Fungi from litter in Amazonian forest ecosystems and biocatalytic aspects in the biotransformation of residues: a review

Fungos do serapilheira de ecossistemas florestais amazônicos e aspectos biocatalíticos na biotransformação de resíduos: uma revisão

Hongos de la hojarasca de ecosistemas forestales amazónicos y aspectos biocatalíticos en la biotransformación de residuos: una revisión

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Iêda Alana Leite de Sousa
PhD Student in Biodiversity and Biotechnology of the Amazon
Institution: Universidade Federal do Pará (UFPA)
Address: Belém, Pará, Brazil
E-mail: ieda.sousa@icb.com.br

Alberdan Silva Santos
Doctor in Biochemistry
Institution: Universidade Federal do Pará (UFPA)
Address: Belém, Pará, Brazil
E-mail: alberdan@ufpa.br

ABSTRACT

Decomposition of Amazonian litter is driven by microorganisms, particularly fungi from the Basidiomycota and Ascomycota, which produce ligninolytic enzymes such as manganese peroxidases, lignin peroxidase, and laccase. These fungi exhibit remarkable capabilities in degrading agro-industrial waste and treating contaminated wastewater, offering a sustainable approach to pollution mitigation. Research has unveiled substantial fungal diversity, notably within the Chaetosphaeriaceae and Russulaceae families. Ligninolytic enzymes demonstrate adaptability and catalytic efficiency, enabling the breakdown of complex lignin bonds into simpler molecules. This process generates compounds, including phenolic acids, methyl gallate, and vanillin, which have significant applications in the food, cosmetics, and pharmaceutical industries. Utilization of agro-industrial waste as substrates for enzyme production not only reduces costs but also fosters sustainable technological solutions. Furthermore,

Amazonian fungi possess immense potential for biotechnological applications, facilitating the transformation of organic and synthetic waste into less toxic by-products. This approach enhances the accessibility and sustainability of these technologies. However, advancing the scalability, as well as the economic and environmental feasibility of these biotechnologies, remains crucial for their sustainable industrial adoption. This review underscores the pressing need for continued research focusing on these aspects to achieve environmentally effective and sustainable industrial applications. Consequently, fungi associated with Amazonian leaf litter emerge as highly promising biological resources, paving the way for innovations in biotechnology, improved waste management, and the production of high-value-added enzymes and products.

Keywords: Ligninolytic Fungi. Enzymes. Bioremediation. Laccase. Peroxidases.

RESUMO

A decomposição da serapilheira na Amazônia é conduzida por microrganismos, especialmente fungos de Basidiomycota e Ascomycota, que produzem enzimas ligninolíticas, como manganês peroxidases, lignina peroxidase e lacase. Esses fungos são capazes de degradar resíduos agroindustriais e úteis no tratamento de águas residuais contaminadas, oferecendo uma abordagem sustentável para a mitigação da poluição. As pesquisas revelaram uma diversidade substancial de fungos, principalmente nas famílias Chaetosphaeriaceae e Russulaceae. As enzimas ligninolíticas demonstram adaptabilidade e eficiência catalítica, permitindo a quebra de ligações complexas de lignina em moléculas mais simples. Esse processo gera compostos, incluindo ácidos fenólicos, galato de metila e vanilina, que têm aplicações significativas nos setores de alimentos, cosméticos e farmacêutico. A utilização de resíduos agroindustriais como substratos para a produção de enzimas não apenas reduz os custos, mas também promove soluções tecnológicas sustentáveis. Além disso, os fungos amazônicos possuem um imenso potencial para aplicações biotecnológicas, facilitando a transformação de resíduos orgânicos e sintéticos em subprodutos menos tóxicos. No entanto, o avanço da escalabilidade, bem como a viabilidade econômica e ambiental dessas biotecnologias, continua sendo crucial para sua adoção industrial sustentável. Esta revisão ressalta a necessidade premente de pesquisas contínuas com foco nesses aspectos para obter aplicações industriais ambientalmente eficazes e sustentáveis. Consequentemente, os fungos associados à serapilheira amazônica surgem como recursos biológicos altamente promissores, abrindo caminho para inovações em biotecnologia, melhor gerenciamento de resíduos e produção de enzimas e produtos de alto valor agregado.

Palavras-chave: Fungos Ligninolíticos. Enzimas. Biorremediação. Lacase. Peroxidases.

RESUMEN

La descomposición de la hojarasca amazónica corre a cargo de microorganismos, en particular hongos de los géneros Basidiomycota y Ascomycota, que producen enzimas ligninolíticas como el manganeso peroxidasa, la lignina

peroxidasa y la lacasa. Estos hongos exhiben notables capacidades para degradar residuos agroindustriales y tratar aguas residuales contaminadas, ofreciendo un enfoque sostenible a la mitigación de la contaminación. La investigación ha revelado una diversidad sustancial de hongos, sobre todo dentro de las familias Chaetosphaeriaceae y Russulaceae. Las enzimas ligninolíticas demuestran adaptabilidad y eficiencia catalítica, permitiendo la descomposición de enlaces complejos de lignina en moléculas más simples. Este proceso genera compuestos, como ácidos fenólicos, galato de metilo y vainillina, que tienen importantes aplicaciones en las industrias alimentaria, cosmética y farmacéutica. La utilización de residuos agroindustriales como sustratos para la producción de enzimas no sólo reduce costes, sino que también fomenta soluciones tecnológicas sostenibles. Además, los hongos amazónicos poseen un inmenso potencial para aplicaciones biotecnológicas, facilitando la transformación de residuos orgánicos y sintéticos en subproductos menos tóxicos. Este enfoque mejora la accesibilidad y la sostenibilidad de estas tecnologías. Sin embargo, el avance en la escalabilidad, así como en la viabilidad económica y medioambiental de estas biotecnologías, sigue siendo crucial para su adopción industrial sostenible. Esta revisión subraya la acuciante necesidad de seguir investigando estos aspectos para conseguir aplicaciones industriales sostenibles y eficaces desde el punto de vista medioambiental. En consecuencia, los hongos asociados a la hojarasca amazónica emergen como recursos biológicos muy prometedores, que allanan el camino para las innovaciones en biotecnología, la mejora de la gestión de residuos y la producción de enzimas y productos de alto valor añadido.

Palabras clave: Hongos Ligninolíticos. Enzimas. Biorremediación. Lacasa. Peroxidasas.

1 INTRODUCTION

In the litter decomposition process, various enzymes are produced by microorganisms, playing a critical role in the chemical transformation of the material. These include fungal enzymes such as laccase (Lac), lignin peroxidase (LiP) and manganese peroxidase (MnP). The production of these enzymes by fungi has been investigated in recent studies, demonstrating their potential in the biodegradation of waste, especially agro-industrial waste, which, like litter, is mainly composed of a lignocellulosic matrix (Shing *et al*., 2019; Diaz *et al*., 2022).

As an example of these investigations, an analysis of the biodegradation of black liquor, a waste product from the paper industry, by isolates of the fungi *Aspergillus uvarum* and *Phanerochaete chrysosporium* revealed that these fungi were able to significantly reduce the amount of this waste (Diaz *et al*., 2022).

Meanwhile, another study carried out with the aim of evaluating the degradation of corn straw showed that the synergistic use of the enzymes Lac, LiP and MnP broke the main chemical bonds of lignin, providing a theoretical basis for the biodegradation of this macromolecule (Zhang *et al*., 2022).

Another biotechnological application using fungi that produces ligninolytic enzymes is their potential for treating wastewater contaminated with industrial dyes. These enzymes are nonspecific in relation to the substrates and can degrade synthetic polymers, such as textile dyes (Ashan *et al*., 2021). The fungi that produce Lac, LiP and MnP are considered promising organisms for the bioremediation of dyes in wastewater (Saratale *et al*., 2020), and their biomass is used as an adsorbent and/or producer of extracellular enzymes responsible for the biodegradation of dyes (Herath *et al*., 2024).

Filamentous fungi isolated from leaf litter are a promising and renewable source to produce oxidative-reducing enzymes, such as lacases and peroxidases, with potential application in the biotransformation of synthetic and organic waste. The careful selection of strains is essential for the development of biotechnological processes aimed at making better use of these organisms and promoting the production of lignolytic enzymes on a large scale. This review sought to evaluate the diversity of fungi associated with litter from forest environments in the Amazon and the role of fungal species in the process of biodegradation of waste, highlighting the main enzymes involved and their catalytic mechanisms, as well as the possible value-added products generated in this process of enzymatic biotransformation of waste. It also addresses possible waste matrices that can act as substrates to produce these enzymes, offering a perspective on this conversion into possible new biotechnological products and a sustainable technological solution for biomass from industrial activity.

2 METHODOLOGY

For this scientific production, different academic publications from various recognized databases, including Scopus, Google Scholar, ACS, Scielo and Web of Science, were analyzed. The keywords used in the literature search were

fungal diversity, litter, Amazon rainforest, biotransformation, lignin, oxidizing enzymes, lacase, dyes, textile dyes, manganese peroxidase, lignin peroxidase, residues, degradation routes, phenolic compounds, antioxidants, anti-inflammatories and antimicrobials. The selection criteria for these studies were limited to fungi identified in litter material related to publications with a study area in the Amazon rainforest, in addition to reporting on the use of these fungi in the biodegradation of agro-industrial waste and studies related to the potential use in biological activities of the new molecules generated after biodegradation. Also, for data analysis of the diversity of fungi found in the published articles, the phylum, class and family of fungi identified in the litter material were corrected and confirmed according to the Mycobank Database (2024).

3 RESULTS AND DISCUSSIONS

3.1 DIVERSITY OF FUNGI IDENTIFIED IN LEAF LITTER IN THE AMAZON

Saprophytic fungi of the phyla Basidiomycota and Ascomycota are frequently identified in the substrate of leaf litter and decaying wood and are the main agents of lignocellulosic matrix degradation in nature (Canto *et al*., 2020). These fungi are classified into three groups: white rot, brown rot and soft rot fungi (Hakkinen *et al*., 2014). They are microorganisms known for producing extracellular ligninolytic enzymes released during the decomposition of organic matter, including manganese peroxidases (MnP), lignin peroxidase (LiP) and laccase (Lac), also known as phenol-oxidase (Jasnuz *et al*., 2017). These fungi play a fundamental role in the decomposition of organic matter, releasing essential nutrients for other plants and micro-organisms (Song *et al*., 2023). The use of these microorganisms in the biotransformation of waste can bring significant environmental benefits, such as reducing the amount of solid waste and producing compounds with high added value (Kuthiala *et al*, 2023).

In the litter of Amazon forest ecosystems that have already been studied, a high diversity of fungal species is observed, including representatives of taxa such as Ascomycota, Basidiomycota, Deuteromycota and Mucoromycota.

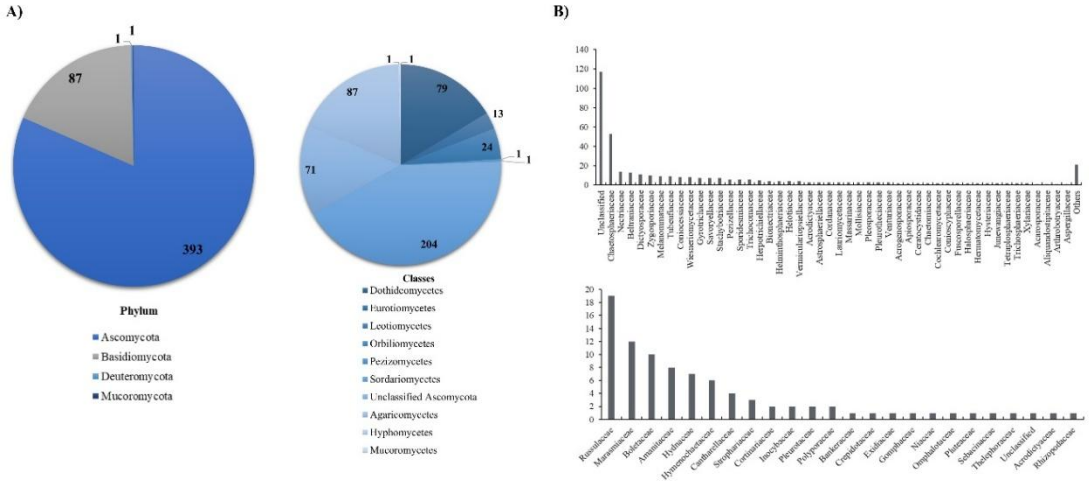
Studies related to the diversity of these fungi in forest environments in the Amazon have reported around 409 species to date. The phyla Ascomycota and Basidiomycota showed the highest abundances and richness of species among those identified in the material (Singer e Araújo, 1979; Braga-Neto *et al*., 2008; Castro *et al*., 2012; Yilmaz *et al*., 2016; Santos *et al*., 2018; Vasco-Palacios *et al*., 2018; Monteiro *et al*., 2019; De Queiroz *et al*., 2021; Gates *et al*., 202; De Sousa *et al*., 2024). Most of the species identified are present in the classes Dothideomycetes and Sordariomycetes, among the ascomycetes, and the class Agaricomycetes is the only one that appears for the phylum Basidiomycota among the species identified, especially abundant in the leaf litter and with the ability to degrade lignocellulosic materials (Figure 1A).

According to data obtained from, the most abundant and diverse family in the Ascomycota phylum is the Chaetosphaeriaceae family with 53 individuals and 42 species, followed by Nectriaceae (14 and 12), Beltraniaceae (13 and 9) and Dictyosporaceae (11 and 8). In the Basidiomycota, the Russulaceae family has 19 species identified in litter from forest ecosystems, followed by Marasmiaceae (12), Boletaceae (10) and Amanitaceae (7). Many representatives of these families play a crucial role as environmental biodegraders. In addition, around 71 species did not have families and/or classes defined (Figure 1B).

The most representative genres found in this survey of the fungal community present in the leaf litter were *Dictyosporium*, *Ellisembia*, *Sporidesmium* and *Stachybotrys*, with 7, 6, 6 and 6 species, followed by *Zygosporium*, *Chloridium* and *Helicosporium*, with 5 species each. In relation to the species, some were common in the leaf litter of different studies in native and planted forest areas in the Amazon, such as *Beltraniella portoricensis*, *Beltrania rhombica*, *Beltraniella portoricensis*, *Brachysporiella gayana* and *Circinotrichum olivaceum* (Braga-Neto *et al*., 2008; Castro *et al*., 2012; Yilmaz *et al*., 2016; Santos *et al*., 2018; Vasco-Palacios *et al*., 2018; Monteiro *et al*., 2019). The distribution of fungi in the litter may be associated with the composition of this material, which will have a direct impact on the enzymatic activities of these microorganisms. Fungi with cellulolytic activities are often found in leaves, while

those with ligninolytic capacity are more common in woodier substrates (Castro *et al*., 2012; De Melo *et al*., 2018).

Figure 1. Distribution of fungal species identified in litter material in forest ecosystems in the Amazon, according to - a) phylum e taxonomic classes; b) phylum Ascomycota Basidiomycota, Deuteromycota and Mucoromycota.



Source: Elaborated by the authors, 2025.

3.2 LIGNINOLYTIC ENZYMES PRODUCED BY FUNGI FROM AMAZONIAN LITTER

The ligninolytic enzymes (LEs) produced by fungi represent a promising biotechnological alternative to overcoming the primary challenge in reusing lignocellulosic biomass residues: the deconstruction of lignin, one of the most recalcitrant components of the organic matrix that has great potential to produce valuable metabolites, turns in this way a biopharm. Lignin is predominantly composed of p-coumaryl (H), guaiacyl (G), and syringyl (S) monomers, linked by chemical bonds such as β-O-4, β-5, and β-β, which confer high structural resistance (Kmimura *et al*., 2019). These bonds can be efficiently broken by the action of LEs produced by fungi, which, due to their high adaptability to organic matter in natural environments, have evolved the capacity to synthesize these enzymes. Among the LEs, laccases and peroxidases stand out, possessing oxidoreductase matrices with high redox potential, making them highly effective in lignin deconstruction (Asemoloye *et al*., 2021).

One of the great difficulties in reusing lignocellulosic biomass waste is due to the lignin component, an aromatic polymer and one of the main components of plant biomass. Lignin is mainly composed of p-coumaryl (H), guaiacyl (G) and syringyl (S) monomers and is connected by β-O-4, β-5 and β-β bonds (Asemoloye *et al*., 2021). However, these strong bonds can be broken through enzymes produced by fungi, which due to their high adaptability to organic matter in natural environments have developed the ability to produce degrading biocatalysts, such as ligninolytic enzymes, also known as lignin-modifying enzymes (LME). Lacases, peroxidases and catalases make up this group of enzymes and present oxidoreductase matrices with intense redox potential (Suryadi *et al*., 2022).

LMEs can be associated with both structural modifications and the degradation of lignin into less complex compounds. These enzymes are divided into two groups: heme-peroxidase and phenoloxidase. In the first group, the main representatives are lignin peroxidase (LiP) and manganese peroxidase (MnP), while the second group includes laccases (Lac). According to the Carbohydrate Active Enzyme Database (CAZy), laccases are classified in the multicopper oxidase superfamily (AA1), and lignin and manganese peroxidases are included in the auxiliary activity family (AA2) (CAZy; http://www.cazy.org/). The three enzymes make up a system that can deconstruct a lignin effectively[23]. In addition, they are enzymes capable of degrading various xenobiotics, including dyes, chlorophenols, polycyclic aromatic hydrocarbons (PAHs), organophosphorus compounds and phenols (Wesenberg *et al*., 2003).

Fungi associated with leaf litter stands out for producing this complex ligninolytic enzyme system, which catalyzes non-specific reactions that lead to the depolymerization of lignin. The genes for these enzymes are constantly reported in white and brown rot fungi present in dead plant material (Lombard *et al*., 2014), such as litter and tree trunks. Among the 30 genera of fungi with the highest abundance of species identified in this review in leaf litter, only 10 have records in the literature that prove ligninolytic enzyme activity. The other genera have been reported to occur in this environment, but without confirmation of the production of these LMEs. The genera *Dictyosporium* and *Stachybotrys* (Castro

et al., 2012; Yilmaz *et al*., 2016; Santos *et al*., 2018; Vasco-Palacios *et al*., 2018; Monteiro *et al*., 2019; De Queiroz *et al*., 2021) have already been described as potential producers of ligninolytic enzymes (Sin *et al*., 2002; Singh *et al*., 2014; Duong *et al*., 2022). On the other hand, for the genera *Ellisembia*, *Sporidesmium*, *Zygosporium*, *Chloridium* and *Helicosporium*, there are no studies that correlate their species with the production of these enzymes. Specifically, the genus *Chloridium* is described as a soft rot fungus, characterized by secondary colonization of the substrate after the degradation of lignin (Gams *et al*., 1976).

3.3 GENERAL PRINCIPLES OF LMES FUNCTIONING

3.3.1 Lignin peroxidase (LiP)

Lignin peroxidase (LiP EC1.11.1.14) of the Class II peroxidase-catalase superfamily, as well as manganese peroxidase (MnP) and versatile peroxidase (PV), which are peroxidases of fungal or bacterial origin, may be related to the degradation of lignin in the presence of hydrogen peroxide as an electron acceptor. In general, during lignin degradation, LiP targets non-phenolic components, while PV and MnP act to oxidize phenolic structures. These enzymes are H_2O_2-dependent, have high redox potential and acidic pH optima, and can oxidize a wide variety of aromatic compounds and non-phenolic structures that make up 90% of lignin (Riley *et al*., 2014).

LiP has the distinction of being able to oxidize methoxylated aromatic rings without a free phenolic group, which results in cation radicals capable of reacting via a variety of pathways, including ring opening, demethylation and phenol dimerization. In contrast to Lac, LiP does not need mediators to degrade compounds with high redox potential, but it does need H_2O_2 to initiate catalysis (Falade *et al*., 2017). The reactions catalyzed by LiP mainly result in the breaking of Cα-Cβ bonds, opening of aromatic rings, oxidation of benzyl alcohols to the corresponding aldehydes or ketones, oxidation of phenol to produce free radicals, hydroxylation of methylene to specific groups and cleavage of phenylglycol (Vandana *et al*., 2019).

In most fungi, LiP is present as a series of isoenzymes encoded by different genes, which have molecular weights ranging from 37 to 47 kDa, ideal enzyme activity temperatures of 35 to 55 °C, with ideal pH values of 3.0 to 4.5 (Singh *et al*., 2021; Zhao *et al*., 2023) found that the fungus *Clonostachys compactiuscula*, a species identified in leaf litter from the Amapá Forest by Monteiro *et al*. 2019, had LME activities, including LiP, with greater stability at acidic pH (equal to 5) and a temperature of 30 °C.

The main inducer to produce this enzyme, which has been widely reported in the literature, is veratryl alcohol, which increases enzyme activity compared to other substrates (Zhao *et al*., 2023). Meanwhile, compounds such as acetone, dioxane, diethyl ether, acetonitrile, dimethylformamide, cationic surfactant, cetyltrimethylammonium bromide and H_2O_2 in high concentrations act as inhibitors, and this inhibition has been reported in different fungi (Parshetti *et al*., 2012).

3.3.2 Manganese peroxidase (MnP)

The manganese peroxidase enzyme (MnP - EC 1.11.1.13) is an H_2O_2-dependent extracellular glycoprotein that requires Mn^{2+} to oxidize monoaromatic phenols and aromatic dyes. This protein has a molecular mass of between 38 and 62.5 kDa. The activity of MnP has already been described for various fungi of the phylum Basidiomycota, such as those belonging to the orders Agaricales, Cortiales, Polyporales and Hymenochaetales of the class Agaricomycetes (Manavalan *et al*., 2015), being species of the order Agaricales. Some genera and species identified in the leaf litter of the phylum show positive activity for this enzyme, such as *Trametes flavida*, *Trametes* sp. (De Sousa *et al*., 2024), and in some species of *Lactarius* sp. (Morgenstern *et al*., 2010), *Lactifluus* sp. (Zhao *et al*., 2021), *Lentinula* sp. (Ematou *et al*., 2020). In addition, there are records of MnP activity in fungi of the phylum Ascomycota, such as *Clonostachys compactiuscula*, *Dictyosporium* and *Stachybotrys* (Sousa *et al*., 2019; Shi *et al*., 2021; Yang *et al*., 2016).

However, some factors can inhibit the production of this enzyme in microorganisms, such as cultivation methods, temperature, pH, metal ions, among others (Suryadi *et al*., 2022). Some species show better production in solid cultures, in the presence of minimal humidity to favor the growth of the microorganism, as in the case of the isolate *Echinodontium taxodii* 2538 (Kong *et al*., 2016). About temperature and pH, the ideal range is 20 to 50 ºC and an acidic pH of 3.5 to 5 (Suryadi *et al*., 2022).

3.3.3 Laccase (Lac)

Among the lignin-modifying enzymes, laccase (Lac - EC 1.10.3.2) is one of the most studied due to its wide applicability and stability. Lac is an oxidoreductase enzyme characterized by the presence of four copper atoms in its catalytic site and is classified as a multicopper enzyme of the extracellular monomeric glycoprotein family. Lac's active site is composed of: Cu type 1 (T1), Cu type 2 (T2) and Cu type 3 (T3). T1 is a mononuclear site, and types T2 and T3 form a trinuclear cluster. The molecular weight of this enzyme varies between 50 and 130 kDa, being higher than LiP and MnP (Debnath e Saha, 2020).

In fungi, Lac not only plays a role in their metabolism, due to its role in the delignification of lignocellulosic material, but also contributes to the process of sporulation, pigment production, basidiocarp formation and plant pathogenesis (Singh e Gupta, 2020). Laccase is one of the main enzymes identified in litter species, especially in basidiomycete fungi. As an example, among the genera identified in litter from the Amazon rainforest (Singer e Araújo, 1979; Braga-Neto *et al*., 2008; Vasco-Palacios *et al*., 2018; Gates *et al*., 2021), include *Coltricia*, *Craterellus*, *Deconica*, *Lactarius*, *Lactifluus* (Ng *et al*., 2004; Morgenstern *et al*., 2010; KALYANI, *et al*., 2012; Martani *et al*., 2017; Zhao *et al*., 2021; Gupta *et al*., 2025).

The ideal conditions reported for this enzymatic activity occur in the temperature range of 25 to 50 °C, in media with a pH varying from 3.5 to 6 (Suryadi *et al*., 2022; Neto *et al*., 2022). As well as the LiP and MnP peroxidases, there are agents that induce Lac production. The main inducers are lignin-derived

compounds such as 2,5-xylidine, lignin and veratryl alcohol, which are known to increase and induce Lac activity (Litwińska *et al*., 2019).

The use of synthetic mediators can also favor an increase in Lac activity, because in the presence of acetosyringone and 2,2'-azinobis(3-ethylbenzthiazoline-6-sulfonate) (ABTS), an increase in Lac activity has already been observed (Neto *et al*., 2022). However, some metal ions can decrease the activity of this enzyme, such as Hg^{+2}, which inhibited *Chalara paradoxa* CH32 (Robles *et al*., 2002). In the same study, reducing agents such as EDTA, potassium cyanide and sodium azide were also shown to inhibit the activity and production of the enzyme. However, in the presence of some organic solvents, such as methanol, ethanol and isopropyl alcohol, enzyme activity was stimulated, with an increase in enzyme production. The species has already been identified in the litter of primary and palm-dominated forests in the Amazon (Monteiro *et al*., 2019; De Queiroz *et al*., 2021).

3.4 BIODEGRADATION ROUTES OF WASTE BY LIGNINOLYTIC FUNGUS AND VALUE-ADDED MOLECULES GENERATED

In the degradation process of dyes and agro-industrial waste, fungi producing LiP, MnP and Lac transform these complex compounds into simpler, less polluting molecules. Enzymes catalyze oxidation reactions that result in the breaking of the chemical bonds of organic molecules, allowing them to be converted into degradation products. The degradation products can have a variety of properties and potential applications, such as the production of substrates in industrial processes, or even the development of new materials and products with added value. The molecules resulting from this process can be used to optimize biodegradation and waste recovery strategies, contributing to environmental sustainability and the circular economy.

3.4.1 Synthetic dyes as a degradation substrate

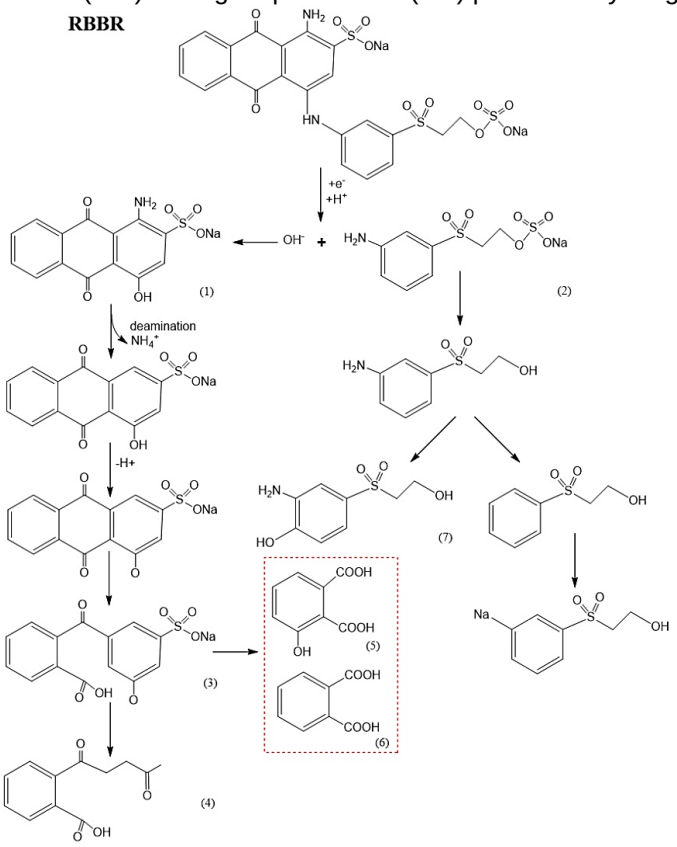
Studies have reported species of genera identified in leaf litter as sustainable and economical alternatives for removing organic dyes from wastewater before they are disposed of. Species of *Crepidotus*, *Dictyosporium* and *Trametes* are described as potential biodegraders of synthetic dyes (Mtui, 2007; Yang *et al*., 2016; De Sousa *et al*., 2024) and can be isolated from litter in terra firme forests, native forests with a predominance of palm trees, cedar plantations and riparian forests (Santos *et al*., 2018; Monteiro *et al*., 2019; De Queiroz *et al*., 2021; Gates *et al*., 202; De Sousa *et al*., 2024).

Crepidotus variabilis in a study carried out for the biodegradation of Azure-B, Poly-B and Poly-R dyes and raw wastewater, revealed a decolorization capacity of 84, 86 and 92% for the dyes and 54% for raw wastewater (Mtui, 2007). The *Dictyosporium zhejiangensis* species is also capable of biodegrading dyes through its enzymatic production, being able to decolorize 11 dyes after treatment for 7 days at rates of 44.78 to 77.87% for strain Sy06 and 46 to 77.41% for strain H-6 (Yang *et al*., 2016). And isolates of Trametes spp. from riparian forest litter were able to decolorize the azo dye RBBR by up to 89.28% (De Sousa *et al*., 2024).

The proposed enzymatic degradation pathway for RBBR reveals that the biodegradation of dyes by fungal enzymes such as Lac and LiP promotes not only the remotion of the dye in wastewater, but also the detoxification of the waste by converting it into less toxic molecules (Figure 2). The enzymatic action, primarily by laccase, promotes the excision of azo dyes, forming a reaction center deficient in electrons. This action generates highly reactive intermediates that are nucleophilically attacked (-OH, -SO, or halogen ions), leading to an asymmetric cleavage of the azo bond (Ardila-Leal *et al*. 2021). After this step, successive deamination, hydroxylation, and oxidation occur, causing the opening of the final ring, as shown by the products (3) and (4) in Figure 2 (Bilal *et al*., 2017). Among the main products accumulated at the end of the degradation of these anthraquinone dyes by fungal enzymes is phthalic acid (molecule (5) in Figure 2), which can be considered a less toxic molecule, reducing the toxicity of

residues containing these dyes and providing a sustainable alternative for their disposal (Bucchieri *et al*., 2024).

Figure 2. Proposed routes for biodegradation of azo dyes Remazol Brilliant Blue R (RBBR), by laccase (Lac) and lignin peroxidase (LiP) produced by fungi.



Source: Adapted of Ardila-Leal *et al*., 2021.

3.4.2 Lignocellulosic waste as degradation substrate

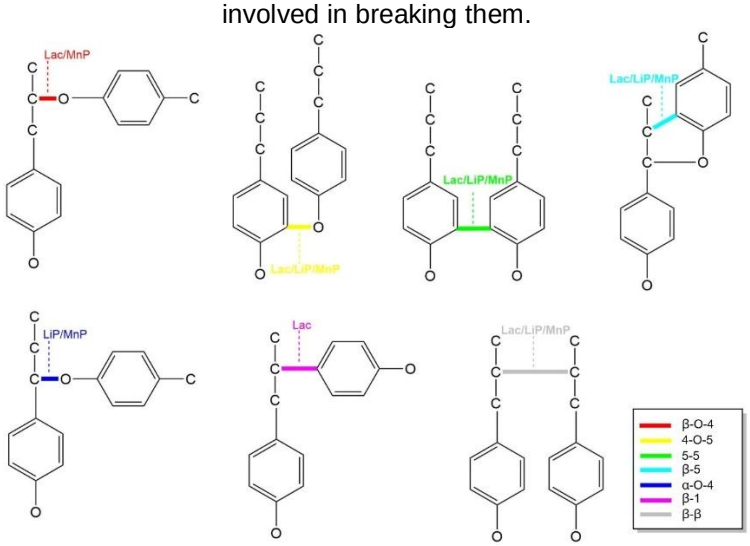
Lignocellulosic waste from agro-industrial residues can be effectively degraded by extracellular ligninolytic enzymes, which initiate the process by breaking key bonds in lignin, such as the β-O-4 ether (β-aryl ether) and β-β (biphenyl) bonds. This enzymatic action generates free cationic radicals that undergo further chemical reactions like hydroxylation and C–C bond cleavage, resulting in hydrophilic degradation products (Asemoloye *et al*., 2021). As lignin is fragmented, it releases lignin monomers such as ρ-coumaryl, coniferyl, and sinapyl alcohols, which are precursors to the phenylpropanoid polymers p-hydroxyphenyl, guaiacyl, and syringyl. This breakdown facilitates the release of

cellulose and hemicellulose, which are further hydrolyzed by specific enzymes into monomeric sugars such as xylose, mannose, galactose, rhamnose, and arabinose.

Different ligninolytic enzymes exhibit varying specificities for bond cleavage. For instance, lignin peroxidase (LiP) is particularly effective at breaking Cα–Cβ bonds in phenolic structures but has significantly lower activity on β-O-4 bonds (Li *et al*., 2022). Manganese peroxidase (MnP) also acts on Cα–Cβ bonds and can catalyze reactions involving β-1 and β-O-4 phenolic substructures (Adriani *et al*., 2020). Laccase (Lac) can degrade β-1 and β-O-4 bonds in the presence of oxygen and phenolic compounds (Pype *et al*., 2019) (Figure 3).

Enzymatic depolymerization of lignin not only supports biomass deconstruction but also enables the production of valuable aromatic compounds. These include gallic acid and 2-pyrone-4,6-dicarboxylic acid from sinapyl alcohol, ferulic acid and its derivatives vanillic acid and 4-hydroxybenzoate from coniferyl alcohol, and protocatechuic acid from ρ-coumaryl alcohol (Higuchi, 2004; Pype *et al*., 2019; Li *et al*., 2022).

Figure 3. Representation of the different types of lignin molecular bonds and the main enzymes involved in breaking them.



Source: Adapted from Datta *et al*., 2017.

3.5 BY-PRODUCTS OF BIODEGRADATION

Ligninolytic fungi play a significant role in the degradation of both synthetic compounds, such as dyes, and organic materials, like agricultural waste, leading to the generation of various bioactive molecules. Aounallah *et al*. 2024 demonstrated that enzymatic treatment of the Congo Red azo dye using *Geotrichum candidum* resulted in a decolorization efficiency of up to 85.4 ± 2.6%, along with the production of metabolites that were less phytotoxic to the shoot and root growth of *Lactuca sativa* and *Solanum lycopersicum*. Similar findings from other studies confirm that dye degradation mediated by fungal ligninolytic enzymes (LMEs) produces metabolites with reduced toxicity to plants and aquatic organisms, including zebrafish larvae and *Daphnia magna* (Przystś *et al*., 2013; Zouari-Mechichi *et al*., 2024). These results underscore the environmental benefits of fungal LMEs in reducing pollutant toxicity and promoting sustainable waste management.

Beyond detoxification, lignin degradation also yields valuable phenolic compounds with diverse industrial applications. For instance, vanillin derived from the cleavage of coniferyl alcohol is widely used in the food and cosmetics industries (Przystś *et al*., 2013). Gallic acid, another byproduct, has applications in food packaging, where it enhances antioxidant activity and extends shelf life (Beckham *et al*., 2016). Additionally, protocatechuic acid, formed from ρ-coumaryl alcohol, exhibits pharmacological properties including antioxidant, anti-inflammatory, neuroprotective, anti-tumor, and organ-protective effects (Sharma *et al*., 2022). These multifunctional compounds highlight the potential of ligninolytic processes not only in environmental remediation but also in the development of value-added bioproducts for various industries.

Recent studies have demonstrated the effectiveness of fungal consortia in lignin biodegradation from agricultural residues. For example, the combined use of *Lenizites betulina* and *Trametes versicolor* on corn stalk-derived lignin led to a 50% lignin reduction over 17 days, with increased enzymatic activity of laccase (Lac) and manganese peroxidase (MnP). The degradation process produced several valuable compounds, including substituted aromatics, small molecule

acids, and aliphatic acids, such as 4-methylcinnamic acid, p-hydroxybenzoic acid, benzoic acid, oxalic acid, succinic acid, maleic acid, and adipic acid (Song *et al*., 2020).

Similar degradation products were identified when lignin in bamboo waste was treated with *Phanerochaete chrysosporium* and *Pleurotus ostreatus*, yielding organic acids, esters, and aromatic substances like benzoic acid, propanoic acid, 3,5-dimethylphenol, and ethyl alcohol (Cui *et al*., 2021). Many of these organic acids have industrial value, particularly in the food and beverage sector, where they are used as acidulants to lower pH, inhibit microbial growth, and extend shelf life (Jin *et al*., 2021).

Fungal degradation of lignocellulosic waste also enables the recovery of high-value aromatic compounds. Vanillin (4-hydroxy-3-methoxybenzaldehyde), a product of coniferyl alcohol degradation, is widely used in the food and cosmetics industries. A notable yield of vanillin (162 µg/mL) was obtained after 96 hours of fungal transformation of black liquor from *Aleppo pinecones* (Zhao *et al*., 2022; Chilakamarry *et al*., 2022). Another valuable compound, gallic acid—derived from sinapyl alcohol—can be extracted from grape pomace treated with fungi like *Rhizopus oryzae*, *Ganoderma* spp., *Phanerochaete chrysosporium*, and *Trametes gibbosa*. The highest gallic acid yield reached 586.43 ± 12.48 µg/g after three days using *R. oryzae* (Šelo *et al*., 2022). Gallic acid is used to enhance antioxidant properties in food packaging and shows promise in drug development due to its selective apoptotic effect on cancer cells without harming healthy cells (Messaoudi *et al*., 2019; AL Zahrani *et al*., 2020).

Additionally, protocatechuic acid, a product of ρ-coumaryl alcohol degradation, has been recovered in high quantities—up to 699.30 ± 20.78 µg/g—through fermentation of grape pomace with *Humicola grisea* (Messaoudi *et al*., 2019). This compound has multiple pharmacological benefits, including antioxidant, anti-inflammatory, neuroprotective, anti-tumor, anti-osteoporotic, and organ-protective properties (Šelo *et al*., 2022).

4 CONCLUSIONS

The ability of fungi to degrade leaf litter highlights their potential for the production of ligninolytic enzymes (LMEs), especially in the generation of value-added molecules during the breakdown of lignin. This review shows that leaf litter is an important natural source for isolating fungi that produce biocatalytic enzymes that can be used to reuse and treat chemical and organic waste. However, there is still a need to investigate other promising species isolated from this material. This study has some limitations, such as the limited number of fungal strains evaluated and the lack of in-depth enzymatic characterization under industrial conditions. Future research should prioritize expanding the screening of different taxa of fungi obtained from leaf litter, optimizing the production of enzymes under industrial-scale conditions, and assessing the environmental impact and economic viability of using agro-industrial waste as a substrate. Progress in this field strengthens industrial biotechnology, sustainable alternatives for organic waste management, and the development of greener technologies and practices associated with the circular economy.

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