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Review

Laccase: A Green Solution for Environmental Problems

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Abstract

A multicopper oxidase, laccases catalyze the four-electron reduction of the substrate with the use of molecular oxygen. Laccases are abundant in nature and can be found in virtually every form of life on the planet. Generally speaking, laccases are classified into three types: blue, white, and yellow. Plant, bacterial and fungal laccases all have the same trinuclear copper site for substrate reduction. Non-phenolic as well as phenolic molecules are both capable of being catalyzed by this enzyme. Laccases are used in a wide range of industries that make use of phenolic chemicals. Laccases have been the subject of recent research because of their unique features. Laccase, its sources, manufacture, purification, and applications in many sectors are discussed in length in this review.

Keywords

Laccases; sources of laccases; application

1. Introduction

The search for ecologically friendly technologies has increased interest in using enzymes to replace conventional non-biological methods, which are increasingly becoming popular. Laccases (benzenediol: oxygen oxidoreductases; EC 1.10.3.2) have received the most attention in recent decades when comparing the many oxidant enzymes currently exist. In nature, laccases are multicopper oxidases that may be found in abundance. They catalyze the one-electron oxidation of phenolic compounds, resulting in the simultaneous reduction of oxygen to water in the presence of oxygen.

Laccases are found in various organisms, including higher plants, bacteria, fungi, and insects. Laccases were found for the first time in the exudates of the Japanese lacquer tree *Rhus vernicifera* in the nineteenth century, which is where they earned their name [1]. Laccase has been discovered in microorganisms mostly in fungi [2] and it is especially common in white-rot fungi engaged in lignin metabolism. In addition, certain bacterial laccases have been discovered in the last few years [3].

Laccases have a wide range of substrate specificities. They can catalyze the oxidation of both phenolic and non-phenolic substances [4]. Laccases are useful biocatalysts for a variety of biotechnological applications, including biobleaching of pulp, textile dye decolorization, xenobiotic bioremediation, biosensors, and the food industry [5]. This is due to their high and non-specific oxidation capacities, lack of requirement for cofactors, and ability to repeatedly use oxygen as an electron acceptor.

This review summarizes the detailed information about laccase's production, purification and applications to date.

1.1 Sources of Laccases

Laccases have been observed in plants, insects, fungi, archaea and bacteria.

1.1.1 Plant Laccases

In plants, laccases belong to the multigene family. Laccase was initially isolated from the sap of the Japanese lacquer tree *Rhus vernicifera* [1]. Other plants have been reported to contain laccases, including lacquer, mango, mung bean, peach, pine, prune, and sycamore [6]. Laccases come in a variety of forms in some plants. Eight laccases have been identified in *Pinus taeda* and five distinct laccases in poplar (*Populus trichocarpa*) xylem tissues [7]. Sycamore maple (*Acer pseudoplatanus*) cell suspension culture was also found to excrete laccase-like multicopper oxidases (LMCO) [8]. Four closely linked LMCOs had been recognized in yellow-poplar xylem tissues (*Liriodendron tulipifera*) [9]. Other species have been found to contain LMCOs, including *Zinnia elegans* [10], tobacco (*Nicotiana tabacum*) [10], and Zea mays [11]. A monocot laccase was also cloned and characterized from ryegrass also (*Lolium perenne*) [12].

Plant laccases are glycosylated enzymes having 22-45% glycosylation than the fungal laccases (10-25%). Mannose, *N*-acetyl glucosamine, and galactose are the major carbohydrate moieties of laccases. Thus, fungal laccases have lower molecular weight than plant laccases [13], 10-50% of their MW was due to glycosylation. Glycosylation is advantageous for secretion, copper retention, thermal stability, and enzyme activity [12, 14].

Plant laccases have found a role in lignin polymerization [8]. Transgenic approaches utilizing laccase genes for overexpression and down-regulation and using plant biomass for various purposes including energy production, phytoremediation, and alteration of phenolic metabolism, have also been used in the last decade or so [15].

1.1.2 Insect Laccase

In insects, laccases have been observed in the pharate pupal cuticle of *Drosophila virilis* [16], tobacco hornworm, *Manduca sexta* [17], the malaria vector mosquito, *Anopheles gambiae* [17] and the silkworm, *Bombyx mori* [18]. Laccase is also found in insects of many genera, *viz. Diploptera, Oryctes, Papilio, Bombyx, Calliphora, Phormia, Rhodnius, Drosophila, Lucilia, Manduca, Musca, Sarcophaga, Schistocerca* and *Tenebrio* [19]. Laccase is believed to be involved in cuticle sclerotization in insects due to its ability to catalyze the oxidation of phenolic compounds to their corresponding quinines [17].

1.1.3 Fungal Laccase

Numerous fungus species have been shown to possess laccase activity (Table 1). But several fungi do not produce laccase, such as *Zygomycetes* and *Chytridiomycetes* [20]. In fungi, laccase is thought to play a role in lignin biodegradation and infestation of decaying wood. Laccase is most commonly produced by basidiomycetes that cause white rot and the saprotrophic fungi that decompose trash. Laccase secretion has been observed in nearly all species of white rot fungi [21]. *Agaricus bisporus*, *Botrytis cinerea*, *Coprinus cinereus*, *Trametes versicolor*, *Pleurotus ostreatus*, *Ganoderma* sp., *Pleurotus sajor-caju*, *Schyzophylum commune* and *Flammulina velutipes*, *Mycena purpureofusca* and *Ceriporiopsis subvermispora* are some examples of basidiomycetes that produce laccases [22].

Table 1 Properties of different fungal laccases.

S. No.	Organism	Cellular localization	Optimum Temperature/Thermal Stability	Optimum pH/stability	Molecular Weight kDa	Km (µM)/Kcat (s^{-1})	Spectroscopic Properties	References
1	*Phytophthora capsici (rlac)*	Extracellular	30°C;	4.0/ABTS;	68	ND	Blue	[23]
2	*Trichoderma harzianum* S7113 LacA and LacB	Extracellular	50°C; 100%/40°C/3 h	LacA: 2.0/ABTS; 3.0/DMP; 3.5/SGZ; LacB: 5.0/ABTS; 100%/7.0/2 h 8.0/DMP; 7.0/SGZ 100%/7.0/2 h	Lac A-63; Lac B-48	0.1 mM/ABTS; 0.064 mM/ABTS	Blue	[24]
3	*Ganoderma lucidum* MTCC-1039	Extracellular	50°C; 90%/50°C/0.5 h	5.0/guaiacol	57	3 mM/ABTS; 21.36 mM/Guaiacol	Blue	[25]
4	*Phlebia brevispora*	Extracellular	40°C;	4.0/ABTS	180	-	Blue	[26]
5	*Agrocybe pediades*	Extracellular	45°C	5.0/DMP	55-60	100 µM/DMP	Blue	[27]
6	*Ganoderma leucocontextum*	Extracellular	70°C; > 90%/60°C/16 min	3.0/guaiacol	65	1.658 mM/Guaiacol;	Blue	[28]
7	*Gymnopus luxurians*	Extracellular	55°C-65°C; 63%/50°C/24 h	2.2/ABTS; 86%/2.2/24 h	64	539 µM/140 mM^{-1} s^{-1}	Blue	[29]
8	*Arthrographis* KSF2	Extracellular	50°C; 69%/60°C/1 h	74.4%/11/24 h	55	15 µM/ABTS	Blue	[30]
9	*Trametes polyzona*	Extracellular	55 °C; 64.38%/40°C/2 h	4.5/ABTS; 93%/6.5/2 h	66	8.66 µM/ABTS	Blue	[30]

10	*Trametes pavonia* EDN 134	Extracellular	27 °C	4.0/ABTS	45	-	Blue	[31]
11	*Pleurotus tuber-regium*	Extracellular	60 °C	4.0/ABTS	52	7.82 μM/ABTS	Blue	[32]
12	*Peniophora lycii*	Extracellular	Lac5 50%/70°C/10 min; LacA 50%/70°C/8 min;	-	Lac5 62 LacA74	-	Blue	[33]
13	*Marasmius* sp. BBKAV79	Extracellular	40°C	5.5/ABTS	75	3.03 mM/guaiacol	Blue	[34]
14	*Marasmius scorodonius*	Extracellular	75°C; 80%/70°C/100 min	3.4/ABTS	67	3.4/ABTS; 4.0/guaiacol; 4.6/DMP	Blue	[35]
15	*Cerrena unicolor* BBP6	Extracellular	60°C/ABTS; 80°C/guaiacol; 80°C/2, 6-DMP; 80%/50°C/2 h	2.5/ABTS; 4.0/guaiacol; 5.5/DMP; 82%/4.0/12 h	55	49.11 μM/ABTS; 1238.6 μM/guaiacol; 3430.8 μM/DMP	Blue	[35]
16	*Ceriporiopsis subvermispora*	Extracellular	50°C	2.0/ABTS	45	-	Blue	[36]
17	*Myrioconium sp.* UHH 1-13-18-4	Extracellular	>80%/15°C/1 h	>80%/4.0-6.0/1 h	72.7	4.2/SGZ; 104.9/ABTS; 67.8/DMP	Blue	[37]
18	*Hexagonia hirta MSF2*	Extracellular	40°C	3.4/ABTS	66	-		[38]

19	*Moniliophthora perniciosa* FA553	Extracellular	60°C/ABTS; 45°C/SGZ; 45°C/Guaiacol; 55°C/DMP; 50%/40°C/35 min	6.0/ABTS; 7.5/SGZ; 6.5/Guaiacol; 6.5/DMP; 70%/6-8/24 h	57	170/21.2/ABTS; 21/0.45/SGZ; 180/7.3/Guaiacol; 108/0.3/DMP	Blue laccase	[39]
20	*Pleurotus ostreatus*	Extracellular	40-70°C; 100%/40°C/5 h; 100%/50°C/10 min	3.5/DMP; 5.5/Guaiacol; 4.5/ABTS	68.4	46.51 mM/244.32/ABTS; 400 mM/208.33/DMP	Yellow	[40]
21	*Pleurotus fossulatus*	Extracellular	50°C; >50%/50°C/5 h; >50%/60°C/2 h	7.0/Guaiacol; 100%/3-6/1 h	Not given	0.083 mM/Guaiacol; 0.454 mM/ABTS; 0.041 mM/o-dianisidine	NA	[41]
22	*Coprinus comatus* rlac 3	Extracellular	60°C; 20%/60°C/30 min	3.0/ABTS; 5.5/SGZ; 5.0/Guaiacol; 5.0/DMP	75	0.087 mM/31.96/SGZ; 0.136/3.485/ABTS; 1.114/0.418/Guaiacol; 1.374/0.307/DMP	Blue laccase	[42]
23	*Coprinus comatus* rlac 4	Extracellular	65°C; 30%/60°C/30 min	3.0/ABTS; 5.5/SGZ; 6.0/Guaiacol; 6.0/DMP	70	0.204 mM/44.71/SGZ; 0.205/1.467/ABTS; 0.455/0.196/Guaiacol; 7.131/1.468/DMP	Blue laccase	[43]

24	*Pycnoporus sanguineus* CS43	Extracellular	Lac I-70°C; 50%/60°C/18 h Lac II-60°C; 50%/60°C/2.25 h	Lac I –2.5/ABTS; 3.5/DMO; 4.0/Guaiacol; 64%/6.0/100 h Lac II-2.5/ABTS; 3.0/DMP; 4.0/Guaiacol; 52%/6.0/100 h	Lac I –68 Lac II-66	Lac I-6.9/519.2/ABTS; 89.2/184.2/DMP; 1484.5/2472.5/Guaiacol Lac II-12.0/447.2/ABTS; 191.6/155.6/DMP; 1100.8/2084.4/Guaiacol	Blue	[44]
25	*Fomitopsis pinicola*	Extracellular	80°C; 40%/60°C/1 h; 20%/70°C/1 h	3.0/ABTS; 80-90%/1.5-11.0/1 h	92	200/ND/ABTS	Blue	[45]
26	*Panus conchatus*	Extracellular	50%/45°C/24 h; 50%/60°C/10 h	100%/4-12/24 h	56.1	11.6/ABTS; 101.1/DMP	White	[46]
27	*Trametes polyzona*	Extracellular	30°C; 90%/50°C/1 h	2.0/ABTS; 4.0/DOPA/Guaiacol/catechol; 5.0/DMP; 100%/6.0-8.0/24 h	71	150/594/ABTS; 503/38.2/DMP; 1890/92.2/Guaiacol; 4080/125/Catechol; 6280/83.2/DOPA	Blue	[47]
28	*Pleurotus florida*	extracellular	50°C; 50%/60°C/2 h	5.5/ABTS; 50%/6.0/1 h	54	21/364/SGZ; 38/1121/ABTS; 210/1466/DMP; 550/3310/Guaiacol	Blue	[48]
29	*Pycnoporus sanguineus* CS-2	Extracellular	65°C; 98%/60°C/24 h; 50%/70°C/4 h	3.5/DMP; 4.5/SGZ; 3.0/ABTS;	64.4	41/88/DMP; 23/231/ABTS	Blue	[49]
30	*Mycena purpureofusca*	Extracellular	50°C; 50%/40°C/40 min	2.2/ABTS; 100%/6-8/24 h	61.7	296 μM/ABTS	Blue	[50]

31	*Coriolopsis floccosa* MTCC-1177	Extracellular	40°C; 100%/45°C/1 h	5.0/DMP; 100%/4.0/1 h	64	112.5/5.16/DMP; 58/5.16/ABTS; 100/5.16/SGZ	yellow	[51]
32	*Psathyrella candolleana* HLS-2	Extracellular	60%/20°C/16 days; 50%/30°C/16 days	90%/7-8/40 days	-	-	Blue	[52]
33	*Ganoderma* sp.	Extracellular	50°C; 100%/30°C/150 min;	4.5/Guaiacol; 50%/6.0/6 h; 95%/5.0/64	62	217/guaiacol; 77/ABTS	Blue	[53]
34	*Coriolopsis byrsina*	Extracellualr	50°C; 33%/50°C/5 h	5.5/ABTS	57.7	31.6/37.4/ABTS	Blue	[54]
35	*Trematosphaeria mangrovei*	Extracellular	65°C; 55.71%/45°C/1 h; 2%/80°C/1 h	4.0/ABTS; 87.34%/4.5/30 min; 8%/6.0/1 h	48	1400/NDABTS	NA	[55]
36	*Shiraia sp.* SUPER – H168	Extracellular	50°C; 60°C/ABTS; 45%/60°C/2.5 h	4.0/DMP; 6.0/SGZ; 5.5/Guaiacol; 3.0/ABTS; 80%/6-7/96 h	70.78	190/7109/ABTS; 40/938/SGZ; 370/1476/DMP; 380/30.44/Guaiacol	Blue	[56]
37	*Ganoderma lucidum*	Extracellular	55°C; 50%/60°C/1 h	5.0/ABTS; 100%/	38.3	47/54/ABTS; 94/37/Guaiacol	Blue	[57]

Brown-rot fungi have not been reported to produce laccase. However, laccase-coding genes have been discovered in some brown rot fungi like *Gloeophyllum trabeum, Postia balsamea* and *Postia placenta* [58]. Laccase synthesis by ascomycetes has been reported numerous times. Phytopathogenic ascomycetes like *Melanocarpus albomyces*, *Cerrena unicolor*, *Magnaporthe grisea*, *Trichoderma reesei* and *Xylaria polymorpha* are reported to produce laccase [59]. Some soil ascomycete species of the genera *Aspergillus*, *Curvularia*, and *Penicillium* as well as some freshwater ascomycete species have been found to produce laccases [60].

In both ascomycetes and basidiomycetes, yeasts are a physiologically distinct category. The human yeast pathogen *Cryptococcus neoformans* (Filobasidiella) has been found to have laccase [61]. The laccase produced by this yeast can oxidize phenols and aminophenols but not tyrosine, indicating that it is a real laccase [62].

1.1.4 Acinomycetes Laccase

Actinomycetes are prokaryotic filamentous microorganisms. Various species of the genera *Streptomyces* are known to produce laccases, such as *S. griseus* NBRC 13350, *S. cyaneus* CECT 3335, *S. psammoticus* MTCC 7334, *S. ipomoea* CECT 3341, *S. cinnamomensis*, *S. sviceus*, *S. chartreusis* NBRC 12753, *Thermobifida fusca* [63].

1.1.5 Bacterial Laccase

Laccases from prokaryotic organisms have been overlooked because of a lack of knowledge regarding the variety and distribution of laccases within bacteria (Table 2). Over 2,200 bacterial genomes were studied by Ausec et al. [64]. They found that more than 1,200 laccase-like enzyme genes were present in bacteria. So many genes showed the presence of predicted signal peptides which demonstrated the possibility of extracellular transport of these laccase-exporting bacterial entities [65].

Table 2 Properties of different bacterial laccases.

S. No.	Organism	Cellular localization	Optimum Temperature/Thermal Stability	Optimum pH for different substrates	Molecular Weight kDa	Km (µM)/Kcat (s^{-1})	Heterologous expression	Spectroscopic Properties	References
1.	*Azospirillum lipoferum*	Intracellular	30°C; 70°C/10 min/100%, 80°C/10 min/40%	6.0/SGZ	Two fragments 81.5 and 16.3	34.65 µM	-	Blue laccase	[65]
2.	*Marinomonas mediterranea*	Intracellular	-	5.0/DMP; 6.5/SGZ	59	4800 µM, 8 s^{-1}/ABTS; 1.5 µM/19.13 s^{-1}/SGZ; 170 µM/28.80 s^{-1}/DMP	*E. coli*	Blue laccase	[66]
3.	*Bacillus sphaericus*	Spore coat protein	60°C	6.0/DMP	-	-	-	Blue laccase	[67]
4.	*Bacillus subtilis*	Spore coat protein	75°C; 80°C/240 min/50%	3.0/ABTS	65	106 µM/16.8 s^{-1}/ABTS; 26 µM/3.7 s^{-1}/SGZ;	-	Blue laccase	[68]
5.	*Sinorhizobium meliloti*	Intracellular	30°C	5.0/ABTS; 5.0/SGZ	95	4 µM/SGZ	---	Blue laccase	[69]
6.	*Bacillus halodurans*	Recombinant /Spore coat protein	45°C	7.5-8.0/SGZ	56	--	*E. coli*	Blue laccase	[70]
7.	*Thermus thermophilus* HB 27	Intracellular/recombinant	92°C; 80°C/14 h/50%	4.5/ABTS; 5.5/SGZ	53	900 µM/24.6 s^{-1}/ABTS; 1880 µM/6.47 s^{-1}/SGZ	*E. coli*	Blue laccase	[71]
8.	*Pseudomonas putida* F6	Intracellular	30°C; 30°C/91%	7.0/SGZ	59	110 µM/SGZ	-	-	[72]

9.	γ-proteobacterium JB	Intracellular	55°C; 60°C/30 min/50%; 55°C/120 min/50%	6.0/SGZ; 6.5/Guaiacol	120	10 μM/SGZ; 580 μM/Guaiacol	---	Blue laccase	[73]
10.	*Bacillus licheniformis*	Recombinant /Spore coat protein	85°C; 70°C/60 min/43%; 80°C/60 min/8%	4.2/ABTS; 7.0/SGZ; 7.0/DMP	65	6.5 μM, 83 s^{-1}/ABTS; 4.3 μM, 100 s^{-1}/SGZ; 56.7 μM/28 s^{-1}/DMP	*E. coli*	Blue laccase	[74]
11.	*Klebsiella* sp. 601	Recombinant /Intracellular	37°C;	8.0/DMP; 3.0/ABTS; 7.0/SGZ	58.2	490 μM/1.03 × 10^3 s^{-1}/DMP; 5630 μM/6.64 × 10^3 s^{-1}/ABTS 23 μM/4.68 × 10^2 s^{-1}/SGZ	*E. coli*	Blue laccase	[75]
12.	*Aeromonas hydrophila* WL-11	Intracellular	37°C; 70°C/10 min/>40%	2.6/ABTS; 8.0/DMP	58	940 μM/81.98 s^{-1}/ABTS; 1.83 μM/205.99 s^{-1}/DMP	*E.coli*	Blue laccase	[76]
13.	*Bacillus subtilis* WD23	Spore coat protein	60°C; 80°C/2.5 h/50%	6.8/SGZ	-	-	-		[77]
14.	*Bacillus* sp.HR03	Spore coat protein	70°C/250 min/50%; 80°C/45 min/50%	7.4/DMP, 4.0/ABTS, 7.0/SGZ	65	535 μM/127 s^{-1}/ABTS; 53 μM/3 s^{-1}/DMP; 5 μM/20 s^{-1}/SGZ	*E.coli*	Spore formation	[78]
15.	Lac591	Metagenome derived	55°C; 55°C/15 min/30%	7.5./Guaiacol;	57.4	1037 μM/10.81 s^{-1}/Guaiacol; 8 μM/0.031 s^{-1}/SGZ; 340 μM/96.25 s^{-1}/DMP	*E.coli*	Blue laccase	[79]

16.	*Bacillus pumilus*	Recombinant /Spore coat protein	70°C;	4.0/ABTS; 7.0/DMP; 6.5/SGZ	58	80 µM/291 s^{-1}/ABTS; 680 Mm/11 s^{-1}/DMP; 66 s^{-1}/SGZ	*E. coli*	Blue laccase	[80]
17.	*Bacillus* sp. ADR	Extracellular	40°C; Lost complete activity/50°C/1 h	3.0/o-tolidine; 4.0/DMP; 5.0/Guaiacol	66	----	-	Non-blue laccase	[81]
18.	*Ochrobactrum* sp.	Intracellular	37-40°C;	8.0/DMP; 3.6/ABTS; 7.5/SGZ	57.8	90 µM,7.94 s^{-1}/DMP; 72 µM, 2.95 s^{-1}/ABTS; 15 µM, 2.4 s^{-1}/SGZ	*E.coli*	Blue laccase	[82]
19.	Lac21	Metagenome derived	45°C	7.5/SGZ	-	-	*E.coli*		[83]
20.	*Stenotrophomonas maltophilia* AAP56	Intracellular	40°C;	5.0/ABTS; 7.0/DMP	66	2250 µM/1.07 s^{-1}/DMP; 160 µM/1.18 s^{-1}/ABTS	---	Yellow Laccase	[84]
21.	Bacillus sp.	Extracellular	35°C; 23 min/75°C/50%	3.0/ABTS	70	-	-		[85]
22.	*Bacillus vallismortis*	Spore bound	82°C; 70°C/10 h/50%; 80°C/4 h/50%	4.8/ABTS; 7.4/SGZ; 10 days/80%/pH 7.0/	55	22.7/ABTS; 476.8/DMP; 1062.4/Guaiacol	-	Non-Blue	[86]
23.	*Bacillus tequilensis* SN4	Extracellular	85°C/ 70°C/24 h/>80%; 65°C/24 h/100%;	8.0/Guaiacol, DMP, 5.5/ABTS, 6.5/SGZ	32	840 µM/73.15 s^{-1}/DMP;	-	Blue laccase	[87]
25.	*Micrococcus sp.*	Extracellular	40°C; 50°C/1 h/100%;	9.0;	23	---	-		[88]
27.	*Geobacillus thermocatenulatus* MS5	Extracellular	55-60°C;	4.0-5.0/ABTS;	Two subunits of 42.5 and 65	-	-		[89]

28.	*Bacillus subtilis strain* R5		55°C; 80°C/2.5 h/50%	7.0/SGZ;	58.5	12.72 µM/302 min^{-1}/SGZ	*E. coli*	Blue laccase	[90]
29	*Bacillus pumilus* ZB1	Extracellular/ Recombinant	25°C	4.8/ABTS;	55	35.454 µM/20.155 s^{-1}/ABTS; 6097.515 µM/0.252-^{1}/2,6-DMP;	*E. coli*	---	[91]
30	*Meiothermus ruber*	Recombinant	70°C; 70°C/half life/120 min	5.0/ABTS; 8.0/2,6-DMP; 7.5/SGZ;	50	27.3 µM/325 min^{-1}/ABTS; 3.01 µM/115 min^{-1}/2,6-DMP; 4.2 µM/106 min^{-1}/SGZ;	*E. coli*	Blue laccse	[92]

31	*Aquisalibacillus elongatus*	Extracellular	40°C; 25-55°C/6 h/80%; 75°C/6 h/50%;	6.0/ABTS; 8.0/2,6-DMP; 7.0/SGZ;	75	39. 2 µM/2150 s^{-1}/ABTS; 8.2 µM/1009 s^{-1}/2,6-DMP; 16.1 µM/918.8 s^{-1}/SGZ; 77.3 µM/414.5 s^{-1}/Catechol; 102 µM/318.8 s^{-1}/L-DOPA; 51.4 µM/675.0 s^{-1}/Gallic acid; 366.7 µM/56.3 s^{-1}/Guaiacol; 68.6 µM/44.3 s^{-1}/Hydroquinone; 14.0 µM/1231 s^{-1}/Pyrogallol; 25.1 µM/1471.9 s^{-1}/Tannic acid; 51.8 µM/462.5 s^{-1}/LTyrosine; 16.1 µM/282.4 s^{-1}/2,5-Xylidin;	-	---	[93]
32	*Sinorhizobium meliloti*	Intracellular	80°C; 50°C/2 h/58%;	5.5/SGZ; 2.2/ABTS; 3.5/Caffeic Acid; 5.0/2,6-DMP; 6.0/Ferulic Acid;	70	0.088 mM/3.46 s^{-1}/ABTS; 0.342 mM/48.7 s^{-1}/2,6-DMP; 0.019 mM/11.2 s^{-1}/SGZ; 0.244 mM/2.51 s^{-1}/Guaiacol;			[94]

33	*Bacillus sp.* PC-3	Extracellular	60°C: 60°C/180 min/99.1%; 60°C/240 min/70.2%;	7/Guaiacol;	36(single subunit)				[95]
34	*Bacillus sp.* MSK-01	Extracellular	75°C; 100°C/50%/5 min	4.5/ABTS; 8.0/Guaiacol	32	5.481 mM/19.32 μM min^{-1} ml^{-1}/Guaiacol; 1.624 mM and 25.53 μM min^{-1} ml^{-1}/ABTS	-	White	[96]
36	*Sphingobacterium* ksn-11	Extracellular	40°C; 40°C/48 h/100%;	4.5/ABTS; 7.0/SGZ;	90	2.12 mM/ABTS; 2.5/SGZ; 2.5/Guaiacol;			[97]
37	*Anoxybacillus ayderensis* SK3-4	Recombinant	75°C	7.0/SGZ	29.8	14.2 μM/SGZ	*E. coli*		[98]
38	*Bacillus licheniformis* NS2324`	Recombinant	45°C; 45°C/8 h/50%	8.0/Guaiacol; 7-9/24 h/50%	66	11.55/Guaiacol; 0.05 mM/ABTS	*E.coli*	Blue laccase	[99]

The first intracellular bacterial laccase was discovered in *Azospirillum lipoferum,* a non-moving soil bacterium [65]. The enzyme was discovered to be involved in the manufacture of melanin in this bacterium. *Marinomonas mediterranea*, a melanogenic marine bacterium, has also been found to produce laccase [66]. Polyphenol oxidase (PPO) from this laccase can oxidize substrates characteristic of laccase and tyrosinase enzymes [66].

Bacillus subtilis Cot A, an endospore coat component, is the most extensively researched laccase-producing bacterium [100]. The outer spore coat protein contains the Cot A gene, which encodes for a 65-kDa Cot A protein that produces brown spore pigment, a melanin-like substance, to protect the bacteria against UV light and hydrogen peroxide [100]. The protein has improved thermal stability compared to other laccases, with a half-life of around 2 hours at 80°C and an optimal activity temperature of 75°C [100]. In addition to this, *B. halodurans* [70], *B. licheniformis* [74], *B. safensis* [101], *B. tequilensis* SN4 [102, 103], *Bacillus sp.* MSK-01 [96], *B. amyloliquefaciens* [104], *B. marisflavi* strain BB4 [105], *B. licheniformis* VNQ [106], *B. licheniformis* NS2324 [99] are some other laccases reported till date.

Most of the reports of laccases are available from *Bacillus*; however, bacteria other than *Bacillus* have also been reported to produce laccase. Rosconi *et al.* [107] reported an intracellular laccase of 95 kDa in melanin-producing strain of *Sinorhizobium meliloti*. This lacacse is active at 30°C and has optimum pH of 5.0 for syringaldazine and ABTS as substrate. Tyrosinase activity was also detected in this strain.

Other intracellular laccases have been reported from *Stenotrophomonas maltophilia* AAP56 [84], *Aeromonas hydrophila* WL-11 [76], *Ochrobactrum* sp. [82], and *Proteus hauseri* [108]. A non-melanogenic alkalotolerant γ-proteobacterium JB isolated from industrial wastewater-drained soil has also been reported to produce a pH-stable laccase with no tyrosinase activity. This laccase is present intracellularly but secreted out after 16 h due to cell lysis. The enzyme was highly stable in the pH range 4–10 even after 60 days at 4°C [73].

Laccases have also been identified and characterized from thermophiles. Intracellular laccase from the hyperthermophilic bacterium *Aquifex aeolicus* VF5 [109] and *Thermus thermophilus* HB27 [71] have been isolated. HB27 laccase is active at 92°C and has a half-life of 14 h at 80°C and is the most thermophilic laccase reported to date.

Lac591 gene encoding a novel multicopper oxidase with laccase activity was identified through activity-based functional screening of a metagenomic library from mangrove soil [79]. Sequence analysis revealed that lac591 encodes a protein of 500 amino acids with a predicted molecular mass of 57.4 kDa. The recombinant enzyme demonstrated activity towards syringaldazine (SGZ), guaiacol and 2,6-dimethoxyphenol (2,6-DMP). The purified Lac591 exhibited maximal activity at 55°C and pH 7.5 with guaiacol as substrate and was stable in the pH range. This laccase was found to be active at 45°C and pH 7.5.

Recently, some extracellular laccase from bacteria has also been isolated and characterized *viz. Bacillus* sp. ADR [81], *Bacillus* sp. [85], *Micrococcus sp.* [88], *Geobacillus* sp. ID17 [110], *Anoxybacillus ayderensis* SK3-4 [98] etc.

1.2 Cellular Localization of Laccases

Laccases have been observed in plants, insects, fungi, archaea and bacteria. Despite their occurrence, their presence in a particular system depends on the laccase's role for that system. In

plants, laccases are found in the sap or tissue extracts. Most laccases from fungi reported so far are extracellular [19]. However, intracellular laccases from wood-rotting fungi have been reported. When cultivated on glucose, wheat straw, and beech leaves, *Trametes versicolor* produced laccases in both extracellular and intracellular fractions [111]. *P. chrysosporium* and *Suillus granulates* were also have intracellular and extracellular laccases [112]. There are also intracellular or cell wall laccase enzymes from *Neurospora crassa, Rigidoporus lignosus*, and one of the laccase isozymes from *Pleurotus ostreatus* [113]. *Irpex lacteus*, a white-rot basidiomycete, has laccase activity nearly completely connected with its cell walls [114].

Laccase's function in the body and the variety of substrates it can use are linked to the enzyme's location in the body. Melanin and other protective cell wall chemicals were formed by a cell wall and spore-associated laccases [7]. Laccase from actinomycetes is mainly extracellular. Laccase from *Streptomyces cyaneus* CECT 3335 [115], *S. psammoticus* [116], *S. ipomoea* CECT 3341 [117], *S. cinnamomensis* [118], *S. sviceus* [119] and *Thermobifida fusca* [120] have been reported to be secreted in the culture supernatant. However, intracellular laccase from *S. lavendulae* [121] and *S. coelicolor* [122] have been isolated and characterized.

In bacteria, mostly laccases are present in cytoplasm or spore bound [123]. Most of the laccases reported from different species of *Bacillus* are found as a component of spore coat protein Cot A. However, in recent years, extracellular laccase-producing bacteria have also been isolated. The Laccase from *Bacillus* sp. ADR has been reported to be produced extracellularly but ADR laccase is a non-blue laccase [81]. Another extracellular laccase has been reported from *Bacillus* sp. [85] and *Geobacillus thermocatenulatus* MS5 [89], *Micrococcus* sp. [88] and *B. tequilensis* SN4 [87], *Bacillus* sp. MSK-01 [124] and *B. licheniformis* NS2324 [99].

1.3 Characteristics of Laccase

Besides being similar in structure, laccases from different organisms exhibit different properties. Therefore, to study the properties of laccase, purification of the enzyme is necessary as the presence of other enzymes and media components in crude preparation may alter some of the characteristics of the enzyme. Laccases can be purified using a variety of methods. These techniques include membrane filtration, precipitation, anion exchange chromatography, gel permeation chromatography, and hydrophobic interactions. Purification efficiency can be increased by employing affinity chromatography with a phenolic group as the ligand. SDS-PAGE and the absorbance ratio at 280 nm to 600 nm are commonly used to determine laccase purification effectiveness.

1.3.1 Purification of Laccases

Purification of any protein is crucial for a better understanding of its functioning. Despite the diversity in the origin of enzymes and types, their purification can be carried out by a generalized approach, which includes the recovery of proteins, their concentration, and then purification using high-resolution chromatographic techniques [125]. The first step in the purification of any enzyme is its recovery. As most of the fungal laccases are extracellular, they are released into the fermentation media and separation of cells from the supernatant is generally done by centrifugation or filtration. Bacterial laccases are intracellular or spore-bound proteins; therefore, extraction of laccase involves a few steps. For intracellular laccases, cells are harvested by centrifugation and then

lysed by ultrasonication. Laccase from the spores of bacteria can be isolated by the method of Held et al. [126]. After the recovery, the next step is the concentration of enzyme which makes the volume manageable for subsequent purification steps [125]. This can be achieved either by ultrafiltration or by precipitation. Although ultra-filtration has been used by some workers [127] precipitation is the most commonly used concentration method. Protein precipitation is promoted by agents such as organic solvents, neutral salts, and high molecular mass polymers or by appropriate pH adjustment. Organic solvents and salts like ammonium sulfate, which lowers the solubility of the proteins in an aqueous solution leading to their precipitation, are generally employed for precipitation [128]. Ammonium sulfate precipitation has been used in various studies. Organic solvents mostly used for precipitation include ethanol and acetone. Various acetone concentrations such as 50-80% [96] have also been used to precipitate proteins having maximum laccase activity from the supernatant. Some researchers have used different concentrations of ethanol *viz.* 70% and 95% for the precipitation of laccases [129].

For further purification of laccase a combination of one or more chromatographic techniques *viz.* gel filtration chromatography, ion exchange chromatography (IEC), affinity chromatography (AC) etc., are used:

Ion Exchange Chromatography: Ion exchange chromatography using DEAE-cellulose resin has been widely employed in the purification of laccases [130]. Researchers have used other ion exchange resins to purify laccase include CM-Cellulose, Q-Sepharose FF, and DEAE sepharose CL-6B [130].

Affinity Chromatography: Most of the laccase are glycoproteins, so the concanavalin A-sepharose 4B affinity column was used to purify laccases [131]. The enzyme was eluted with a linear gradient of α-D-mannopyranoside [132]. Phenyl sepharose is one of the most commonly used hydrophobic interaction chromatography (HIC) matrices in the purification of laccase [133]. Other affinity adsorbents used for the purification of laccases include Con-A CL agarose [134], $Cu2^{+}$–iminodiacetic (IDA)–Sepharose [135] etc. Though this technique is a highly selective method of protein purification, the labile nature of some affinity ligands and high cost are the major limitations of this technique [125].

Gel Filtration Chromatography: The Sephadex range of fractionation gels (Sephadex G-75, G-100, G-200) are widely used for the purification of laccases [31, 136] Sephacryl based matrix such as sephacryl S-200 [137] have also been used by various workers for purification of laccases.

1.3.2 Molecular Weight of Laccases

A laccase consists of a single, two, or four glycoproteins. In addition to secretion, proteolytic destruction, copper retention, and thermal stability, laccase is thought to have a role in glycosylation [3]. 10-45% of the molecular weight of laccases is contributed by the covalently linked carbohydrate moieties [138]. Compounds of monosaccharides including hexoamines, galactose, fructose, and arabinose are found in the carbohydrate compound [7]. Mannose is one of the major components of carbohydrates attached to laccase [139]. Most bacterial laccases have a molecular weight of 55-65 kDa. Singh et al. [73] showed that the laccase from α-proteobacterium JB had a mass of 120 kDa. The molecular weight of some laccase was found to be around 30-36 kDa [140].

Laccase from actinomycetes mainly *Streptomyces* are of variable sizes [141]. Laccases from *S. sviceus* [119] are reported to be of 32 kDa. Laccase from *S. lavendulae* [121] and *S. cyaneus* [115] has a molecular weight of 70-75 kDa. Other reported *Streptomyces* laccases are in the range of 40-45 kDa. Laccase from *S. griesus* has the highest molecular weight of 114 kDa [142].

Fungal laccases reported to date are also of variable sizes. The laccase reported from *Ascomycetes* is generally in the range of 70-80 kDa [2]. Laccases from *Basidiomycetes* are generally from 50-75 kDa [142]. However, extracellular laccase from *Pluerotus sajor-caju* [143], *Postia placenta* [144], *Ganoderma lucidum* [145] and *Fomitopsis pinicola* [146] are in the range of 90-95 kDa.

1.3.3 Effect of pH

The optimum pH for laccase activity varies from substrate to substrate [70]. Generally, laccases have alkaline pH optima for phenolic compounds while the non-phenolic substrates like ABTS are oxidized by laccase in the acidic range [70]. The redox potential difference between the compound and the T1 Cu of laccase, which rises with pH, is the driving force for electron transfer between the phenolic substrate and laccase [70]. Fungal laccases generally have acidic pH optima for phenolic and non-phenolic substrates. Bacterial laccases have alkaline pH optima for phenolic substrates and acidic pH optima for non-phenolic substrates. The low pH optima for fungal laccases are because they grow in acidic conditions.

Generally, laccases are stable in wide ranges of pH. Bacterial and actinomycetes laccase are more stable in alkaline pH ranges. Laccase from *S. coelicolor* retains 100% activity for 48 h at pH 3.0-9.0 [122]. Similarly, *Streptomyces ipomoea* CECT 3341 laccase remains 100% stable for 36 h in the buffers of pH 5.0-9.0 [117]. Fungal laccase also exhibits broad pH stability. Laccase from *Xylaria polymorpha* retains 86% activity at pH 10.0 for 4 h [59]. Laccase from *Fomitopsis pinicola* is 80-90% active in the pH range of 1.5-11.0 for 1 h [147]. *Abortiporus biennis* J2 laccase retains 80% activity in the pH range of 4.0-7.0 for 24 h [148].

1.3.4 Effect of Temperature

The optimum temperature for laccase activity varies from strain to strain. Spore-bound bacterial laccases are generally highly thermostable because of their very nature. Laccase from *Thermus thermophilus has* optimum temperature of activity at 92°C [71]. Cot A laccase from *B. subtilis* is active at 75°C [149]. Extracellular laccase from bacteria has a temperature optima range of 35-50°C [88]. Laccase from *B. tequilensis* SN4 is active at 85°C and could retain more than 80% activity at 70°C in 24 h [103]. Laccase from actinomycetes has an optimum temperature range of 60-70°C [63]. Fungal laccases generally have optimum temperatures of 50-60°C [150]. However, laccase from *Fomitopsis pinicola* is active at 80°C, thus having the highest temperature optima reported among the fungi [147]. Fungal laccases are less thermo-stable than bacterial and actinomycete laccases.

1.3.5 Substrate Specificity of Laccases

Laccases of different origins have different preferences for different substrates. Laccases can oxidize a wide diversity of substrates, but kinetic studies have only been conducted on a few laccase-specific substrates. Guaiacol, syringaldazine, and 2,6-DMP (2,6-DMP) are the most commonly

studied phenolic compounds, while many authors have also looked at ABTS as a non-phenolic substrate. It has been found that laccase kinetic catalytic constants are highly variable [151]. Laccase *Km* values range from 1.5-7,500 nM [3]. 2,6-DMP and guaiacol have low affinity for laccases, while ABTS and syringaldazine have high affinity. There is no significant difference in the laccase's *kcat* values between different substrates.

1.3.6 Inhibitors of Laccase

As laccase is a copper-containing enzyme, metal ion chelators such as EDTA, and dimethyl glyoxime are good inhibitors of laccase activity. Anions such as F^-, Cl^-, N_3^-, CN^- and OH^- bind to the T2 and T3 copper atoms of laccases disrupting the electron transfer between substrate and oxygen, resulting in enzyme inhibition [70]. OH^- also prevents catalysis of substrates by laccases at higher pH causing inhibition of the enzymatic reaction. The inhibition by halides varies with different laccases. This can be due to the difference in the size of the solvent channel of TNC [70]. Several laccase inhibitors, such as Hg^{2+}, Fe^{2+}, fatty acids, sulfhydryl reagents, hydroxylysine, kojic acid, and ammonia detergents, can be employed in various ways [42]. They may chelate the Cu (II) atoms, modify amino acids, or change the conformation of the glycoprotein by affecting the laccase.

1.4 Laccase's Industrial and Biotechnological Applications

Laccases are useful enzymes due to their potential applications in various industries like the pulp and paper industry for biobleaching and bioremediation of effluent water, the textile industry for dye decolorization, the cosmetic industry for hair coloring, nanobiotechnology, the food and beverage industry, etc. [152, 153]. Laccases have also been applied to remove many recalcitrant compounds such as alkenes, para chlorophenols, dyes, herbicides, polycyclic aromatic hydrocarbons, benzopyrene, etc. [154]. Some of the applications of laccase are discussed below:

1.4.1 Food Industry

Recently, Mayolo-Deloisa *et al.* [155] reviewed the use of laccase in the food industry. Phenols and other aromatic compounds present in foods are good substrates of laccase. Waste from food industries is utilized to produce laccase. Banana peels were utilized for laccase production from *Aspergillus sydowii* NYKA 510 [156]. Akpinar and Urek [157] have utilized peach waste as a substrate for laccase production. Sweet lime peels were used as solid substrates for laccase fermentation from *Bacillus sp.* MSK-01 with a total activity of $687IU^{-g}$ [158]. Sondhi and Saini [159] have utilized fruit juice waste to produce laccase. They observed a maximum laccase yield of 1645 IUg^{-1} in solid-state fermentation conditions. Backes *et al.* [160] utilized pineapple crowns to produce laccase in a recent study.

Laccases can improve the quality of fruit products and lower their costs by altering them. Oxidation/cross-linking of the tyrosyl group in myofibril protein leads to rheological changes in meat products [161]. Laccase is widely used in the food industry for various purposes, including clarifying wine and beer [155] Ethanol, salts, organic acids, and phenolic compounds are some of the active components of wine, beer and must. Alcohol and organic acids are responsible for wine aroma while the phenolic compounds contribute to the color and taste of wine. Oxidative reactions (modernization) in musts and wines cause turbidity, color intensification, aroma, and taste

alteration. Laccase can oxidize the polyphenolic compounds in wine and beer thus causing clarification [139]. Laccase is also added at the end of the beer production process to remove unwanted oxygen and thus increase the shelf-life of beer [162]. Laccases are also responsible for cross-linking the biopolymers in wheat flour to improve the quality of baked products. Laccases oxidize the ferulic acid unit in arabinoxylans, pentosans, and pectins, leading to the gelling of cereal foods [163]. In flour and gluten dough, laccase from *Trametes hirsuta* has increased maximum resistance while decreasing dough extensibility [164]. The use of laccase in the baking industry has been reported to increase the textural quality of bread [165].

Laccases have also found application in fruit juice processing. During the juice extraction from fruits, various proteins, and polyphenols interact with each other, leading to haze formation in fruit juices. Using laccase to reduce the phenolics in fruit juices results in the clarity of juices [162]. Laccases are also applied to remove phenolics in food industry effluent water.

The olive mill effluent (OMW) is a byproduct of the olive oil production. The color of OMW depends on the age and type of olive used. Olive mill effluent contains high salt and organic matter levels, including pectins, sugars, tannins, and phenolic compounds. Laccase can be used to reduce the phenolic content of effluent and thus reduce the color of the effluent [166].

1.4.2 Cosmetics

Laccases have also found a role in the cosmetic industry. The use of laccases has been reported in hair dyeing to replace H_2O_2 in the developer. It is simpler to handle laccase-based hair colors than current hair dyes since they are less irritating to the skin. Laccase can also be used to make natural colors such as gallic acid, syringic acid, catechin, catechol, ferulic acid, and syringic acid, among other phenolic compounds, as a color for hair [140].

Laccase-containing dermatological preparations for skin lightening has also been documented [167]. Laccase can also be used to treat poison ivy dermatitis due to urushiol. Urushiol is a catechol derivative with alkene/allyl side chains found in the saps of trees. Laccase can polymerize urushiol to urushi and thus can be used as a topical agent for treating ivy dermatitis [167].

The use of laccase in deodorants has also been proposed. Sulfides, thiols, ammonia, amines, short-chain fatty acids, and other volatile chemicals can cause foul body odors. Because laccase can oxidize thiols and other sulfur-containing compounds, it can be used as an deodorant additive [31].

1.4.3 Nanobiotechnology

Electron transfer reactions may be carried out by laccases without extra cofactors, making them useful in biosensors [168]. Biosensors based on laccase for the detection of morphine and codeine [169], catecholamines [169], plant flavonoids [170], azo-dye tartrazine [171] and for electro-immunoassay [172] have also been developed.

1.4.4 Bioremediation & Biodegradation

Toxic chemical contamination of soil, water, and air has become one of our most pressing environmental issues. The pollution comes mainly from the industrial and agriculture sector where releasing harmful chemical compounds and pesticides to the air and water bodies results in serious health problems. Some hazardous chemicals such as benzene, toluene, 1,1-trichloro-2,2-bis (4-

chlorophenyl) ethane (DDT), xylene (BTEX), ethylbenzene and tri chlorotoluene (TNT) remain in the environment and are well-known carcinogens [173]. Laccases can be used for the degradation of these compounds [174]. Polyhydroxy hydrocarbons have also been reported to be degraded by laccases [19].

1.4.5 Plastic Degradation

Plastics are synthetic polymers obtained by polymerizing ethylene gas. Based on their density and branching, they are classified into low-density (LDPE) and high-density (HDPE) polyethylene plastics [175]. Plastic has persisted in the environment for as long as 1000 years. Degradation is extremely difficult with these materials. Researchers are working to solve the problem because of environmental concerns about the buildup of this type of plastic. In the past few years, plastic-degrading microorganisms that utilize plastic to grow and degrade have been reported. It was observed that laccase is the only ligninolytic enzyme produced in the culture of plastic-degrading bacteria [176]. Thus, laccase can also be applied to the degradation of plastics [175].

1.4.6 Disinfection

Laccase has also found application in the generation of iodine *in situ.* Iodine is widely used as a reagent in disinfectants. Laccases can oxidize iodide to iodine [177]. A laccase-iodide (LIS) used for disinfection can have several advantages compared to direct iodine use. Using iodide salt for handling, storage, and transportation is safer than using iodine. The amount of laccase in LIS can be easily adjusted to regulate the release of iodine from the iodine storage solution. LIS can be applied to sterilize drinking water, swimming pools, etc. It can also be used to disinfect minor wounds [178].

1.4.7 Pulp and Paper Industry

In the pulp and paper sector, natural resources are consumed at the highest rate globally (i.e., water, wood and energy). Therefore, it is a major contributor to water, air and soil pollution. Laccase can be used in the pulp and paper industry for bio bleaching of kraft pulp, bioremediation of effluent water and recycling of waste papers.

Bio Bleaching of Kraft Pulp. The use of laccases has been extensively studied for the bio-bleaching of kraft pulp and was first patented in 1994 [179]. Fungal laccases are widely used for the biobleaching of pulp [179]. Despite high thermo-alkali-stability, using bacterial laccase for pulp bio-bleaching is rare. This might be due to their intracellular/spore-bound localization which makes the subsequent purification and large-scale production steps difficult. Using bacterial laccase from γ-proteobacterium JB and *Streptomyces cyaneus* has shown a 21.1 and 18.4% reduction in kappa number by using ABTS as a mediator [180].

Mediators increase the efficiency of laccases for delignification [181]. Several natural and synthetic mediators, e.g., ABTS, HOBT, viol uric acid, etc., are used for pulp delignification. Using fungal laccases in the presence of HOBT resulted in a 20-27% decrease in the kappa number of eucalyptus kraft pulp [182]. Laccase from *B. tequilensis* SN4 was known to reduce the kappa number of pulp by 28% and increase brightness by 7.6% [103].

Moreover, using laccases in combination with hemicellulases has broadened the use of enzymes in the pulp and paper industry. Hemicellulases facilitate the removal of hemicelluloses such as xylan

and mannan, making the lignin layer accessible for degradation by laccase thereby reducing chlorine consumption [183]. Using dual/triple enzymes for bio-bleaching is a novel approach [184]. Woldesenbet *et al.* [185] have reported using laccase and/or xylanase and/or mannanase for the bio-bleaching of kraft pulp. When mannanase was used with a laccase mediator system, a 32.6% reduction in kappa number was observed, while a 40% reduction was observed with the triple enzyme. Anugral *et al*. [186] have treated pulp with a cocktail of laccase, xylanase, and mannanase enzymes which led to a 49.35% reduction in kappa number and considerable enhancement in the brightness (11.59%), whiteness (4.11%), and other pulp properties. Most importantly, no mediator system was used for the pulp biobleaching by laccase. They showed that 40% less chlorine consumption was required to obtain a paper of the same quality as that of pulp treated without enzyme but with 100% chlorine.

Bioremediation of Paper Industry Effluent. Laccase has also been used for the decolorization of paper industry effluent. Pulp and paper mills generate ample amounts of dark brown colored, highly alkaline effluent water called black-liquor which is characterized by having toxic chlorinated compounds such as chlorolignins, chlorophenols, and chloroaliphatics [187].

Various white rot fungi have been reported to treat paper industry effluent. *Gliocladium virens*, a saprophytic soil fungus had been reported to decolorize paper and pulp mill effluents by 42% [188]. Although fungal treatment of pulp and paper mills effluent showed significant results, the treatment is not feasible at the industrial level because high pH, high temperature, and oxygen limitation in the effluent treatment plant of pulp and paper mills prevent fungi from proliferating [189].

Laccase from *Bacillus tequilensis* SN4 reduced the color of effluent water by 83% BOD and COD were also reduced by 82% and 77% respectively [190]. Kumar et al. [191] reported a significant reduction of pollutants, i.e., kraft lignin 72.5%, color 62.0%, COD-45.05% and reduction in toxicity (80%) of effluent treated with *B. cereus* laccase. Kumar and Chandra [192] also reported up to 78.67% of decolorization by laccase from *Bacillus cereus* AKRC03.

Recycling of Waste Papers. Laccases have also found a role in the recycling of waste papers. Old newspapers (ONP) are one of the major sources of waste paper. Deinking of ONP pulp by laccase has attracted awareness for its reuse. Laccase can also be employed for deinking of ONP pulp as they are rich in lignin [193].

1.4.8 Textile Industry

Dye Synthesis. Laccase can also be used to synthesize natural dyes [194]. Laccases can naturally produce reactive colored quinones by the oxidation of various substrates. Some people, especially those in textile industries, develop allergic reactions from synthetic dyes. Natural dyes based on laccase are less irritant and not allergic to the individual. The colored products formed by laccase are soluble in water and thus can be used for dyeing fabrics [195].

Dye Degradation. The use of laccases has been reported for the degradation of textile dyes for bioremediation and denim finishing. Second, only to agriculture, India's textile industry is a major source of employment for its people. Textile manufacturing contributes to the national economy and environmental pollution [196]. Various inorganic, polymeric, and organic compounds are among the dyes employed by textile mills when dying fabrics [197]. To make clothing and other

products, the textile industry relies on three types of fibers: cellulose fibers like cotton, and rayon linen; polyester fibers like spandex polyester nylon acetate and protein fibers like wool angora mohair cashmere silk, etc. [198]. The textile industry uses a variety of dyes and chemicals depending on the type of fabric being produced. Many different types of reactive dyes (such as remazol and cibacron F), direct dyes (such as congo red, direct yellow 50), naphthol dyes (like fast yellow GC and fast scarlet R), and indigo dyes (like indigo white or indigo carmine) are used by manufacturers to color cellulose fibers. Protein fibers are dyed with lancet dyes and acid dyes (azo dyes, triarylmethane dyes, and anthraquinone dyes) (Blue 5G and Bordeaux B). Dispersed (yellow 218), basic (orange 37), and direct dyes (red 1) can be used to color synthetic fibers [154].

The fabric absorbs 70% of the dye in the dyeing process, while the effluent stream receives the remaining 30%. Dyes in the water absorb and reflect sunlight, disrupting algae's ability to photosynthesize [199]. Thermal and photochemical stability makes toxic dyes persistent in the environment for long periods [200]. According to India's Central Action Plan, the Ministry of Environment and Forests has designated the textile industry as a Red category polluter.

Effluent water from dyeing industries is treated utilizing chemical and biological methods [197]. Treatment processes for these effluents include simple sedimentation, aerated lagoons, and aeration of activated sludge, a flocculant, chemical flocculation, coagulation, and trickling filters and reverse osmosis [201]. Conventional treatment methods, even the most cutting-edge ones, cannot handle the highly colored wastewater generated during textile manufacturing [201]. Aside from that, these methods use a lot of energy and degrade dyes ineffectively. Because of this, reducing textile dye pollution also necessitates addressing the issue of dye degradation.

Laccase can decolorize dyes in effluents from the dye industry [154]. Literature has documented various degrees of decolorization in various types of dyes. As well as being used to remove the color from textile waste, laccase is also useful for bleaching fabrics and making dyes [5].

Synthetic Chemistry. Laccases play different roles in nature depending on the organism, and they are actively engaged in both catabolic and anabolic processes. A laccase-mediated reaction is a valuable tool in green chemistry for synthesizing biologically active compounds such as antimicrobial substances due to mild and environmentally friendly reaction conditions such as room temperature, atmospheric pressure, and the avoidance of organic solvents. Low molecular weight phenolics (monolignols and flavonoids) are typically oxidized to radical and/or quinone intermediates in normal anabolic reactions [202]. They combine to produce various dimeric products, many of which have biological activity. These dimers can make dimeric radicals, which can then self- or cross-couple to produce trimers, oligomers, and polymers because they still have phenolic activities [202]. As a result, laccases produce several dimers, such as lignans and related compounds, and polymeric products such as lignin, flavonoid polymers, melanins, quinones, cross-linked to cuticular proteins (for insect cuticle sclerotization), etc. Laccase-mediated homo- and heteromolecular coupling reactions result in antibiotics that have been derivatized or synthesized for the first time [203].

2. Conclusion

This review highlights the importance of laccase in different industries. The review encompasses detailed reports on different laccases and their properties. Laccase because of its very nature is a non-specific enzyme catalyzing both phenolic and non-phenolic substrates. Laccases are in various

industries for reducing the load of chemicals in industries. The complex nature of effluent water and chemical processes can be overcome by engineering laccases with site-directed mutagenesis and isolating more laccases from different sources. Existing literature suggests that laccase can be used for the bioremediation of various industrial effluents; however, the commercialization of said technologies is still in its infancy. In the future, developing more suitable immobilization techniques and increased production of laccase at a cost-effective rate can make its commercial application possible.

Author Contributions

Dr. Sonica Sondhi has written this manuscript and done all the communication. Ms. Navleen Chopra has also contributed in article formulation and Table formation. Dr. Naveen Gupta and Dr. Aditya Kumar helped in revision of the manuscript.

Competing Interests

The authors have declared that no competing interests exist.

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