIONS**

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**Competing Interests**
The authors declare that they have no competing interests. Andrii P. Gryganskyi is employed by LF Lambert Spawn Co as researcher, molecular biologist.

**Author Contributions**
- Alona S. Sekan conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, approved the final draft.
- Olena S. Myronycheva conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, approved the final draft.
- Olov Karlsson contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper, approved the final draft.
Andrii P. Gryganskyi performed the experiments, analyzed the data, prepared figures and/or tables, approved the final draft. Yaroslav Blume contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper, approved the final draft.

Data Availability
The following information was supplied regarding data availability:

The research in this article did not generate any data or code. The sequence of analysis is included in the article.

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