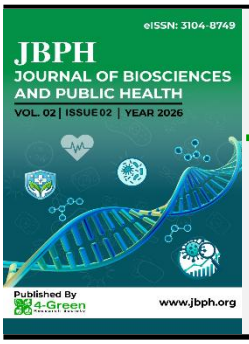


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Review Article

# Laccase as a Potential Biological Catalyst in Green Circular Bioeconomy and Public Health: From Mechanistic Insights to Sustainable Applications

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## ABSTRACT

Laccase, a multicopper oxidase, has emerged as a promising biocatalyst in advancing the green circular bioeconomy and sustainable public health solutions. This review critically synthesizes current knowledge on laccase, integrating mechanistic insights with emerging applications. Its capacity to oxidize substrates such as phenols, anilines, and lignin, while reducing molecular oxygen to water, enables eco-friendly applications in paper pulp bleaching, textile dyeing, nanobiotechnology, woodworking, food processing, biorefining, wastewater treatment, organic synthesis, and biofuel production. Their structural complexity, including a multicopper catalytic core and variable glycosylation, underpins their catalytic versatility and stability across diverse conditions. This review advances beyond descriptive summaries by providing (i) a comparative evaluation of production platforms, including microbial, recombinant, and waste-derived systems; (ii) a critical assessment of natural versus synthetic mediator systems; and (iii) roles of laccase in green and circular bioeconomy applications in bioremediation, industrial processing, biosensing, and medical diagnostics are discussed with emphasis on pollutant degradation and risk reduction. Emerging trends (2023–2026), such as laccase-like nanozymes and circular production strategies, are highlighted. Despite significant progress, challenges related to enzyme stability, scalability, and cost remain. Addressing these limitations will be crucial for translating laccase-based technologies into large-scale sustainable and public health applications.

# 1. INTRODUCTION

Over the past few decades, enzymes have emerged as indispensable tools in advancing sustainable technologies, particularly within the framework of the green circular bioeconomy, where waste valorization, resource efficiency, and environmental protection are central priorities. Among these biocatalysts, oxidoreductases have gained significant prominence due to their ability to catalyze redox reactions under mild conditions while minimizing toxic by-products [1]. In this context, laccase (benzenediol: oxygen oxidoreductase; EC 1.10.3.2) has attracted considerable attention as a versatile and eco-friendly enzyme with wide-ranging applications across environmental, industrial, and public health domains [2, 3]. First identified in 1883 from the Japanese lacquer tree (*Rhus vernicifera*) and later found to occur in fungi, this copper-ligated polyphenol oxidase belongs to the family of blue oxidases, which is the largest class of multinuclear copper oxidases found in plants, fungi, insects, bacteria, lichens, and sponges [2]. Fungal laccases, particularly those from Basidiomycetes, have been extensively studied and are the primary producers compared to bacterial laccases [3]. Laccase research, initiated in the 19th century, has focused on its oxidative capabilities, including its ability to oxidize both phenolic and non-phenolic compounds, including environmental pollutants, as well as its applications in other sectors [4]. Laccase genes comprise a multigene family that encodes ionic isozymes with distinct functions under various conditions [5]. Laccases oxidize substrates such as phenols and anilines, reducing molecular oxygen to water as the primary by-product, making them environmentally friendly catalysts [6, 7]. Laccases are tetrameric or dimeric glycoproteins with four copper atoms in the monomer disposed around a catalytic core at three centers: $T_1$ (Blue copper), $T_2$ (standard copper), and $T_3$ (binuclear copper), with electronic paramagnetic resonance signals [2]. The substrates donate electrons to the $T_1$ center, which then transfers them to the $T_2/T_3$ cluster, 13 Å away from the cysteine-histidine complex, where oxygen is reduced to water [8]. High glycosylation of laccases shields them against proteases, and they are selective toward substrates such as p-diphenols, o-diphenols, aryldiamines, and aminophenols [9]. In addition to bioremediation, laccases catalyse polymerisation and depolymerisation, supporting reactions such as lignin formation in plants and breakdown in fungi and bacteria [4]. This evoked further interest in structural and functional research. Their application in the degradation of pollutants is a primary use, alongside applications in the pulp, food, textile, and paper industries, especially in delignification and bleaching of paper and pulp [10-12].

The broad substrate specificity and catalytic versatility of laccases have positioned them as key biocatalysts in multiple industrial sectors. Their applications span bioremediation (degradation of dyes, pesticides, pharmaceuticals, and endocrine-disrupting compounds), pulp and paper processing (biobleaching and delignification), textile treatment, food processing, and biosensor development [9–11, 13]. In environmental contexts, laccases play a crucial role in detoxifying hazardous pollutants, thereby contributing to ecosystem restoration and reducing human health risks associated with contaminated air, soil, and water [3, 13]. Recent advances have expanded the scope of laccase applications beyond traditional uses. Emerging areas include biofuel cells, nanobiotechnology, and medical diagnostics, where laccase-based biosensors enable sensitive detection of toxins and biomarkers [4]. Additionally, the integration of laccases into nanozyme systems and waste-derived

production platforms has opened new avenues for cost-effective and scalable applications, aligning with circular economy principles [14, 15].

Despite these advancements, challenges such as enzyme stability, variability in optimal operating conditions, and dependency on mediators continue to limit large-scale implementation. Due to their ability to polymerise phenols, these compounds are used in various cosmetic products, including hair dyes, deodorants, and mouthwashes. One of the more recent applications is in nanoparticle-based biosensors for medical and pharmaceutical use [4]. Although excellent reviews exist, they remain largely descriptive. The present review differentiates itself by (i) quantitative comparison of production platforms, (ii) side-by-side evaluation of synthetic vs natural mediators, (iii) critical discussion of conflicting optimal pH/temperature data, and (iv) emphasis on emerging 2023–2026 trends such as laccase-like nanozymes and waste-derived production. Collectively, this review aims to bridge mechanistic understanding with translational applications in green bioeconomy and public health.

## 2. ENZYME FUNDAMENTALS, CATALYTIC MECHANISM, AND QUANTITATIVE COMPARISONS

### 2.1. Structural topology of laccase

The structural and physicochemical properties of laccase, including its molecular organization and glycosylation, have been characterized through spectroscopic and crystallographic studies of purified enzymes (**Figure 1**). Laccases differ in their biochemical characteristics and molecular organizations. They are usually glycoproteins with molecular masses ranging from 50 to 130 kDa, for which carbohydrates constitute 10-45% of the total mass. Carbohydrates play different roles, including stability, copper binding, secretion, and resistance to proteolytic degradation [12, 16]. While laccase's core structure is genetically regulated, the degree and composition of glycosylation, which influences enzyme stability and activity, can be modulated by the growth medium's composition [17]. Laccases occur as monomeric, dimeric, and polymeric forms. They contain several copper atoms and are called blue oxidases [18]. The optimal pH for laccase activity varies (typically 3-8) depending on the substrate type and the enzyme's source, such as fungal or bacterial laccases [19 ]. The optimal temperature also varies significantly among strains, most often reported as 30–50°C. Kinetic constants of the enzyme (Km and Vmax) also differ based on substrate, enzyme type, and conditions, with Km ranging most often between 2 and 5000 μm [18, 20].

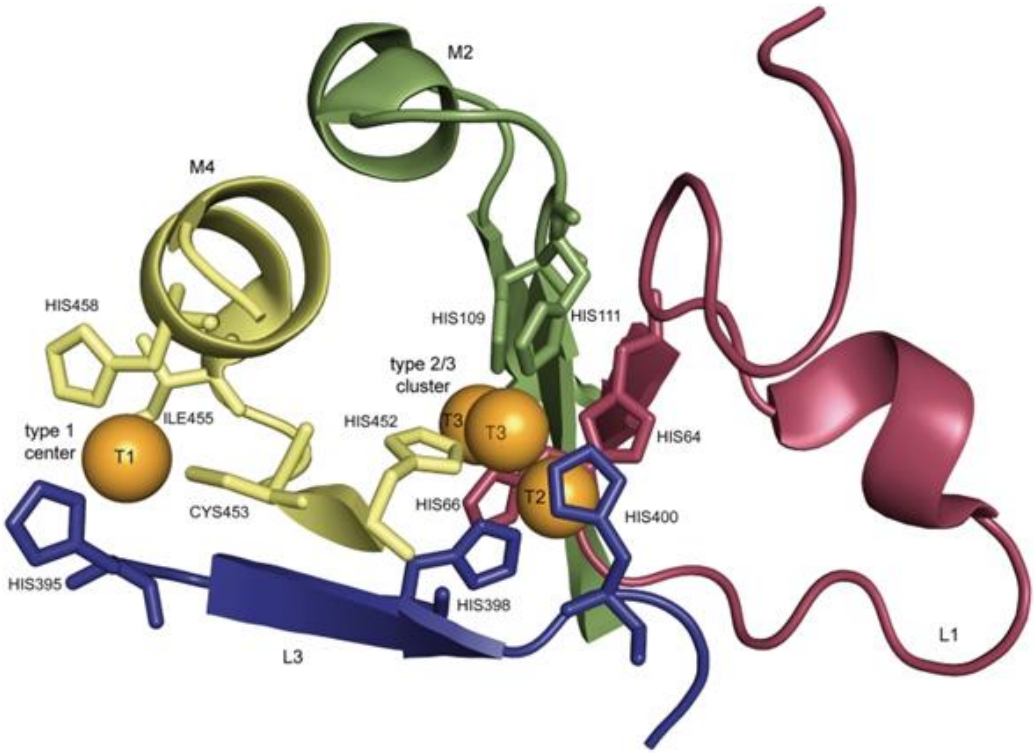


**Figure 1.** Structural topology and catalytic mechanism of laccase (Laccases, EC 1.10.3.2) ($C_{66}H_{109}N_{19}O_{25}$). (A) The three-dimensional schematic representation of the laccase monomer, highlighting the Greek-key fold structure. (B) The active site architecture, depicting the three distinct copper centers: Type 1 (T1, blue), Type 2 (T2, green), and the binuclear Type 3 (T3, orange). (C) Schematic illustration of the electron transfer pathway, showing the distance (13 Å) between the T1 copper site (substrate oxidation site) and the trinuclear T2/T3 cluster (oxygen reduction site).

### 2.2. Catalytic mechanism of laccase

Laccases are glycosylated broad-spectrum oxidases catalyzing single-electron oxidation of a wide variety of organic and inorganic substrates e.g., phenolics, polyphenols, methoxy-monophenols, aromatic amines, lignin, ascorbic acid, and certain inorganics while molecular oxygen is reduced to water [21]. Their catalytic site consists of four copper ions: one Type 1 ($T_1$), one Type 2 ($T_2$), and two Type 3 ($T_3$). Characterized by UV/visible and EPR spectroscopy, the blue color of the oxidized enzyme arises from the EPR-detectable $T_1$ copper at 610 nm. $T_2$ is colorless, but EPR-detectable, and $T_3$ is weakly UV-absorbed and is EPR-silent. Substrate is bound at the $T_1$ site, while the $T_2/T_3$ coppers form a trinuclear cluster to reduce $O_2$. Two histidine nitrogens and an oxygen ligate $T_2$, while three histidine nitrogens ligate each $T_3$. Structural analysis of most variants confirms that these copper-binding sites are well conserved in multicopper oxidases [22].

As illustrate in **Figure 2**, the catalysis process of the enzyme includes three key steps: copper $T_1$ oxidizes by accepting electrons from a reducing substrate, the electrons are transferred from copper $T_1$ to a ternary complex of $T_2$ and $T_3$, and an

oxygen molecule is coordinated to the ternary complex, where it becomes reduced to $H_2O$ by accepting electrons from copper $T_2$. A single-electron oxidation process enables the laccase enzyme to oxidize substrates. The enzymes can be used to treat a variety of substrates, such as monophenols, aromatic compounds, methoxyphenols, para- and ortho-phenols, aminophenols, lignins, nonphenolic aromatic compounds, inorganic compounds, oxides, aromatic amines, ascorbic acid, and polyphenols, simultaneously reducing the molecular oxygen to water [15, 16]. For instance, oxidation of different types of organic and inorganic pollutants by laccase are discussed briefly in the following section.

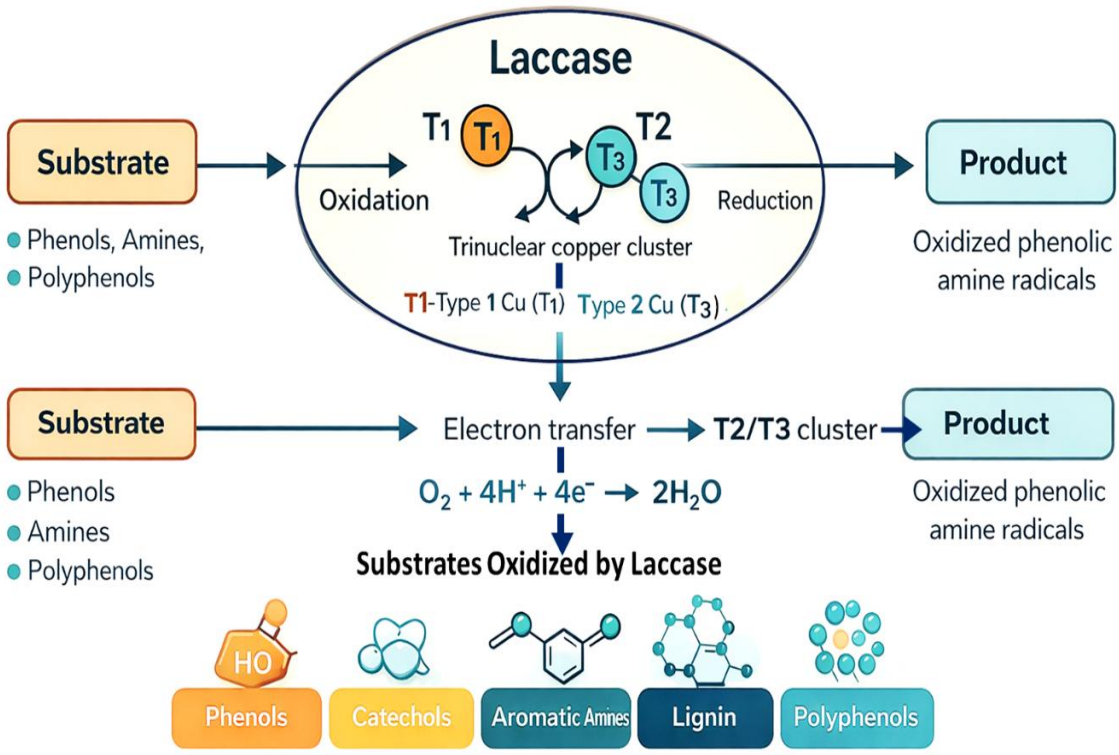


**Figure 2.** Catalytic mechanism of laccase and substrate oxidation pathway. Laccase catalyzes the oxidation of phenolic and aromatic substrates at the Type 1 (T1) copper site via single-electron transfer. Electrons are transferred to the trinuclear T2/T3 copper cluster, where molecular oxygen ($O_2$) is reduced to water ($H_2O$), generating oxidized radical intermediates. The electrons are then transferred to the T2/T3 cluster, where molecular oxygen ($O_2$) is reduced to water ($H_2O$), as the only by-product.

### 2.3. Microbial sources of laccase production with quantitative comparisons

Laccases are multicopper oxidases produced by various types of organisms, including fungi, bacteria, actinomycetes, plants, and even certain insects. **Table 1** provides a concise, analytical overview of the variability in optimal pH and temperature across different laccase sources. It lists typical ranges for fungal, bacterial, and thermostable variants, as well as emerging laccase-like nanozymes. Each entry includes the organism/source, optimal pH and temperature ranges, commonly used substrate in assays, and implications for industrial applications, addressing a key gap in prior descriptive reviews.

**Table 1.** Comparative overview of optimal pH and temperature ranges among major laccase sources.

| Source | Organism | Optimal pH | Optimal Temperature (°C) | Substrate used | Reference |
|---|---|---|---|---|---|
| Fungal | Trametes versicolor | 3.0–5.0 | 30–50 | ABTS, guaiacol | [19] |
| Bacterial | Bacillus subtilis CotA | 6.0–8.0 | 60–80 | SGZ, ABTS | [20] |
| Thermostable variants | Streptomyces spp. | 7.0–9.0 | 70–90 | ABTS | [21] |
| Nanozyme mimics | Cu-based nanozymes | 3.5–8.0 | 25–80 | Various | [22] |

**Table 2** presents a quantitative comparison of typical laccase production yields across major heterologous systems (bacteria such as *E. coli*, yeast such as *Pichia pastoris*, filamentous fungi such as *Aspergillus oryzae/niger*, and waste-based solid-state fermentation (SSF)). Columns include the host system, typical yield range (in U/mL or U/kg substrate, with mg/L where available), fermentation time, and relative cost level. It highlights trade-offs: yeast systems often achieve the highest volumetric yields (up to ~15,000 U/mL), while waste-based SSF offers very low-cost, high per-substrate yields (50,000–300,000 U/kg on olive mill waste).

**Table 2.** Recombinant production yields.

| Host System | Typical Yield | Time | Cost Level | Recent research findings | Ref. |
|---|---|---|---|---|---|
| E. coli | 50–500 U/mL (1–20 mg/L) | 24–48 hours | Low | CotA variants, ~300 U/mL | [23, 24] |
| Pichia pastoris | 500–15,000 U/mL (20–300 mg/L) | 96–144 hours | Medium | Up to 12 g/L | [25, 26] |
| Aspergillus oryzae/niger | 100–3,000 U/mL | 5–10 days | Medium-High | 2.6 g/L | [ 27, 28] |
| Waste-based fungal SSF | 50,000–300,000 U/kg substrate | 7–14 days | Very low | Olive mill waste | [29-31] |

Fungal laccases' unparalleled capacity to oxidize a wide variety of aromatic, phenolic, and nonphenolic molecules, lignin, mineral substances, and other compounds has attracted significant interest for their application across various industries [2, 3]. Mass production is required to make them available for commercial applications. The inability to meet this objective, primarily due to poor enzyme yields from natural sources, hinders their widespread use. Different ways to enhance laccase production include reducing costs by identifying appropriate fungal strains, optimizing fermentation medium formulations, implementing new, more effective fermentation processes, and utilizing genetic engineering to achieve high-yield production through recombinant strains [32]. Laccase production via fermentation processes requires extended growth periods, which increase production costs. Genetic modification is a helpful tool for laccase production. Currently,

considerable efforts are being made to achieve cost-efficient enzyme production in heterologous hosts, while also improving their chemical and genetic engineering methods [2, 3].

To address the challenges of industrial scalability and post-translational modification, a comparative analysis of major heterologous hosts is crucial (**Table 3**). While Pichia pastoris offers the highest volumetric yields, filamentous fungi remain the most scalable option for bulk production, especially when utilizing waste-based solid-state fermentation. Conversely, *E. coli*, despite its high scalability in fermentation tanks, often exhibits low extracellular secretion and a lack of glycosylation, both of which are critical for laccase stability.

**Table 3.** Comparative evaluation of heterologous hosts for laccase production.

| Host System | Typical Yield Range | Glycosylation Issues | Industrial Scalability and Cost | Ref. |
|---|---|---|---|---|
| Filamentous Fungi (Aspergillus, Trichoderma) | High (Native)<br>Low-Moderate (Recombinant) Up to 10,000–50,000 U/L in SSF | Compatible<br>Natural hosts; correct folding and modification. | High<br>Well-established fermentation; low-cost waste-based substrates (SSF). | [ 33-35] |
| *E. coli* | High (Intracellular)<br>Low (Extracellular)<br>Often <500 U/mL | None (Prokaryotic)<br>Lacks glycosylation machinery; may form inclusion bodies. | High (Lab), Low (Industrial)<br>Simple and cheap, but downstream processing for inclusion bodies is costly; low extracellular secretion. | [36-38] |
| Pichia pastoris | Very High<br>Up to 10,000–15,000 U/mL | Hyper-glycosylation<br>Glycans are longer than native; they may affect enzyme stability/activity. | Moderate-High<br>Excellent for high-density fermentation; requires methanol induction (safety concerns); higher media cost. | [39] |
| Plants/Insects | Low<br>mg/kg (Plants) or low titer | Plant-like/Insect-like<br>Different from fungal glycosylation; potential allergenicity. | Low<br>Long growth cycles (plants); expensive bioreactors (insects); mainly for niche pharmaceuticals. | [40-43] |

Due to their broad substrate tolerance, these enzymes are in high demand as renewable biocatalysts for various industrial applications. One limitation is that they do not have large-scale production from natural sources, which cannot meet the increasing market demand. Low productivity is also unsuitable for conventional industrial fermentation processes, which require a large number of microorganisms to be cultured, thereby increasing production costs. In next section, heterologous expression of laccase has been described to date in bacteria, yeasts, fungi, plants, and insects.

### 2.3.1. Bacterial source

E. coli is a general and easy host for the expression of recombinant proteins and thus is a good choice for producing a wide range of valuable proteins, i.e., vaccines, immunotoxins, and biopharmaceuticals [44-48]. Heterologous expression in E. coli is employed to overcome the limitation of the availability of minute quantities of laccase from natural sources. Different laccases are synthesized in bacterial hosts. The cotA enzyme of Bacillus subtilis has been directly and successfully recombinantly expressed in *E. coli,* and its structure and properties have been elucidated, even allowing for alterations in its functions. Cyathus bulleri laccase, of the ligninolytic fungus, is also produced in *E. coli.* Streptomyces strains are also

utilized for recombinant laccase production. *S. coelicolor laccases* produced in *S. lividan*s yield high rates of highly pure product [49, 50].

### 2.3.2. Fungal source

Fungi also qualify as hosts for recombinant expression because they can secrete high levels of protein into the growth medium. Up to today, only a few species of fungi are suitable for recombinant expression. The most frequently used filamentous fungi are Aspergillus niger, A. oryzae, and Trichoderma reesei; hence, most studies and reports focus on these organisms. A. nidulans, which is genetically modified and has a tailor-made expression system for A. sojae, is also available. Heterologous laccase expression in fungi has enabled more detailed studies of these enzymes, yielding valuable insights. For instance, high yields of recombinant protein enabled the determination of the three-dimensional structures of Coprinus cinereus, S. coelicolor, and M. albomyces laccases [51].

### 2.3.3. Yeast source

Yeasts are valued for their rapid microbial growth, ease of genetic manipulation, and capacity for posttranslational modifications, including disulfide bridge formation, glycosylation, and proteolytic processing. The two most popular yeasts used to express recombinant laccases are Pichia pastoris and Saccharomyces cerevisiae. Numerous laccases, including plant laccases, are described in both of these yeasts. P. pastoris has overall performed better as a recombinant laccase producer, yielding approximately 8–17 mg/L. The laccases expressed in these organisms tend to be hyperglycosylated [52].

### 2.3.4. Plants and insects sources

Plants have also been successfully employed as host organisms in the recombinant expression of plant and fungal laccases. Secretory laccase expression has potential applications in phytoremediation technology. In addition, increased expression of potato laccase (PPO) in tomato has also conferred significant resistance to bacterial pathogens in the transgenic plant. Recombinant expression of laccase in insect SF9 cells was carried out using the baculovirus system, which facilitated the investigation of laccases from Manduca sexta and Tobacco hornworm [53, 54].

## 3. EMERGING ROLES OF LACCASE IN GREEN AND CIRCULAR BIOECONOMY APPLICATIONS

In recent years, growing environmental concerns and the global transition toward sustainable development have intensified interest in laccase-based processes. The concept of a green and circular bioeconomy emphasizes the efficient use of renewable biological resources, waste minimization, and the transformation of residues into value-added products. Within this framework, laccases play a crucial role by enabling the biodegradation of industrial pollutants, detoxification of xenobiotics, and valorization of lignocellulosic biomass [55, 56]. Emerging research also highlights the integration of laccase with mediators and engineered systems (including immobilization on bio-derived supports) to enhance catalytic efficiency, expand substrate range, and improve stability for industrial-scale applications, further strengthening their

relevance [57, 58]. As a result, laccases are positioned as key biocatalysts bridging environmental sustainability and industrial innovation, aligning closely with the principles of a green and circular bioeconomy [56, 59]. The integrated outcomes demonstrate significant public health benefits, including improved water quality, reduced exposure to toxic pollutants, ecosystem protection, and enhanced human well-being. Overall, **Figure 3** illustrates the alignment of laccase-driven processes with key sustainability principles, including low-carbon technologies, circular resource use, economic value creation, and societal health advancement. Some of the important applications of laccase have been discussed in next sections.

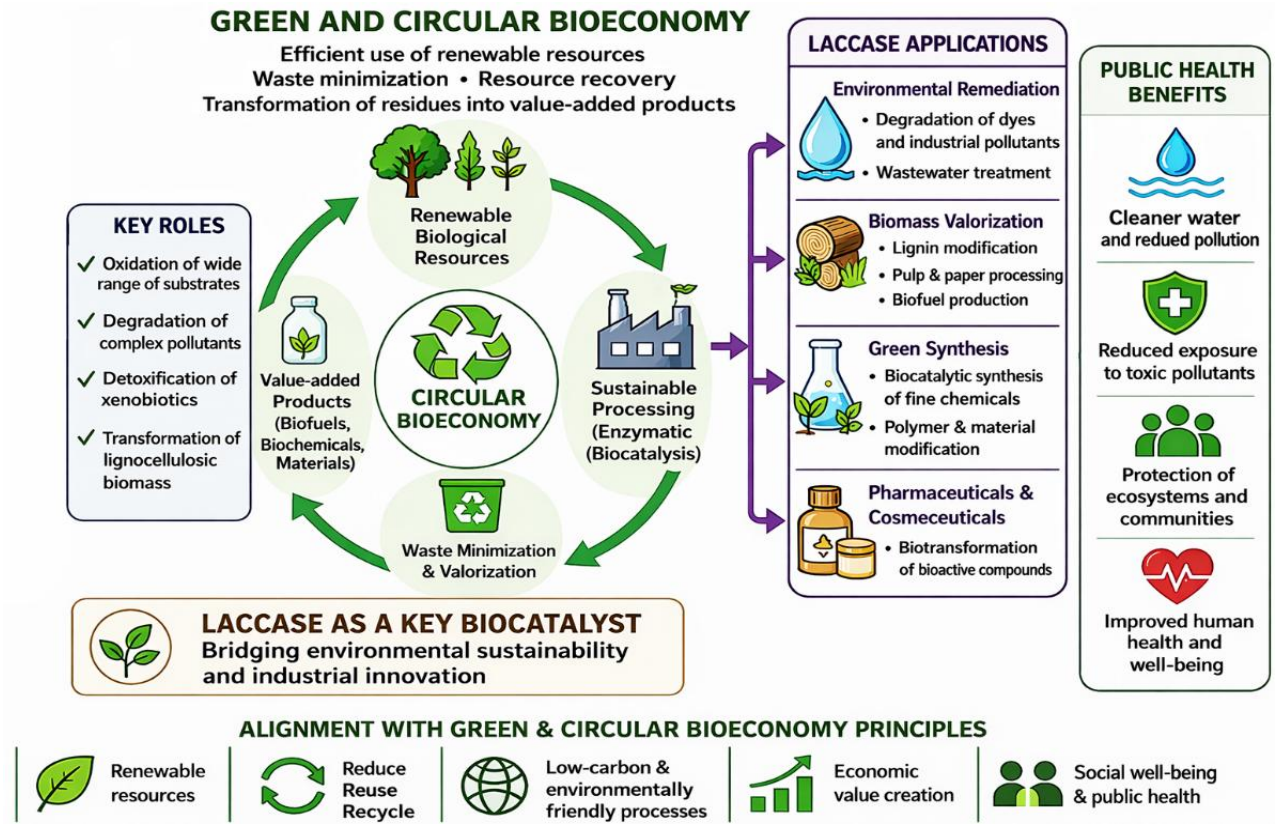


**Figure 3**. Role of laccase in advancing a green and circular bioeconomy and its public health implications.

## 4. LACCASE IN ENVIRONMENTAL BIOREMEDIATION

Laccases have emerged as one of the most promising biocatalysts for environmental remediation owing to their ability to oxidize a wide range of organic and inorganic compounds under mild and eco-friendly conditions. Multiple herbicides and pesticides have been used recently to maximize agricultural yields. However, the downside is the detrimental effect these chemicals have on environmental health. Air, water, and soil resources are their primary targets. Among the numerous pesticides and herbicides, chemicals such as benzene, dichlorodiphenyltrichloroethane, polychlorinated biphenyls, and

polycyclic aromatic compounds are the most carcinogenic and mutagenic, causing damage to both environmental and human health [2, 3, 60]. Luckily, laccases are highly effective in inactivating these pollutants. Population growth, bad global management, and inadequate disposal practices have significantly impacted potable water resources in recent decades. Emerging pollutants, such as chemical substances with unrecognized mechanisms that disrupt ecosystems, are significant environmental pollutants [61, 62]. Endocrine disruptors (EDs) constitute another significant subclass of pharmaceutical and personal care products [63]. Specifically, EDs are chemicals that can imitate the hormonal activity in various organisms, causing disruptions in the endocrine system, most notably linked with sexual abnormalities, cancers, and chronic diseases. Laccase-based systems can degrade these chemical disruptors [60, 63].

### 4.1. Oxidation of phenols

Phenols are one of the primary substrates for laccase. The reaction involves the oxidation of phenols to quinones, and phenol is oxidized to benzoquinone. Industrial wastewater often contains toxic phenolic compounds (phenol and cresols) from chemical manufacturing, petroleum refining, and the pharmaceutical industry [64].

$$C_6H_5OH + \frac{1}{2}O_2 \xrightarrow{Laccase} C_6H_4O + H_2O$$

Laccases are now considered versatile biocatalysts in a variety of industrial and environmental applications, especially for the oxidation of phenols, thanks to this environmentally friendly mechanism. Laccases efficiently break down phenolic pollutants in bioremediation, including bisphenol A, chlorophenols, azo dyes, polycyclic aromatic hydrocarbons (PAHs) like anthracene and benzo[α]pyrene, pesticides like atrazine and lindane, xenobiotics like 2,4-dinitrophenol, and polychlorinated biphenyls (PCBs) [65]. Their broad substrate specificity, low toxicity, minimal sludge formation, and high efficiency in mineralizing recalcitrant compounds into $CO_2$ and $H_2O$ make them an affordable, mediator-enhanced alternative to conventional chemical treatments [66].

### 4.2. Oxidation of catechols

Catechols are dihydroxy derivatives of benzene that laccase oxidizes to o-quinones. Catechol is oxidized to o-benzoquinone. Catechols and related phenolic compounds in wine contribute to haze formation and affect the color and taste during storage [67]. They catalyze the oxidation of catechols using molecular oxygen as the terminal electron acceptor, producing water as the only by-product. This environmentally benign catalytic mechanism enables radical-mediated reactions that support polymerization, oxidative coupling, and degradation processes under mild conditions [68]. Consequently, laccases have been widely explored in green chemistry and organic synthesis, where they facilitate reactions such as oxidative coupling of phenolic polymers, synthesis of biaryl compounds from substituted catechols, and polymerization of catechols into polycatechols. These reactions are also utilized in the production of synthetic urushi-type polymers and functional phenolic materials [69]. Although high concentrations of organic solvents may destabilize enzymes and mediators can increase costs, laccase-based processes offer advantages including broad substrate specificity, use of atmospheric oxygen, and reduced reliance on toxic oxidants [70]. In addition, laccase-mediated catechol oxidation also has significant applications in pharmaceutical and biomedical synthesis, enabling the production of compounds such as β-lactam–catechol hybrids,

sulfonamide–catechol derivatives, phenoxazinones, and antioxidant molecules derived from catechin oxidation. These reactions can achieve yields of up to 98% under mild and environmentally friendly conditions [71]. In environmental biotechnology, laccases contribute to the removal of emerging contaminants including triclosan and bisphenol A (BPA) from wastewater. Laccase–mediator systems (LMS) can significantly enhance oxidation efficiency, achieving removal rates approaching 100% within hours under optimal conditions [72, 73]. In cosmetic and textile applications, catechol oxidation contributes to the formation of natural pigments and antimicrobial coatings [74]. Furthermore, laccases have been investigated as cathode catalysts in enzymatic fuel cells, where catechol oxidation supports bioenergy generation under mild conditions [75].

### 4.3. Oxidation of aromatic amines

Laccase can oxidize aromatic amines to form cationic radicals or polymerized products. Through radical formation, laccases facilitate diverse transformations of aromatic amines, including azo coupling reactions, polymerization of anilines to polyanilines, oxidation of ortho-aminophenols to phenoxazinones, and synthesis of heterocyclic compounds such as benzimidazoles and quinoxalines in green organic synthesis [76]. In addition, laccase-mediated oxidation of aromatic amines also has significant applications in pharmaceutical synthesis, where it is used to generate hydroxyindole derivatives, antimicrobial phenoxazinones, actinocin-like antibiotic hybrids, antitumor compounds, and sulfonamide–amine conjugates. These reactions can achieve yields of up to 95% under environmentally friendly conditions, although challenges related to mediator dependency, byproduct toxicity, and enzyme cost remain [66, 71].

In environmental remediation, laccases are effective in degrading aromatic amine dyes, azo dyes, aniline derivatives, and polycyclic aromatic amines, contributing to the removal of hazardous contaminants from wastewater and soil. Removal efficiencies can reach up to 90%, although the use of mediators may increase operational costs and potential toxicity [77]. Recent developments include laccase–mediator systems (LMS), nanomaterial immobilization, oxidase combinations, and microbial consortia, which can improve degradation efficiency by 20–50% and enhance applicability in real effluent treatment [78]. Laccase-based technologies have also been explored in biosensing applications for detecting aromatic amines in food and water through electrochemical oxidation [79].

Moreover, in cosmetic formulations, laccases catalyze the oxidation of aromatic amines such as tyramine and p-phenylenediamine, producing melanin-like pigments used in hair coloring with reduced irritation and improved sustainability [80]. In materials science, laccase-catalyzed oxidation of aniline derivatives enables the biodegradable synthesis of conductive polymers, protein cross-linking, and surface functionalization, offering potential applications in bioelectronics, adhesives, and smart textiles [81]. Furthermore, laccases have been investigated in biofuel and bioelectrochemical systems, where oxidation of amine-containing intermediates contributes to improved lignocellulose processing and catalytic reactions in fuel cell cathodes [82]. Overall, **Table 4** summarize the ability of laccases for the potential in green synthesis, environmental remediation, biosensing, and advanced materials development with some challenges for broader industrial implementation.

**Table 4.** Laccase-mediated oxidation of phenols, catechols, and aromatic amines: applications, advantages, and challenges.

| Substrate Class | Purpose / Sector | Key Examples | Advantages | Challenges / Disadvantages | Mediators and Substrates | Ref. |
|---|---|---|---|---|---|---|
| **Phenols** | Bioremediation | Degradation of bisphenol A, chlorophenols, azo dyes, PAHs, pesticides, xenobiotics | Eco-friendly, $O_2$ as acceptor, broad range, reduces toxicity | Toxic byproducts, enzyme inactivation, high cost | ABTS, HBT, phenols, dyes | [83] |
| | Pulp and Paper | Biopulping, biobleaching, delignification, recycled paper bleaching | Reduces energy, improves brightness | Low stability, mediator need, potential fiber strength loss | HBT, lignin, N-hydroxy compounds | [84] |
| | Textile | Dye decolorization (e.g., Reactive Black 5, indigo, Malachite green), denim finishing | Low water/energy use, minimal fabric damage, effective on diverse dyes | Dye-dependent efficiency, mediator depletion | ABTS, synthetic dyes, indigo, ionic liquids | [85, 86] |
| | Food | Juice, wine stabilization, phenolic reduction, dough cross-linking | Enhances shelf life, texture, quality, reduces additives, energy-saving | Low stability in matrices, turbidity, variable browning control | Polyphenols, ferulic acid | [87] |
| | Organic Synthesis | Polymerization (lignin/phenolic resins, biopolymers) | Green/mild conditions, novel compounds, biodegradable catalyst | Scalability limited by stability/cost | Catechol, guaiacol, lignin monomers | [88] |
| | Pharmaceuticals | Antibiotic degradation (tetracycline), drug synthesis/removal | High efficiency, eco-friendly, precursor synthesis | Byproduct toxicity, mediator/stability issues | ABTS, antibiotics, HBT | [89] |
| | Cosmetics | Hair dyeing, skin lightening | Safer/less irritant, natural pigments | Stability/mediator needs | Catechol, hydroquinone | [90] |
| | Biosensors | Detection of phenolics in food, water | High sensitivity, real-time, low cost, eco-friendly | Interference, short lifetime, denaturation | ABTS, phenols, catechols, nanomaterials | [89] |
| | Biofuel | Cathode in enzymatic fuel cells, lignocellulose pretreatment | Clean energy, neutral pH, yield increase | Low power, denaturation, cost | $O_2$, phenolics, TEMPO | [91] |
| **Catechols** | Organic Synthesis | Polycatechol polymerization, biaryls, phenolic polymers, artificial urushi | Green (air/$O_2$, water byproduct), mild, broad specificity | Co-solvent unfolding, mediator toxicity/cost | ABTS, HBT, TEMPO, (acetosyringone), catechols | [92, 93] |
| | Pharmaceuticals | Antimicrobial hybrids, phenoxazinones, antioxidants, drug derivatives | High yields (≤98%), eco-friendly, enhanced bioactivity | Mediator dependency, cytotoxicity, cost | HBT, ABTS, natural mediators, catechols, β-lactams | [94] |
| | Bioremediation | BPA, triclosan, phenolic pollutants | High efficiency (≤100%), neutral pH/room temp | Instability, cost, mediator dependency | HBT, ABTS, humic acid, BPA/triclosan | [95] |
| | Biosensors | Polycatechol films, functionalization (lignin/wood) | Sensitivity/reproducibility, sustainable materials | Interference, lifetime issues | ABTS, catechols, nanomaterials | [96] |
| | Cosmetics | Phenoxazinones, antimicrobial surfaces, fuel cell cathodes | Safer pigments, antimicrobial, mild energy production | Stability, mediator needs | Catechol, hydroquinone, TEMPO | [97] |
| **Aromatic Amines** | Organic Synthesis | Phenoxazinones, heterocycles (benzimidazoles), azo compounds, polyanilines | Green ($O_2$/water), mild/selective, no toxic reagents | Low potential (mediator need), solvent denaturation | ABTS, HBT, TEMPO, anilines, aminophenol | [98] |
| | Pharmaceuticals | Antimicrobial,antitumor compounds | High yields (≤95%), eco-friendly, anti-resistant activity | Mediator/byproduct issues, cost | HBT, ABTS, amines, sulfonamides | [99] |
| | Bioremediation | Azo/aniline dyes, amine xenobiotics | Efficient (≤90%), ambient, low toxicity | Inactivation, mediator cost | ABTS, HBT, humic, anilines | [100] |
| | Biosensors, Cosmetics | Amine detection, hair dyeing/melanin pigments | Sensitivity/selectivity, safer/natural colors | Interference, stability | ABTS, amines (dopamine, p-phenylenediamine) | [101] |
| | Materials, Energy | Conducting polymers, surface modification, fuel cells | Enhanced properties, clean energy | Scalability, recycling, low density | Aniline, TEMPO/ABTS | [102] |

## 5. BIOCATALYTIC APPLICATION OF LACCASE

Laccases are excellent biocatalysts with various applications, including nanobiotechnological production, biodegradation, and bioremediation in the food industry, as well as in the woodworking, textile, cosmetics, and pulp/paper industries [103]. As quantitatively summarized in **Figure 4**, the industrial footprint of laccase is rapidly expanding. Notably, the combined biofuel cell and biosensor sector accounts for 22% of applications, reflecting the growing integration of laccase into nanobiotechnology and renewable energy. Conversely, the minimal allocation to 'Paints' (0%) suggests a shift away from traditional coating applications towards more high-value, eco-innovation sectors.

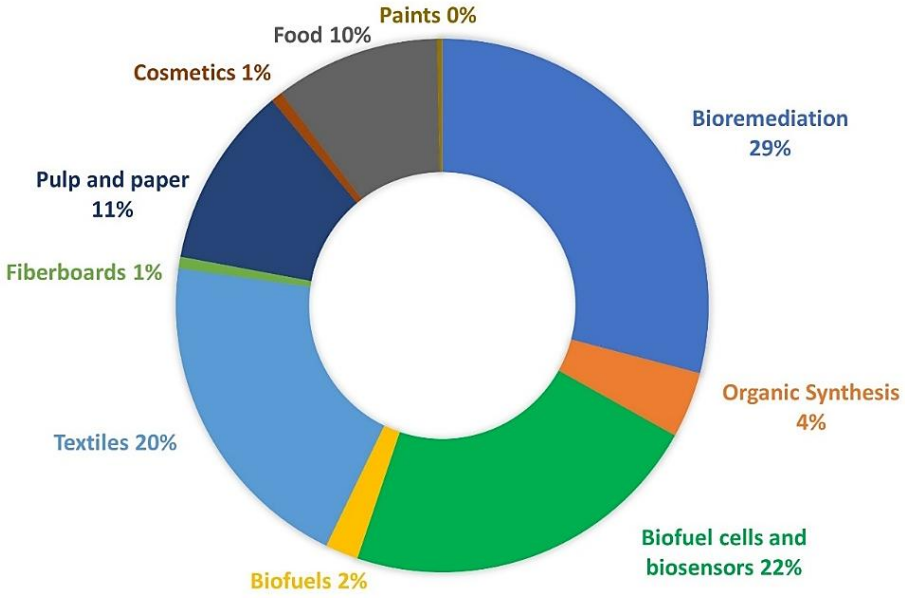


**Figure 4.** Global distribution of laccase applications across various industries (estimated market share). The data, synthesized from recent industrial reports and literature (2023–2026), indicates that bioremediation (29%) and bio-electrochemical systems (22%) currently dominate the application landscape. This distribution underscores the enzyme's critical role in sustainable technologies, particularly in wastewater treatment and energy generation, while highlighting the growing demand in the textile (20%) and food (10%) sectors [5, 103].

Industrially, laccase often enhanced by mediators including natural phenolics like syringaldehyde facilitates eco-friendly processes such as pulp delignification and biobleaching, lignocellulosic pretreatment for enhanced biofuel yields, bioremediation of effluents and soils, and valorization of lignin into high-value aromatics. Ongoing advancements in enzyme engineering, immobilization, and mediator optimization continue to address limitations in stability, cost, and scalability, positioning laccase as a cornerstone of green biotechnology. **Table 5** provides a concise overview of key biocatalytic and industrial applications of laccase enzymes, with a special focus on uses involving syringaldazine (SGZ) as a direct substrate or mediator, alongside broader environmental and industrial sectors.

**Table 5.** Biocatalytic and industrial applications of laccase with advantages and challenges.

| Category | Purpose / Sector | Key Examples | Advantages | Challenges / Disadvantages | Mediators / Substrates | Ref. |
|---|---|---|---|---|---|---|
| **Biocatalytic (Syringaldazine-Focused)** | Laccase Activity Assay | Spectrophotometric quantification in fungal cultures (e.g., Trametes, Pleurotus) | Highly specific, sensitive, quantitative for purified enzymes | Poor solubility, precipitation of products, unstable expensive, pH 5.5–7.0 limited | Syringaldazine (SGZ; direct substrate), phosphate/ acetate buffers | [104, 105] |
| | Antioxidant Activity Assay | SGZ radical generation vs. DPPH, reduction by antioxidants (e.g., ascorbic acid, Trolox) | Enzymatic fresh radical generation, eco-friendly | Limited to phenolics, enzyme activity control needed, interference in complex samples | SGZ radicals, reducing antioxidants | [106] |
| | NAD(P)H Oxidation / Cofactor Regeneration | Coupled system for $NAD(P)^+$ recycling in biocatalysis | Efficient recycling, sustainable ($O_2$ acceptor), active at pH ~8.0 for some laccases | pH/solvent inhibition, variable specificity, scalability issues | SGZ, NAD(P)H | [107] |
| | Detection in Complex Matrices | Activity in soils, litter, wastewater; hydrophilic SGZ analogues | Functional in natural samples, stable analogues reduce underestimation | Original SGZ insoluble interference/ radical side reactions | Modified SGZ, ABTS (comparison) | [108] |
| **Industrial / Environmental** | Pulp and Paper | Delignification/biobleaching of kraft pulp, hardwood/softwood | Reduces chlorine/energy use, improves brightness/strength, eco-friendly | Low thermostability/ pH tolerance, mediator need for non-phenolics, slow rates | HBT, ABTS, violuric acid, lignin (guaiacyl/syringyl) | [109] |
| | Biofuel Production | Pretreatment of lignocellulose (wheat straw, corn stover, bagasse) for ethanol/biogas | Enhances saccharification (up to 50%), mild/selective lignin removal, no cellulose loss | Incomplete degradation, high enzyme/mediator costs, toxicity | Natural (acetosyringone, syringaldehyde), synthetic (HBT, TEMPO), lignin subunits | [110] |
| | Bioremediation | Effluent/soil detoxification (pulp wastewater, lignocellulosic pollutants) | Reduces COD/BOD, detoxifies, promotes microbial growth | Matrix inhibition (metals/phenols), variable efficiency | ABTS, HBT, humic acids, lignin phenolics | [111] |
| | Value-Added Compounds | Lignin depolymerization to vanillin, syringic acid, phenolics | Sustainable bio-aromatics from waste, mild process | Low yields, product inhibition, separation issues | HBT (recalcitrant bonds), kraft/organosolv lignin | [112] |
| | Soil/Compost Enhancement | Lignin breakdown in residues, humus formation | Improves fertility, accelerates composting, reduces accumulation | Slow rates, environmental dependency | Natural lignin (straw/wood chips) | [113] |
| | Textile and Dye | Lignin/dye degradation in effluents, biofinishing | Eco-friendly decolorization, fiber property enhancement | Variable efficiency, potential damage | ABTS, lignin co-substrate | [114] |
| | Pharma/Cosmetics | Bioactive phenolics/antioxidants from lignin | Natural sourcing, anti-inflammatory potential | Purity/low yield issues | Ferulic acid, lignin fractions | [115] |

**Some specific industrial applications of laccase have been discussed in the following section.**

### 5.1. In food industries

Laccases are essential in food industry applications such as baking, juice processing, and wastewater treatment [116]. For instance, haze formation during long-term beer storage can make it insoluble, reducing its shelf life and stability. To reverse this effect, laccases are added to eliminate residual oxygen, extending the beer's lifespan[117]. Similarly, during wine making, repeated pressing operations yield polyphenols and phenolic compounds that may lead to color darkening or flavor shifts. Laccases are used in immobilized forms to remove certain phenols and polyphenols [118]. Laccases can also cross-link biopolymers, increasing bread volume, texture, freshness, and flavor. Therefore, it applied to dough stabilize gluten networks during baking [119]. Studies show that laccase from the white-rot fungus *Trametes hirsuta* increases dough's maximum resistance, decreasing extensibility in flour and dough. In addition, fruit juices contain phenolic compounds and their oxidative derivatives, which impact flavor and color. So, fruit juices are stabilized by removing phenols and enzyme-substrate complexes through the use of laccases, thereby increasing color stability [119].

### 5.2. In textile industries

Laccases are used in the textile industry for denim finishing, indigo bleaching, and the decolorization of dyes such as Reactive Black 5, Malachite green, Reactive Orange 96 etc [120]. Around 1–20% of dyes produced globally are lost during textile industry dyeing processes. Regrettably, these carcinogenic waste textile productions are colored wastewater, which is organic in nature, severely disturbed ecosystems. Various physicochemical and biological treatments are available for removing dyes, but biological processes are more cost-effective and do not produce undesirable by-products [121]. Industrial dyes with tailored structures are stable against light, water, or chemical degradation. Given the limitations of traditional dye-removal processes, employing laccases has proven a viable means of eliminating dyes. Laccases, with the addition of specific stabilizers, are efficiently utilized to decolorize waste materials and also find application in bleaching various cloths and fabrics, one of the major textile applications being the bleaching of denim [122]. Laccases also contribute to color development by oxidizing aromatic compounds to produce dyes such as phenoxazines and azo dyes [123]. Laccases also remove odors during textile production and are therefore of immense value in washing detergents. Therefore, recent research is focused on laccase cocktails and condition tailoring. Biodegradable coatings and ongoing decolorization procedures are examples of emerging applications [124, 125].

### 5.3. In cosmetics and pharmaceuticals

The cosmetic industry has recently seen an increase in the number of laccase-related registered patents. Hydrogen peroxide ($H_2O_2$) and phenylenediamines, which are highly toxic and carcinogenic compounds, are prevalent in hair-dyeing products and may cause allergic reactions [124]. Consequently, laccases can detoxify these toxic chemicals based on their oxidizing capacity [120]. They are utilized as major biocatalysts in the production of hair dyes, deodorants, perfumes, soaps, and toothpastes [2, 3]. Laccases are also used as hair bleaches in combination with hydroxystilbenes. Notably, laccase-based

hair dyes are less irritating and simpler to apply. Protein-based skin whitening creams, newly formulated for dermatological use, contain some laccases [126].

In the pharmaceutical industry, laccases (multi-copper oxidoreductases) serve dual roles as green biocatalysts: they facilitate the synthesis of bioactive anticancer phenolics and degrade antibiotics, such as tetracycline, as well as contaminants such as diclofenac, ibuprofen, carbamazepine, bisphenol A, and triclosan [127-129]. Although byproduct toxicity, mediator dependence, and expenses are problems, they provide effective, environmentally friendly remediation and drug precursors.

Laccases also efficiently degrade a range of emerging contaminants commonly found in pharmaceutical wastewater and hospital effluents. For antibiotics like tetracycline (and related tetracyclines such as oxytetracycline or chlortetracycline), laccase-mediator systems (LMS) achieve high removal efficiencies often >90-100% within hours via ring opening, demethylation, deamination, or hydroxylation pathways, frequently resulting in complete loss of antimicrobial activity in the transformation products [130, 131]. Non-phenolic or recalcitrant pharmaceuticals, including diclofenac (an NSAID), ibuprofen, carbamazepine (an antiepileptic), bisphenol A (an endocrine disruptor), and triclosan (an antimicrobial), are similarly transformed [132, 133]. Phenolic compounds such as bisphenol A and triclosan undergo direct oxidation by laccase, whereas mediators (e.g., ABTS, syringaldehyde, or natural polyphenols) extend the substrate range to non-phenolics like carbamazepine, diclofenac, and ibuprofen by generating diffusible radicals, leading to reported removals frequently exceeding 80–100% under optimized conditions in batch or immobilized systems [134].

### 5.4. Laccase in woodworking and paper industries

Laccases bind lignin-derived material to create medium-density fine tiles, an affordable alternative to natural wood [135]. In addition, sawdust or wood shavings use to make noncircular (glueless, synthetic) woods, which is a potential application [136]. Therefore, it can help limit deforestation, a pressing environmental challenge, given that forests serve as the planet's lungs. So, laccases can accelerate the drying of painted surfaces, which is an odor-free, faster, and less toxic option for property owners [2, 3].

Paper manufacturing involves numerous processes, ranging from pulp manufacture and bleaching to the final production of paper. Paper is manufactured from wood-based and non-wood-based pulps, with eucalyptus as the primary source for commercial production due to its low-cost cultivation and high yield potential. Laccases play a significant role in the biological bleaching of kraft pulp from eucalyptus [137]. In recent era, laccases have transformed the paper industry and the pulping process in improving pulp brightness. It also facilitates the removal of lipophilic compounds from wood- and non-wood-based paper pulps, enhance the physicochemical and mechanical properties of pulp [138]. Another possible application is laccase mediator systems (LMS) confer energy-saving and high-yield pulp characteristics [139]. Lignocellulosic biomass is the primary raw material base for the pulp and paper industry. This energy-intensive sector focuses on separating lignin and the cellulosic fraction from biomass. Laccases have proved to be an incredibly potent reagent for delignification and detoxification of the pretreated lignocellulosic substrates, and subsequent saccharification

and fermentation processes are significantly improved [140]. In addition, they detoxify paper and pulp mill effluents [141]. Such versatile applications have made laccase one of the most powerful enzymes used in both present and future trends in industrial papermaking.

### 5.6. Laccase in green synthesis in nanobiotechnology

Laccases are used as biodegradable catalysts in organic synthesis to polymerize lignin monomers, create phenolic resins, polyphenols, biopolymers include nanobiotechnology, adhesives, and biobased plastics [142]. However, fabricating biofuel cells as pollution-free energy generators is a prominent nanobiotechnological innovation [143]. Entrapment of laccases on the cathode of miniature biofuel cells offers a more environmentally friendly power source [144]. However, fabricating biofuel cells as pollution-free energy generators is a prominent nanobiotechnological innovation [143]. Entrapment of laccases on the cathode of miniature biofuel cells offers a more environmentally friendly power source [144]. It is reported that laccases have been used to detect various molecules and compounds, such as phenols, oxygen, opioids (including morphine and codeine), and plant flavonoids, as well as for biosensor technology [145]. Laccase-based biosensors identify phenolic indices in juices, olive oil, honey, and beer; catechols in tea; polyphenols in wine; and lignins and phenols in water. They offer low cost, miniaturization, reproducibility, real-time monitoring, and high sensitivity, IoT integration and wearable sensors [146]. In addition, laccases are utilized as cathode catalysts in microbial and enzymatic biofuel cells to produce bioethanol at neutral pH with high selectivity, increase biogas yields by 25–46% [147]. These applications are significant in enhancing human health and well-being [148].

## 6. CHALLENGES OF APPLICATIONS OF LACCASE IN INDUSTRIAL SECTORS

Despite significant advances in laccase production, translating laboratory success into industrial-scale applications remains challenging due to cost, stability, and process robustness. To support non-specialist stakeholders like process engineers, investors, and sustainability officers, **Table 6** outline a strategic roadmap based on current evidence and emerging solutions.

**Table 6.** Key industrial barriers in laccase applications and actionable solutions.

| Barrier | Evidence from Literature | Recommended Action | Ref. |
|---|---|---|---|
| High production cost of recombinant strains | *P. pastoris* and *A. oryzae* show high yields (Table 9), but fermentation media and purification are expensive. | Shift to low-cost substrates: Use agro-industrial waste (olive mill waste, wheat bran) in solid-state fermentation (SSF). Studies report yields of 50,000–300,000 U/kg using SSF with minimal input cost | [149, 150] |
| Enzyme instability under industrial conditions | Laccases degrade at high temperature, extreme pH, or in the presence of inhibitors (heavy metals, halides) | Adopt enzyme immobilization: Use magnetic nanoparticles, CNTs, or biopolymers to immobilize laccase. This enhances thermal/pH stability, allows reuse (>5 cycles), and enables easy recovery from effluents | [151, 152] |
| High cost and toxicity of synthetic mediators | HBT increases decolorization efficiency but is expensive and potentially toxic. | Transition to natural mediators: Use non-toxic, low-cost alternatives like syringaldehyde, acetosyringone, or vanillin. Though slightly less efficient (60–90% vs. HBT), they are sustainable and safe for food/textile effluents | [153, 154] |
| Inhibitor sensitivity in real wastewater | Heavy metals ($Hg^{2+}$, $Pb^{2+}$), chelators (EDTA), and high salinity reduce activity. | Implement pre-treatment or enzyme engineering: For complex effluents, combine laccase with a pre-treatment step (pH adjustment, metal precipitation). Alternatively, engineer inhibitor-resistant mutants (directed evolution) or use robust fungal laccases (e.g., *Trametes* spp.). | [155] |

## 7. FUTURE TRENDS OF APPLICATIONS OF LACCASE

As visualized in **Figure 5**, the keyword analysis highlights a clear transition in the field: recent research (indicated by yellow nodes) is increasingly converging on industrial scalability and novel materials, moving beyond traditional descriptive studies on enzyme kinetics.

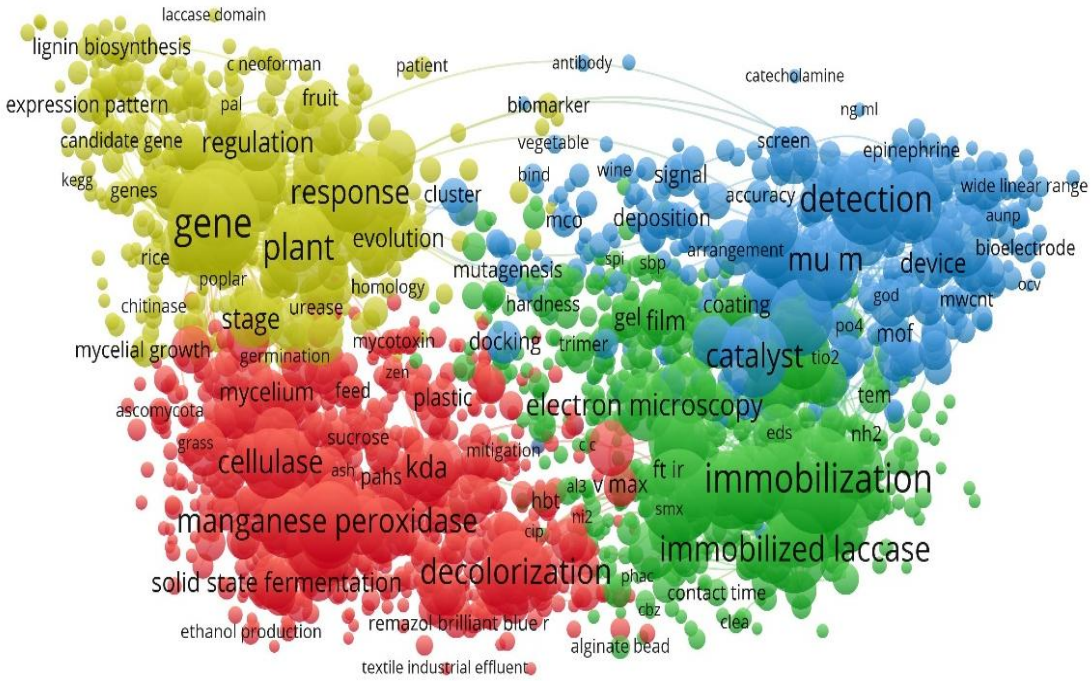


**Figure 5.** Science-mapping visualization of laccase research trends (2018–2025) generated using VOSviewer (Version 1.6.20). The network illustrates keyword co-occurrence, where node size corresponds to citation frequency. Color gradients indicate temporal shifts, with red nodes representing foundational studies (2018–2020) and yellow nodes highlighting emerging frontiers (2023–2025). The analysis reveals a significant shift from basic enzymology ('gene', 'expression') towards applied biotechnology, particularly in 'nanobiotechnology', 'waste-derived production', and 'laccase-like nanozymes.

The transition of laccase technology from laboratory to industrial application continues to evolve, driven by advancements in enzyme engineering, immobilization strategies, and integration with sustainable processes [156, 157]. Recent developments emphasize metagenomic discovery of extremophilic laccases for enhanced stability under harsh conditions (e.g., high temperature, pH, or salinity) [158, 159], molecular modifications via directed evolution and site-directed mutagenesis to improve redox potential and inhibitor resistance [157], and hybridization with advanced nanomaterials (e.g., metal-organic frameworks (MOFs), graphene, carbon nanotubes) for superior reusability, electron transfer, and catalytic efficiency in wastewater treatment [160, 161]. These innovations address longstanding barriers such as cost, operational

stability, and scalability, positioning laccase as a key player in circular bioeconomy initiatives, including lignin valorization for bio-aromatics, biofuel pretreatment, and micropollutant removal (e.g., pharmaceuticals, dyes) [162, 163]. Emerging applications extend to sustainable food packaging (biodegradable active films) [164], biosensors, and pharmaceutical degradation, while market projections indicate steady growth fueled by green chemistry demands, with the global laccase market expected to expand significantly through 2030–2034 at CAGRs of approximately 4–7% [165, 166]. However, successful scale-up remains contingent on co-development with process-specific conditions, robust piloting, and economic modeling to mitigate risks in complex matrices. These trends underscore laccase's potential as a cornerstone of eco-friendly industrial biotechnology, with phased implementation and interdisciplinary collaboration critical for widespread adoption.

In addition, future research should focus on microcredential based education for facilizing engineering microbial strains using tools like CRISPR to boost laccase yields in bacteria, yeasts, and fungi, enabling cost-effective production for bioremediation, biofuels and wellbeing of public health [167]. Developing low-toxicity natural mediators and Cu-based nanozymes could expand applications by improving stability across wider pH and temperature ranges, reducing environmental risks. Standardizing kinetic assays for optimal pH (3–9) and temperature (25–90°C) with substrates like ABTS is essential to resolve discrepancies and enhance enzyme tailoring for industrial use. Utilizing agro-industrial wastes, such as olive mill wastewater or grape marc, in solid-state fermentation promotes sustainable, low-cost laccase production through circular economy models.

## 8. CONCLUSIONS

Laccases exhibit diverse characteristics and are produced by a wide range of bacteria, fungi, and plants. The catalytic activities of laccases differ among microorganisms. The catalytic activity of laccase has found multiple applications, including the paper and pulp industries, industrial wastewater treatment, enzymatic bleaching, and bioremediation. Typically, parameters such as environmental conditions, culture conditions, and bioreactor dimensions must be optimized to maximize laccase production. Recently, emphasis has been given to expressing heterologous laccases to achieve large-scale production and enhance their catalytic activity and stability. Given the significant role of laccases in modern applications, it is not surprising that the enzyme remains a fascinating subject of global research, with further studies needed to fully explore its intricate biological character. These analytical insights and recent developments position laccase as a truly sustainable industrial biocatalyst in the 2025–2030 horizon.

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## CONFLICTS OF INTEREST

The authors declare no competing interests.

## ETHICS STATEMENT

This study did not involve any experiments on human participants or animals.

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