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REVIEW ARTICLE

Bacterial laccase: recent update on production, properties and industrial applications

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Abstract Laccases (benzenediol: oxygen oxidoreductase, EC 1.10.3.2) are multi-copper enzymes which catalyze the oxidation of a wide range of phenolic and non-phenolic aromatic compounds in the presence or absence of a mediator. Till date, laccases have mostly been isolated from fungi and plants, whereas laccase from bacteria has not been well studied. Bacterial laccases have several unique properties that are not characteristics of fungal laccases such as stability at high temperature and high pH. Bacteria produce these enzymes either extracellularly or intracellularly and their activity is in a wide range of temperature and pH. It has application in pulp biobleaching, bioremediation, textile dye decolorization, pollutant degradation, biosensors, etc. Hence, comprehensive information including sources, production conditions, characterization, cloning and biotechnological applications is needed for the effective understanding and application of these enzymes at the industrial level. The present review provides exhaustive information of bacterial laccases reported till date.

Keywords Bacterial laccase · Phenolic compound · Laccase-mediated system · Response surface methodology · Multi-copper oxidase · Biotechnological applications

Introduction

Laccases (benzenediol: oxygen oxidoreductase; EC 1.10.3.2) are a versatile oxidoreductase enzyme having the capability to oxidize a wide range of phenolic and non-phenolic compounds by converting oxygen molecule to water on concomitant four-electron reduction (Hakulinen and Rouvinen 2015). These free electrons catalyze the oxidation of different aromatic and non-aromatic compounds as well as phenolic ring-containing amines substituted with various functional groups such as methoxy, amino, diamino and hydroxyindols and few other metal compounds $[Mo(CN)8]^{4-}$, $[Fe(CN)6]^{4-}$ and $[Os(CN)6]^{4-}$ (Chandra and Chowdhary 2015; Rezaei et al. 2017).

Laccases are ubiquitously found glycoproteins, ranging from various fungi to higher plants. It is mainly produced from fungi, especially white rot, and has been extensively exploited for the application in industrial processes due to their high redox potential. The commercial exploration of fungal laccases is usually hindered due to high fermentation period, low laccase yield and also their applicability only under mesophilic and acidic reaction condition. However, the majority of the industrial operations are carried out in extreme conditions, i.e., higher temperature and pH, and high salt concentration, and fungal laccase

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generally fails to work in these extreme environments (Du et al. 2015; Wang and Zhao 2016).

In recent years, the use and application of bacterial laccases are growing rapidly due to their many remarkable features in comparison to fungal laccase from the industrial point of view, such as work in a broad range of temperature and pH with enormous stability against various inhibitory agents (Guan et al. 2015). Moreover, bacterial laccases have some additional advantages because of their cost-effective use in industrial applications, which include broad substrate specificity, enzyme production in a short time, and easiness to clone and express in the host with suitable manipulation (Fernandes et al. 2014; Prins et al. 2015). Bacterial laccase is also useful in applications such as pulp and paper biobleaching, decoloration and degradation of textile dyes/effluent and biosensor development (Mathews et al. 2016).

Various bacterial laccases from different microorganisms are isolated, expressed in a suitable host and studied at the molecular level (Sharma et al. 2007; Singh et al. 2011; Narayanan et al. 2015; Chandra and Chowdhary 2015). In the proposed review, comprehensive information of all laccase-producing bacterial sources, characteristics of the enzyme, gene information and their application have been summarized.

Mechanistic aspect of bacterial laccase

Mode of action

Aromatic compounds are oxidized by polyphenolase which has copper proteins. This copper protein helps in the oxidation of the benzene ring-containing compounds, in which oxygen acts as the last electron receptor. Polyphenols are oxidized by a group of enzymes having oxidase activities: catechol oxidase (EC 1.10.3.1); laccases (EC 1.10.3.2); cresolase (EC 1.18.14.1) (Mathews et al. 2016).

The basic reaction mechanism of laccase involves the formation of two water molecules on the concomitant electron loss of a single oxygen molecule. This abstracted electron further leads to oxidation of various benzene ring-containing compounds (Solomon et al. 1996; Chandra and Chowdhary 2015). The catalytic properties of laccase have increased significantly; it plays an important role in the degradation of aromatic compounds which leads to cation generation. The cation formed from this reaction is generally less stable, and therefore converted into the stable product in the presence of laccase (e.g., quinine → phenol) or non-enzymatic reactions (e.g., hydration, degradation or polymerization) (Rubilar et al. 2008). The redox mechanism takes place due to the presence of four copper atoms that form the central part of this reaction. This is classified into three types: type 1 copper (T_1Cu), type 2 copper (T_2Cu) and type 3 copper (T_3Cu) (Fig. 1).

Substrate molecules are bound near the T_1-copper center which is shallower than the oxygen-binding center. One-electron abstraction occurs by an outer-sphere mechanism from the substrate to T_1 copper. Thereby, the substrate molecules are converted into free radicals that can undergo further oxidation or radical coupling reactions, resulting in the formation of oligomers or polymers. The abstracted electron moves from the T_1 center to the trinuclear cluster via a cysteine–histidine pathway that is highly conserved among multi-copper oxidases. This so-called super exchange pathway is built by overlapping redox active molecule orbitals of T_1 coordinating cysteine, backbone atoms and T_3 copper coordinating histidine residues (Solomon et al. 2008).

The trinuclear center which plays an important role in the catalytic mechanism is made up of Type 2 and 3 copper. The catalytic process begins after oxygen molecules attach to the trinuclear cluster and inhibit further entry of any other molecule. The T_2Cu site react with two molecules of histidine and one molecule of water, whereas T_3Cu react with three histidines and hydroxide molecules. In the final step, the oxygen molecule is converted to water by laccase in two steps. In the first step, first electron is reduced by T_2Cu and T_3Cu, whereas reduction of the second electron is assisted by the peroxide mediator which is directly entertained by the T_2Cu site and T_1Cu linked to T_3Cu by covalent Cys–His bonds (Madhavi and Lele 2009; Chandra and Chowdhary 2015).

Substrates and mediators for laccase

Laccase is a remarkably substrate-specific enzyme and, in general, it oxidizes a wide range of substrates such as phenolic compounds, phenylpropanoids, azo dyes and indigo dyes by the above-described reaction mechanism (Christopher et al. 2014). The laccase-catalyzed reaction is generally slowed down by a bulky substrate, which has a high redox potential. Laccase enhances the synthesis as well as breakdown reaction of various organic and aromatic compounds. The breakdown of environmentally harmful substances like pollutants leads to an eco-friendly environment, whereas the synthesis of complex compounds leads to bioremediation by producing non-toxic products (Cañas and Camarero 2010). Phenolic compounds such as hydroquinone and catechol are good substrates for the majority of laccases; moreover, methoxy-substituted phenolic compounds, syringaldazine, guaiacol and DMP (2,4-di-methoxy phenol), are commonly used substrates in various reactions (Niladevi et al. 2008).

Some of these mentioned substrates cannot be oxidized directly by laccase due to their large size, lower diffusion of

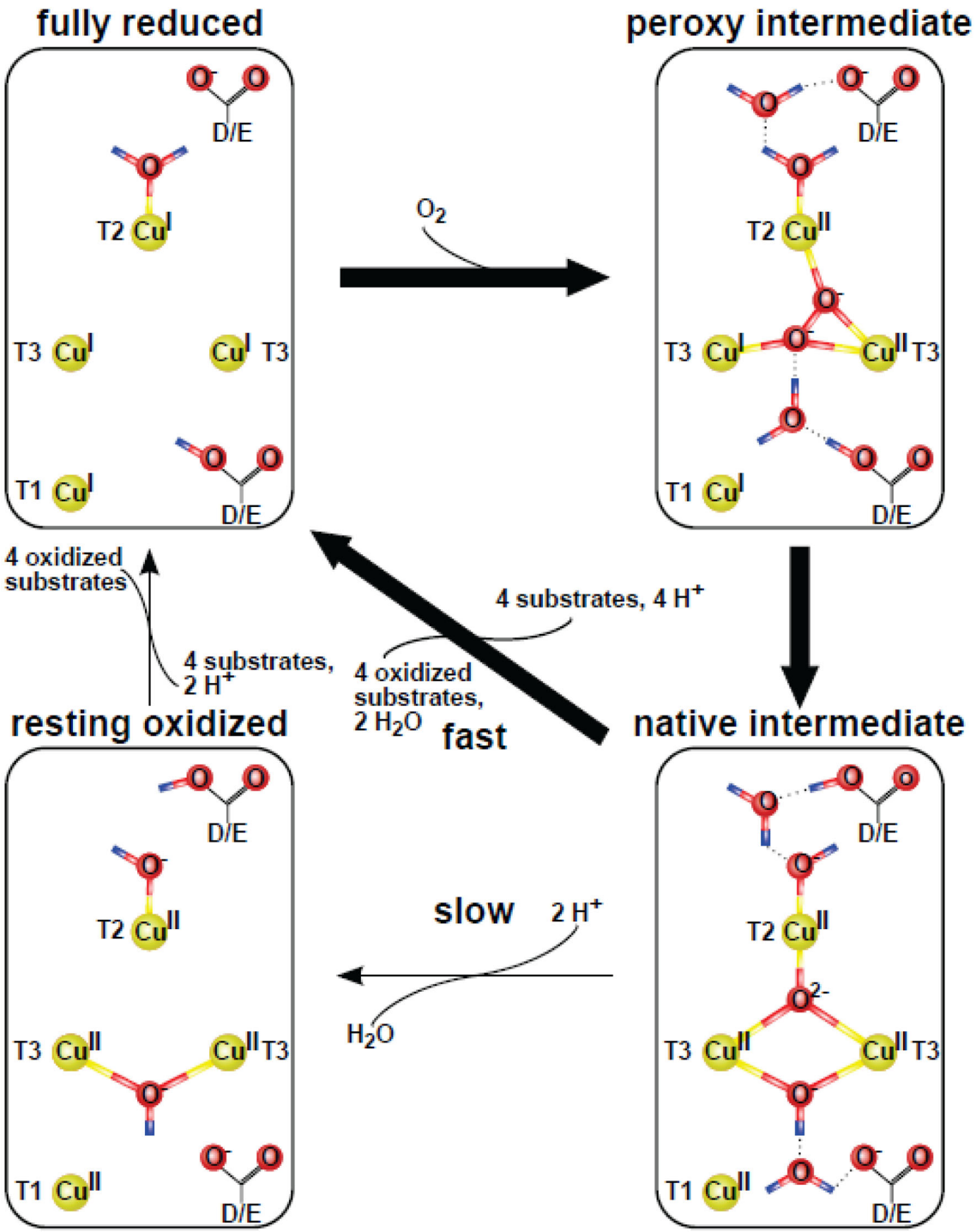

Fig. 1 General reaction mechanism of bacterial laccases (Solomon et al. 2008)

the substrates into the active pocket or due to the high redox potential of substrates. To increase the range of substrates oxidized by laccase, the reaction can be carried out in the presence of different mediators. The redox mediator acts as a intermediator for laccase substrates, which are first oxidized by laccase and thereafter the oxidized radical formed reacts easily with bulky or high redox potential substrates. The first artificial mediator to be used was ABTS (2,2′-azino-bis(3-ethylbenzothiazoline-6-sulfonic acid) (Madhavi and Lele 2009). The most effective mediators are the N-heterocycles bearing N–OH such as violuric acid, N-hydroxy-*N*-phenyl acetamide, *N*-hydroxybenzotriazole (Chandra and Chowdhary 2015). The various substrates and mediators used for laccase have been listed in Suppl Table 1.

Types of laccases

There are two types of laccases, true laccase and false laccase. Laccase which shows activity with tyrosine is called false laccase and that which does not show activity is called true laccase. Till date, blue laccase is the most studied in comparison to yellow/white laccase (Chandra and Chowdhary 2015). They can be further differentiated on the basis of three aspects. Firstly, an absorption spectrum of around 610 nm is always produced by blue laccase. Secondly, requirement of a mediator for degradation of non-phenolic compounds is mandatory for blue laccase. Thirdly, blue laccase can be extracted only from the liquid medium in the absence of lignin, whereas yellow/white laccase can be extracted from the solid medium (Mot et al. 2012; Chaurasia et al. 2013). Modification of blue laccase with lower molecular weight lignin degradation residues leads to the formation of yellow laccase having high redox potentials. It is assumed that yellow/white laccase possesses some endogenous phenolic compounds which are generated from lignin and act as an exogenous mediator for degradation of non-aromatic compounds (Pozdnyakova et al. 2006; Chandra and Chowdhary 2015).

Laccases classification and structural characteristics

Laccase is a versatile oxidase enzyme of the cupredoxin superfamily which comprises more than one copper atom. This superfamily consists many another oxidase enzyme such as manganese oxidase and ascorbate oxidase (Gray et al. 2000; Roberts et al. 2002). This suggests that all of them originated from the same parents having cupredoxin fold as a common signature. Various complex structures showing different functions have been generated by multiplication of cupredoin fold encoding gene. The typical Greek-key motif consists of a total of four β-sheets, each arranged on opposite sides which are joined by a hair pin loop, and the first sheet is directly connected to the fourth sheet by a longer connection (Fig. 2a) (Enguita et al. 2003). Previously, comprehensive information regarding the three-dimensional structure of microbial laccases has been published by Hakulinen and Rouvinen (2015).

Three-domain laccase

Very little information has been available on the structural aspects of bacterial laccase. To our knowledge, only one three-domain bacterial laccase, i.e., outer endospore coat component of *Bacillus subtilis* exhibiting laccase activity has been fully characterized and studied at the structural level (Enguita et al. 2002; Enguita et al. 2003). It is play a major role in the formation of brown pigment of the spore which helps them to protect against harmful ultraviolet ray-oxidizing agents (Hakulinen and Rouvinen 2015). The tertiary structure of very few different bacterial laccase i.e., *Escherichia coli* laccase (CueO) (Roberts et al. 2003) and *Campylobacter jejuni* (Silva et al. 2012) are known, but they show less enzymatic efficiency against phenolic molecules.

Structural analysis revealed that CotA is a monomeric protein and overall possesses three cupredoxin domains, as shown in Fig. 2b. The primary domain (represented in blue color in Fig. 2b) of the bacterial spore coat laccase which makes the N-terminal part has altered the configuration and possesses eight filaments arranged in a β-barrel shape, which joins the first and second domain, the support provided by H-bonds, giving compactness among all the domains (Enguita et al. 2003). The comprehensive loop of domain 2 (shown in green in Fig. 2b) of bacterial cotA laccase possesses a β-barrel made up of 12 filaments. This domain is centrally located among domains 1 and 3 (Fig. 2b); moreover, a small α-helical portion forms the link in the middle of domains 1 and 2, while the big loop portion links domains two and three (Fig. 2b). This specialty is a specific feature of the bacterial spore CotA laccase enzyme (Enguita et al. 2003). At the end, the C-teminal domain of the spore cot laccase (red color in Fig. 2b) comprises the mononuclear copper center and plays an important role in making attachment point from the T_3Cu center, present in the middle of domains 1 and 3 (Fig. 2b). In addition to this, the third domain also possesses an attachment site for the substrate near the T_1Cu center which is important for single-electron oxidations of reducing substrate (Fig. 2c, d). Moreover, additional specific characteristics of this laccase which does not exist in any previously identified multi-copper oxidases are the presence of overhanging cap-type element (made of coil and small loop) above the substrate attachment spot (Enguita et al. 2003). The detailed structure of CotA model showed high amount of hydrophobic bonds in cupredoxin domains and compact packing is a major parameter which plays a role in the thermostability of spore cot laccase (Enguita et al. 2003).

Two-domain laccase

This class of laccases has been described using laccase from *Streptomyces coelicolor* as a reference (Fig. 3). These so-called small laccases consist of only two domains with domain 2 of common laccases lacking. Domain 2 of three-domain laccases is responsible for connection and positioning of domains 1 and 3 in a way that enables the formation of the trinuclear cluster at the interface of domains

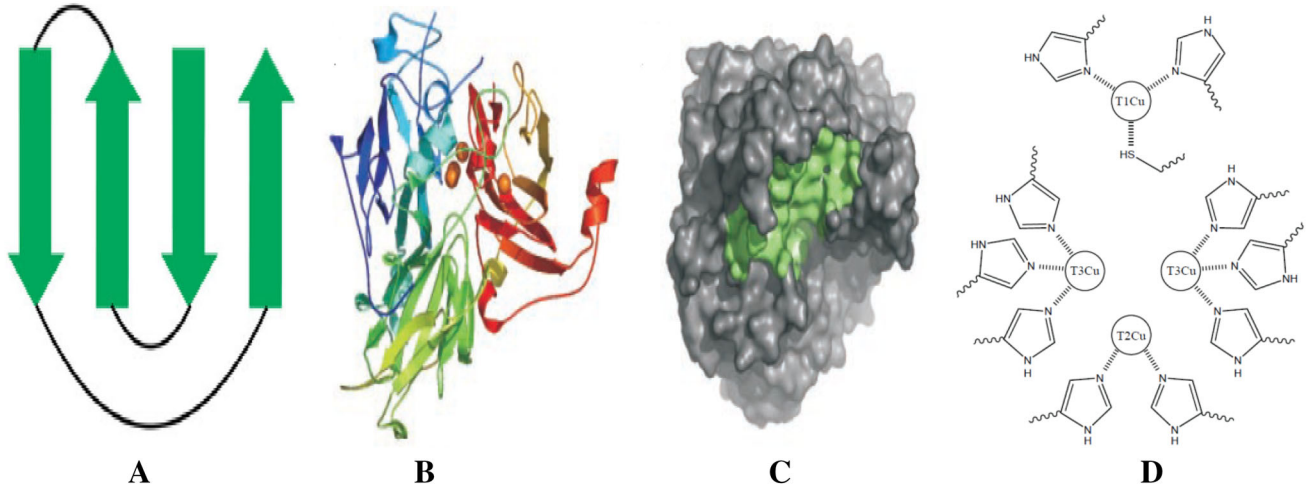

Fig. 2 Three-dimensional structure of cotA laccase from *B. subtilis*: **a** The classical Greek-key motif of multi-copper oxidase superfamily. **b** The trimer assembly of the enzyme with three domains is well represented in ribbon form. Domain 1 (blue; top right [N-termiuns]), Domain 2 (green; bottom right) and Domain 3 (red; right [C-terminus]) are structural domains containing mainly β-sheets including the localization of the copper atoms within the structure (plotted as orange balls) **c** Molecular surface representation of CotA with the putative substrate-binding pocket colored in green (D) Schematic represention of laccase copper sites. T1 copper is coordinated by two histidines and one cysteine in trigonal planar geometry. Two histidines ligate T2 copper, and the T3 copper pair is ligated by six histidine residues. T2 and T3 copper ions together form the trinuclear cluster (Enguita et al. 2003)

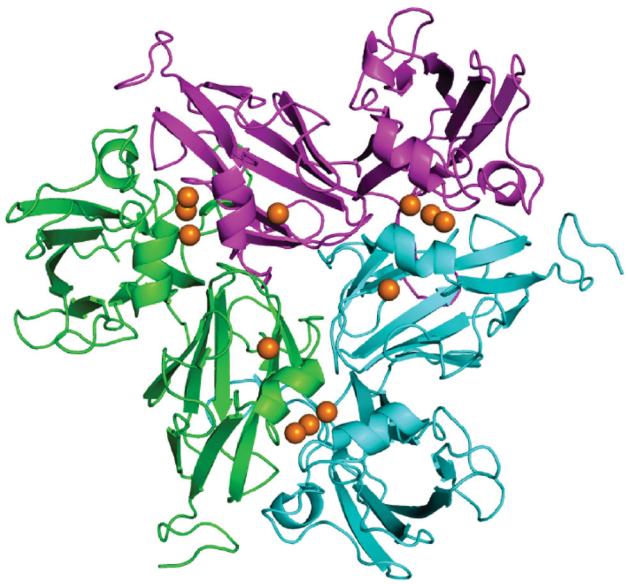

Fig. 3 Structure of the two-domain laccase SLAC from *Streptomyces coelicolor* (PDB: 3CG8); monomers are colored in magenta, green and cyan. SLAC forms homotrimers and the trinuclear cluster is located at the interface of domains 1 and 2 of neighboring monomers (Machczynski et al. 2004)

1 und 3. As a result of the absence of this domain in small, two-domain laccases, the formation of a trinuclear cluster within single molecules is impossible. Instead, the trinuclear cluster is built at the interface of individual laccase monomers (Fig. 3). Therefore two-domain laccases require oligomerization to form intact catalytic sites. Actually, for both two-domain laccases structurally characterized so far, the formation of homotrimers has been reported (Machczynski et al. 2004; Gunne et al. 2014).

Assay methods for bacterial laccase

Various methods are available for identifying laccase-producing bacteria (Kameshwar and Qin 2016). A plating method is effective for qualitative analysis of laccase-producing bacteria in the presence of a substrate. A commonly available method for identifying laccase activity in which the medium is supplemented with a substrate, i.e., DMP/guaiacol/ABTS/naphthol leads to the conversion of the colorless agar medium into a brown/reddish brown/-green/blue color (Neifar et al. 2016; Devasia and Nair 2016). Moreover, laccase activity could also be determined by inoculating a bacterial culture in a medium supplemented with a dye such as Poly-R and Azure-B. Decolorization of the polymeric dye by bacterial culture indicates laccase activity (Pointing 1999; Archibald 1992).

Laccase activity can be rapidly examined by chromatography method in which fractions of eluents are applied on filter paper coated with ABTS or DMP, leading to the formation of blue-green or yellow-brown color (Deker et al. 2000). Another simple, fast and easy method for laccase activity determination among another polyphenol oxidase (PPO) and peroxidase activities is the sodium dodecyl sulfate (SDS) method, which employs 4-amino-diethylaniline (ADA) and 4-tert-butyl-catechol (TBC) as a substrate showing different colors with respect

to enzyme activities. Laccase uses 4-amino-diethylaniline as a substrate, whereas in the presence of H_2O_2 peroxidase activity was observed using the same substrate. On the contrary, polyphenol oxidase, laccase and peroxidase use 4-tert-butyl-catechol as a substrate. All the stated above three enzymes showed step by step activity by producing pink or dark blue patches on the consecutive inclusion of 4-amino-diethylaniline, hydrogen peroxide and 4-tert-butyl-catechol (Rescigno et al. 1997).

Moreover, by flooding the plate with 1% emulsion of ferric chloride and potassium ferricyanide having lignin as a substrate, bacteria form a hollow region around them against a blue-green background (Pointing 1999). In an alternative method, laccase was put in the well made in the media containing different phenolic substrates i.e., guaiacol, ABTS, pyrogallol and 4-hydroxy 3,5-dimethoxybenzaldehyde. The formation of coloration in the vicinity of the well showed the presence of laccase (Pardo et al. 2013). Moreover, laccase activity can be detected (red brown color) by adding a few drops of 0.1% w/v p-cresol on bacterial culture growing on lignin-modifying enzyme basal medium (LBM) (Pointing 1999).

In the colorimetric method, the formation of a specific color is due to the action of the enzyme on various substrates such as ABTS, DMP, guaiacol, pyrogallol and L-DOPA. In PAH (polycyclic aromatic hydrocarbon) biodegradation method, 9,10-anthraquinone released from anthracene due to the existence of sodium borohydride was quantified at 419 nm (Pointing 1999). One unit of PAH activity is the quantity of laccase that produces 1 µmol of 9,10-anthraquinone/min under standard conditions. In iodide assay method, iodine + laccase was incubated (ABTS is added to the solution if mediated activity is required to be assessed) and the absorption measured at 353 nm.

In the fluorometric method, laccase solution pretreated with catalase is incubated with phenolic substrates such as hydroxyphenyl acetic acid (HPAA) and homovanillic acid (HVA). The fluorescence was monitored after the addition 0.1 M glycine buffer resulting in the formation of the fluorescence product. Laccase activity against HVA was expressed as H_2O_2 equivalents (Lonergan et al. 1997).

In the voltammetric method, laccase activity could be detected by putting platinum or glassy carbon electrode in Mcilvaine buffer. A specific amount of laccase enzyme and substrate was added and scanned for a specific time point. This method is accurate, simple and allows to monitor the consumption of the substrate. It is more reproducible than using Clark electrode (oxygen measurement) and spectrophotometry (Klis et al. 2007).

Overview of bacterial laccase

Bacterial sources

First, bacterial laccase, known as *Azospirillum lipoferum*, was isolated in the year 1993 from rice rhizosphere (Givaudan et al. 1993). Laccase has been produced from different bacteria that belong to different genera. All the laccase-producing bacteria reported till date have been summarized in Table 1. The bacteria are mainly Gram positive. e.g., *Bacillus*, *Geobacillus*, *Streptomyces*, *Rhodococcus*, *Staphylococcus*, *Azospirillum*, *Lysinibacillus* and *Aquisalibacillus* (Muthukumarasamy et al. 2015; Narayanan et al. 2015; Dhiman and Shirkot 2015; Sondhi et al. 2014; Verma and Shirkot 2014; Demissie and Kumar 2014; Margot et al. 2013; Lu et al. 2012; Wang et al. 2011; Diamantidis et al. 2000; Rezaei et al. 2017). However, some Gram-negative bacteria like *Pseudomonas*, *Enterobacter*, *Delfia*, *Proteobacterium* and *Alteromonas* are also able to secrete laccase (Neifar et al. 2016; Devasia and Nair 2016; Dhiman and Shirkot 2015; Mongkolthanaruk et al. 2012; Singh et al. 2010; Solano et al. 1997).

Production condition and properties of bacterial laccase

Various bacteria are known to produce laccase extracellularly however some bacteria are unable to secrete laccase outside the cell (Givaudan et al. 1993; Diamantidis et al. 2000; Chauhan et al. 2012). Various agricultural wastes such as saw dust, banana peel and rice bran have commonly been used as a substrate for laccase production because of their low cost and accessibility. Different monomeric sugars (lactose, mannose, maltose, glucose, fructose) constitutively produce laccase, but when the levels of those carbon sources decrease, laccase synthesis is further enhanced by lignin and phenolic compounds present in agricultural waste (Muthukumarasamy et al. 2015).

Laccase production is largely affected by nutritional (C/N ratio, the amount of dissolved oxygen, organic salts) and physical elements (optimum growth time, light intensity, pH and shaking conditions) (George et al. 2014; Narayanan et al. 2015; Rezaei et al. 2017). Different microorganisms need a distinct time for optimum laccase yield. This time length varies from 24 h in *Pseudomonas extremorientalis* BU118 (Neifar et al. 2016) to 96 h in *Bacillus tequilensis* SN4 (Sondhi et al. 2014). Like any enzyme, maximum yield of laccase produced from bacteria is found at ambient temperature (Devasia and Nair 2016; Sheikhi et al. 2012; Mongkolthanaruk et al. 2012; Lu et al. 2012; Wang et al. 2011; Singh et al. 2007, 2010) with the exception of

Table 1 Production conditions and characteristics of bacterial laccase from different microorganisms

S. no.	Name of organism	Carbon source/fermentation conditions	Substrate used in enzyme assay	Temp. optima (°C) of activity	Temp. stability	pH optima of activity	pH stability	Molecular weight of protein (kDa)	Reference
1	*Aquisalibacillus elongatus*	LB/37 °C/SF/150 rpm/72 h	DMP	40	>80%/25-55 °C/6 h	8.0	>40%/pH 5.0-10.0/ 6 h	69	Rezaei et al. 2017
2	*Bacillus subtilis* MTCC 1039	NB/37 °C/SF/180 rpm/60 h	Guaiacol	30	100%/30 °C/60 h	5.0	100%/pH 5.0	NR	Mishra and Srivastava, 2016
3	*Bacillus* sp. WT	SWN medium/35 °C/SF/ 150 rpm/14 days/pH 7.5	ABTS SGZ	37	>100%/70 °C/ 90 min	5.0 8.0	NR	180	Siroosi et al. 2016
4	*Pseudomonas extremorientalis* BU118	WB/SSF/72 h/pH 8	DMP	40–50	NR	8.0	100%/pH 7–10/24 h	NR	Neifar et al. 2016
5	*Streptomyces bikiniensis* CSC12	CAM/37 °C/SF/7 days	SGZ	6-7	NR	50–60	NR	69	Devi et al. (2016)
6	*Bacillus subtilis* MTCC 2414	Agro waste/30 °C/SSF/96 h/ pH 7.0	Guaiacol	30–40	NR	7.0	NR	53	Muthukumarasamy et al. (2015)
7	*Bacillus subtilis* MTCC 2414	Dextrose/40 °C/SSF/72 h/ pH7.0	Guaiacol	35	NR	9.0	NR	37	Narayanan et al. (2015)
8	*Bacillus cereus* TSS1	MM/37 °C/SF/12-16 h	Guaiacol	37	NR	7.0	NR	NR	Rajeswari et al. (2015)
9	*Pseudomonas luridas*train LR5.1 *Pseudomonas luridas*train LB6.2 *Lysinibacillussphaericus*strain LH3.4 *Bacillus subtilis* strain LB6.1 *Bacillus subtilis* strain LR6.3	M16 medium/37 °C/ 150 rpm/96 h	ABTS	32	NR	NR	NR	NR	Dhiman and Shirkot (2015)
10	*Bacillus tequilensis* SN4 MTCC 11828	M162/30 °C/150 rpm/96 h	DMP	85	100%/65 °C/24 h	8.0	75%/pH 9.0/24 h	32	Sondhi et al. (2014)
11	*Bacillus safenis* DSKK5	M162 medium/37 °C/ 200 rpm/48 h	NR	37	NR	6.2	NR	NR	Singh et al. (2014)
12	*Geobacillusthermocatenulatus* MS5	NB/60 °C/24-48 h	ABTS	60	NR	4.5	NR	42.5 65	Verma and Shirkot (2014)
13	*Pseudomonas aeruginosa*	MM/30 °C/60 h/pH 6.0	ABTS	37	NR	4.5	NR	NR	Arunkumar et al. (2014)
14	*Streptomycetes* sp.	SM/30 °C/24-72 h	ABTS	35	NR	6.0	NR	NR	Demissie and Kumar (2014)
15	*Streptomycetes cyaneus*	GYM/30 °C/SF/140 rpm/ 96 h/pH 7.2	ABTS	60	NR	4.5	50%/pH 9.0/82 d/25 °C	NR	Margot et al. (2013)
16	*Bacillus subtilis* WPI	NB/37 °C/SF/200 rpm	ABTS	25	NR	NR	NR	55	Sheikhi et al. (2012)

Table 1 continued

S. no.	Name of organism	Carbon source/fermentation conditions	Substrate used in enzyme assay	Temp. optima (°C) of activity	Temp. stability	pH optima of activity	pH stability	Molecular weight of protein (kDa)	Reference
17	*Bacillus licheniformis* LS04	LB/37 °C/SF/200 rpm/48 h	ABTS	60	44.56%/60 °C/10 h	4.4	123%/pH 7.0–9.0/ 10d/30 °C	NR	Lu et al. (2012)
			DMP			6.6			
			SGZ			7.4			
18	*Rhodococcus* sp.	NB/37 °C/48 h	ABTS	37	NR	3.0	NR	NR	Mongkolthanaruk et al. (2012)
	Enterobacter sp.			45		5.0			
	Staphylococcus saprophyticus			32		3.0			
	Delftiatsuruhatensis			37		3.0			
19	*Bacillus. subtilis*WD23	M9 Medium/37 °C/24-48 h	SGZ	60	50%/60 °C/68 h	6.8	50%/pH 5.0–7.0/ 240 h	NR	Wang et al. (2011)
20	*Stenotrophomonas maltophilia* AAP56	LB/30 °C	SGZ	40	100%/25 °C/ 30 min/pH 7.0	7.0	100%/pH 6.0–9.0/ 1 h	NR	Galai et al. (2009)
21	*Pseudomonas desmolyticum* NCIM 2112	NB/SF/30 °C/24 h	Hydroquinon	60		4.0		43	Kalme et al. (2008)
			DAB						
			O-Tolidine						
			ABTS						
22	γ-*Proteobacterium* JB	M162 Medium/37 °C/ 150 rpm/24 h	SGZ	55	>60%/50 °C/30 min	6.5	100%/pH 4–10/60 d/4 °C	120	Singh et al. (2007), (2008)
			ABTS						
			Guaiacol						
			Catechol						
			Hydroquinon						
			L-methly DOPA						
			Catechin						
			p-Phenylenediamine						
23	*Bacillus HR03*	NB/37 °C/170 rpm/18 h	SGZ, DMP	55	NR	5.5	NR	20	Dalfard et al. (2006)
24	*Pseudomonas putida* F6	E2 medium/2 h	SGZ	30	91%/30 °C/30 min/ pH 7.5	7.0	60%/5.0–9.0.0/ 30 min	59	McMahon et al. (2006)
			SGZ			8.0			
25	*Azospirillum lipoferum*	Rice Rhozosphere/ Intracellular	SGZ	70	100%/70 °C/10 min	6.0	NR	81.5	Diamantidis et al. (2000), Givaudan et al. (1993)
								16.3	
26	*Alteromonas* MMB-1	MB/25 °C	Tyrosine	37 °C	NR	5.0	NR	46	Solano et al. (1997)
			L-DOPA			5.0			
			DMP			5.0			
			SGZ			6.5			

NAM nutrient agar medium, *SWN* seawater nutrient agar, *WB* wheat bran, *CAM* Crawford's agar medium, *VMMB* Vogel's mineral media, *NB* nutrient broth, *SM* screening medium, *GYM* glucose yeast malt medium, *LB* Luria–Bertani, *DMP* 2,4-dimethoxy phenol, *ABTS* 2,2′-azino-bis(3-ethylbenzothiazoline-6-sulfonic acid), *SGZ* syringaldazine, *MB* marine broth

Geobacillus thermocatenulatus MS5, which requires 60 °C for production (Verma and Shirkot 2014).

According to literature, both types of fermentations (solid and submerged state) are suitable for maximum laccase production (Neifar et al. 2016; Devasia and Nair 2016; Muthukumarasamy et al. 2015; Sondhi et al. 2014). Statistical tools, i.e., Plackett–Burman and response surface methodology, are helpful in the enhancement of laccase production up to several fold by critical analysis of each factor; in the case of *B. tequilensis* SN4, the laccase activity increased by about 764-fold more in comparison to the control in simple medium (Sondhi et al. 2015). Similarly, under optimized condition, the activity of laccase from γ-proteobacterium JB gives 9.3-fold increases over the control (Singh et al. 2008), whereas laccase from *Pseudomonas aeruginosa* ADN04 produced 46.074 IU ml^{-1} after optimization of four variables (KH_2PO_4, Na_2HPO_4, NH_4Cl, NaCl and $MgSO_4$) (Arunkumar et al. 2014). The laccase production media for the isolated *Bacillus cereus* TSS1 was optimized using response surface methodology. The optimized media (9.03 U ml^{-1}) were found to have fourfold increase in laccase production compared to the unoptimized media (2.05 U ml^{-1}) (Rajeswari et al. 2015).

Summarized and comparative features of bacterial laccase are given in Table 1. Literature shows that the laccase of bacterial origin work in a broad temperature and pH range (30–85 °C and 3.0–9.0) (McMahon et al. 2006; Sondhi et al. 2014; Mongkolthanaruk et al. 2012; Devasia and Nair 2016, Narayanan et al. 2015) with the majority of bacterial laccase having an optimum temperature between 45 and 60 °C. *B. tequilensis* SN4 laccase exhibits maximum working temperature at 85 °C and pH 8.0 which is advantageous in various industrial processes such as pulp biobleaching in paper industry, where thermo-alkali stable laccase becomes mandatory (Sondhi et al. 2014).

Very limited knowledge is available in the literature on the effect of different organic solvents on spore laccase activity. Lu et al. 2012 showed that methanol, ethanol (up to 30%) acetone, acetonitrile and DMSO (up to 20%) promote the laccase activity of *Bacillus licheniformis* LS04, whereas beyond these concentrations these solvents inhibit laccase activity. Similarly, in the presence of various organic solvents (50%) petroleum ether, xylene, ether, acetone, chloroform and ethyl acetate, laccase from *Bacillus subtilis* WD23 retained more than 80% activity (Wang et al. 2011).

Different inorganic metals and detergents affect laccase yield distinctively in various bacteria. In most of the cases, inorganic metals such as Mg^{+2}, Hg^{+2} and Zn^{+2} inhibit the activity to a very high level by changing the conformation of protein, indicating that laccase enzyme yield was not dependent on positively charged metals (Muthukumarasamy et al. 2015; Sondhi et al. 2014). It was hypothesized that Hg^{+2} decreases the yield of laccase, showing the necessary role of thiol possessing amino acid in laccase activity (Liu et al. 2015). Moreover, inorganic minerals in high amounts (5 mM) such as Ca^{+2}, Cu^{+2}, Ni^{+2}, Co^{+2} and Mn^{+2} are generally known to accelerate laccase activity at a remarkable level by modifying the physical state of the substrate which directly increases the rate of reaction (Muthukumarasamy et al. 2015; Sondhi et al. 2014; Mongkolthanaruk et al. 2012). Anionic and cationic detergents such as SDS and CTAB positively affect the enzyme activity, whereas detergents comprising no charge like Tween-80 and Tween-20 did not change the activity (Dalfard et al. 2006; Sondhi et al. 2014). Various halides such as fluoride, chloride, bromide and iodide did not induce laccase activity (Sondhi et al. 2014).

The kinetics of laccases, i.e., Michaelis–Menten constant (K_m) and the catalytic efficiency (K_{cat}) data, have been shown for laccases of bacterial origin reported till date. K_m and V_{max} data for *Bacillus tequilensis* SN4 employing 2, 2,-azino-bis (3- ethylbenzothiazoline-6-sulfonic acid) (ABTS) is 80 ± 4 μM and 291 ± 2.7 s^{-1}; for dimethoxy phenol 680 ± 27 μM and 11 ± 0.1 s^{-1}; and for guaiacol 3.289 ± 0.06 and 63 ± 0.1, respectively (Sondhi et al. 2014), whereas for *Bacillus* sp. strain WT using ABTS the values are 132.7 μM and 309 s^{-1} and for SGZ 3.7 μM and 51 s^{-1}, respectively (Siroosi et al. 2016). Rezaei et al. (2017) calculated the K_{cat}/K_m of *A. elongates* using various substrates and it was found that 2,6-DMP was a good laccase substrate and its Kc_{at}/K_m was about 1.4, 2.1, 2.2 and 2.2 times higher than that of pyrogallol, tannic acid, SGZ and ABTS, respectively. All the information related to enzyme source, their production condition and characteristics of bacterial laccases is summarized in Table 1.

Cloning and expression of bacterial laccase gene

Recombinant protein expression facilitates higher production of a particular protein in a short time period and decreases the cost of production (Sharma et al. 2007; Singh et al. 2011; Chauhan et al. 2015; Mathews et al. 2016; Chauhan and Gupta 2016; Chauhan and Jaiswar 2017; Chauhan and Saxena 2016). Recently, several studies have been carried out on heterologous expression and manipulation of laccase gene of bacterial origin in a suitable host with the objective of overexpression, X-ray crystallographic studies. Moreover protein engineering studies are helpful in changing the characteristics of enzyme to make it more suitable for industrial applications (Guan et al. 2014; Chauhan et al. 2014a, b, c; Menaka et al. 2015; Shi et al. 2015a, b).

In most cases, bacterial laccase gene has been cloned and expressed in *E. coli* (Ghasemi et al. 2014; Mathews et al. 2016; Kalyani et al. 2016). High titer of laccase yield has been attained by expressing the laccase gene in a suitable host such as cloning *Thermus thermophilus* SG0.5JP17 putative laccase gene (LacTT) and *Bacillus licheniformis* in the heterologous host (*Pichia pastoris*) (Liu et al. 2015; Fang et al. 2012; Ihssen et al. 2015; Wang and Zhao 2016). Similarly, to enhance laccase yield (3420 UL^{-1}), the laccase gene from *Bacillus vallismortis* fmb-103 was cloned and heterologously expressed in *E. coli* BL21 (DE3) cells using auto-induction strategy during fermentation (Sun et al. 2017). Xia et al. (2016) optimized the fermentation conditions for the expression of laccase gene *lac1338* into *E. coli* through response surface methodology for maximum production of enzyme, which increased from nearly 2.13 times to 22.8 U mg^{-1}.

Researchers have also performed genetic manipulation experiment for enhancing enzyme yield. The expression of one (pHKFA-LacTT) and four (pHKFA-$LacTT_4$) recombinant plasmids of *Thermus thermophilus* into *P. pastoris* leading to increase in production up to 1.9-fold in the presence of methanol-inducible alcohol oxidase 1(AOX1) promoter (Liu et al. 2015). The activity and expression level of laccase have been increased (1.4- to 118-fold) by providing static culture conditions and simultaneously giving a limited amount of oxygen in the case of *B. pumilus* and *B. subtilis*. It was hypothesized that in a limited amount of oxygen condition, bacteria are unable to form the required amount of protein from the medium because of a decrease in the concentration of fermentable sugar or blend toward lower pH. An additional feature which affects the yield of active laccase enzyme in *E. coli* is the presence or absence of N-terminal signal peptides (Ihssen et al. 2015).

Protein engineering studies have also focused on bacterial laccase-like multi-copper oxidase (LMCOs) (Mate and Alcalde 2015), aiming at improving the activity or thermostability or specificity of an enzyme from *Bacillus* sp. HR03 using site-directed point mutations (Mollania et al. 2011). Secondly, Koschorreck et al. (2009) combined arbitrary and site-directed mutagenesis for enhancing the expression level and activity of cloned CotA laccase gene from *Bacillus licheniformis* in *E. coli.* Interestingly it was found that CotA double mutant showed 11.4-fold increased activity in comparison to the control, performed ferulic acid degradation rapidly (21 vs. 14%) and effective degradation of textile dye in comparison to the control. Similarly, in vitro transformation experiment was carried out for enhancing the substrate specificity (phenolic compound) of versatile metal-dependent oxidase produced from *Aquifex aeolicus*. Up to four cycles of arbitrary mutagenesis of the enzyme (mcoA) gene and thereafter computer-based shortlisting (~94 000 clones) give a variant having a higher catalytic efficiency (K_{cat}/K_m) than the wild-type enzyme. Interestingly, the recombinant variant exhibits enhanced solubility as well as higher kinetics and thermostability (Brissos et al. 2015). In a fourth example, substrate specificity of *B. subtilis* CotA was changed by simultaneous randomization of residues in the active site (Gupta et al. 2010). Moreover Ihssen et al. (2017) used site-specific mutagenesis in combination with DNA shuffling to produce variants of *B. pumilus* LMCO with higher catalytic efficiency for the substrate guaiacol, a model lignin compound. Mutant L9 showed a 1.39 mM K_m for guaiacol and a 2.5-fold increase in turnover rate ($K_{cat}/K_m = 2.85 \cdot 10^4$ $M^{-1}s^{-1}$). All the information related to the origin, host, gene size, molecular weight, fermentation conditions and characteristics of recombinant bacterial laccase is summarized in Table 2.

Application of bacterial laccase

Laccase has become an important industrially relevant enzyme that has a wide range of applications such as delignification of lignocellulosic material, bioremediation applications such as waste detoxification and textile dye decolorization. Some of the important industrial applications have been discussed below (Fig. 4).

Role of laccase in degradation of dye

The use of dyes has increased to the extent that approximately 10,000 various dyestuffs are used and generated yearly. The entire world generates approximately $7 \times 10^5 - 1 \times 10^8$ tons annually; out of this on an average one-tenth of the dyestuff penetrate the environment through industrial wastewater. Some of these dyes become recalcitrant against various environmental (temperature, light, pH) and biological (microorganisms) factors (Chandra and Chowdhary 2015; Shi et al. 2015a, b; Ba and Kumar 2017). Color from wastewater can be removed by various physical and chemical methods such as oxidation and flocculation, but suffer from problems such as cost, generation of chemical sludge. Therefore, the development of a biological process which can act on a wide range of waste is in great demand (Madhavi and Lele 2009; Narayanan et al. 2015). Bacterial laccase comprises many unique properties over fungal laccases, such as work in extreme conditions and salt tolerance which can be taken into consideration (Sharma et al. 2007; Pereira et al. 2008). A recent study displayed the degradation of an azo dye such as Sudan orange by bacterial laccase, giving maximum absorption due to decrease in the concentration of dye, whereas an increment in the absorption at 325 and 530 nm was due to

Table 2 Overview of heterologously expressed bacterial laccase (origin, host, gene size, molecular weight, fermentation conditions, optimum temperature and stability, optimum pH and stability, family, etc.)

S. no.	Origin	Host	Gene size (bp)/enzyme (aa/kDa)	Substrate	Carbon source/ fermentation conditions	Temp. optima (°C) of activity	Temp. stability	pH optima of activity	pH stability	Reference
1	*Bacillus vallismortis* fmb-103	*Escherichia coli* BL21	1542 bp/513 aa/ 70 kDa	ABTS	LB/16 °C/24 h	84	50%/70 °C/pH 4.8/ 10 h	4.8	90%/pH 8.0/ 45 °C/10 d	Sun et al. (2017)
2	*Bacillus subtilis*	*Escherichia coli* DH5α	NR	ABTS	NR	30	NR	11.6	NR	Wang and Zhao (2016)
3	*Meiothermusruber* DSM 1279	*E. coli* DH5α	1497 bp/499 aa/ 50 kDa	ABTS	LB/30 °C/180 rpm	70	50%/60C/120 min	5.0	NR	Kalyani et al. (2016)
4	*Paenibacillusglucanolyticus*SLM1	*Escherichia coli* BL21 (λDE3)	1701 bp/567 aa/ 90 kDa	ABTS	LB/37 °C/200 rpm/6 h	40	76%/60 °C/pH 7.0/ 4 h	7.0	68%/pH 5-7/ 24 h	Mathews et al. (2016)
5	*B. subtilis*	*E. coli*	62 kDa	ABTS	NA/37 °C/48 h/pH 7.0	NR	NR	8.0	NR	Menaka et al. (2015)
6	*Bacillus coagulans* LMCO	*E. coli*	1566 bp/522 aa/ 59.7 kDa	ABTS	LB/30 °C/180 rpm	30	>80%/70°C/30 min	4.0	NR	Ihssen et al. 2015
				DMP				7.5		
				SGZ				7.5		
				Guaiacol				8.5		
7	*Thermus thermophilus SG*0.5JP17-16	*Pichia pastoris*	1398 bp/466 aa/ 46 kDa	ABTS	LB/37 °C/200 rpm	90	>75%/80°C/4 h	4.5	>95%/pH 4-11/30°C/ 12 h	Liu et al. (2015)
				SGZ				6.0		
				Guaiacol				7.5		
				DMP				8.0		
8	*P. ananatis*	*E. coli*	120 kDa	ABTS	LB/30 °C/170 rpm/6 d	30–50	>40%/60 °C/ 10 min/pH 2.5	2.5	100%/pH 3.0/ 4 °C/12 h	Shi et al. (2015a, b)
				Guaiacol				4.5		
9	*Bacillus subtilis*	*E. coli*	1542 bp/513 aa/ 62 kDa	SGZ	LB/37 °C/220 rpm/20 h	37	NR	5.0	NR	Ghasemi et al. (2014)
10	*B. pumilus* strain W3	*E. coli*	NR	ABTS	LB/37 °C/48 h	50	NR	3.0–9.0	100%/pH 7.0–9.0/ 50 °C/10 d	Guan et al. 2014
				SGZ						
				DMP						
11	*B. licheniformis*	*Pichia pastoris*	1542 bp/513 aa/ 59.07 kDa	SGZ	LB/37 °C/200 rpm/12 h	70	50%/70/6.9 h	6.2	100%/7–9/ 30 °C/ 10 days	Lu et al. 2013
12	Uncultured Bacterium lac21	*E. coli*	1389 bp/463 aa/ 52 kDa.	SGZ	NR	45	>60%/35 °C–50 °C	7.5	95%/pH 6.0–8.0/ 4 °C/1 h	Fang et al. (2012)

Table 2 continued

S. no.	Origin	Host	Gene size (bp)/enzyme (aa/kDa)	Substrate	Carbon source/ fermentation conditions	Temp. optima (°C) of activity	Temp. stability	pH optima of activity	pH stability	Reference
13	*Ochrobactrum*.sp.531	*E. coli*	1092 bp/364 aa/ 57.8 kDa	DMP ABTS SGZ	LB/23 °C	37	NR	8.0 3.6 7.5	>80%/pH 7.5/37 °C	Li et al. (2012)
14	*B. pumilus* DSM 27	*E. coli*	1530 bp/510 aa/ 58.6 kDa	ABTS DMP SGZ	SRB/30 °C/150 rpm/24 h	37	NR	4.0 7.0 6.5	NR	Reiss et al. (2013)
15	*B. licheniformis*	*E. coli*	1069 bp/513 aa	ABTS	TB/37 °C/600 rpm/24 h	37	NR	4.0	100%/p H 5.0–7.0/ 37–70 °C	Koschorreck et al. (2009)
16	*Aeromonashydrophila* WL-11	*Escherichia coli*	1605 bp/534 aa/ 58.5 kDa	ABTS DMP	LB/20 °C/200 rpm	37	40%/70 °C/10 min	2.6 8.0	NR	Wu et al. (2010)
17	*Streptomyces ipomoea* CECT 3341	*E. coli*	1008 bp/336 aa	ABTS DMP	YEME medium/28 °C/ 180 rpm	37	NR	5.0 8.0	NR	Guijarro et al. (2009)
18	*B. subtilis*	*E. coli*	1069 bp/513 aa/ 65 kDa	ABTS SGZ	LB/30 °C	75	50%/80 °C/ 112 min	3.0 7.0	NR	Pereira et al. (2008)

LB Luria–Bertani, *NA* nutrient agar, *SRB* sulfate reducing bacteria medium, *TB* Terrific Broth, *YEME yeast extract malt extract medium*, *DMP 2,4 dimethoxy phenol*, *ABTS* 2,2′-azino-bis(3-ethylbenzothiazoline-6-sulfonic acid, *SGZ* syringaldazine

Fig. 4 Various industrial applications of bacterial laccase

the generation of biotransformation products, i.e., oligomeric products (Pereira et al. 2008; Singh et al. 2014).

Lu et al. (2012) reported decolorization of three synthetic dyes: anthraquinone, azo and indigo by spore laccase produced from strain *Bacillus licheniformis* LS04 in the presence and absence of intermediator acetosyringone. However ,the addition of acetosyringone increased the decolorization efficiency and 80% dye decolorization was observed within 1 h. Similarly, there was degradation of triphenylmethane dyes such as malachite green, aniline blue and brilliant green by *B. vallismortis* fmb-103 laccase with the help of a mediator like ABTS, acetosyringone and syringaldehyde (Zhang et al. 2012).

Wang et al. (2011) reported the removal of the color of complicated anthraquinone dyes (due to an aromatic ring) such as Remazol Brilliant Blue R, methyl orange, Congo red, Alizarin red by *B. subtilis* WD23 enzyme at alkaline pH in the deficiency of nutrients and mediator. Moreover, thermoactive laccase produced from *Bacillus subtilis* successfully degraded azo and anthraquinone Sudan orange G (SOG) dye except for reactive yellow (Pereira et al. 2008).

Kalme et al. (2008) reported color removal study of dye by oxidoreductases enzyme from *Pseudomonas desmolyticum* NCIM 2112. Analysis through FTIR suggests that unsymmetric degradation of the azo bond is highly preferred by the laccase, but it was more specific toward the phenolic compounds having NH^{+2} and sulfonic group in the meta position.

Guijarro et al. (2009) showed that recombinant laccase of *Streptomyces ipomoea* CECT 3341 cannot decolorize the azo-type dye Orange-II without the addition of mediator like acetosyringone. Alkaline laccase produced from a recombinant strain of *Bacillus licheniformis* completely degraded synthetic dyes such as carmine and reactive black within 1 h (Lu et al. 2013). Narayanan et al. (2015) reported the decolorization sequence of synthetic dye T Blue > Yellow GR > Orange 3R by immobilized laccase

from *B. subtilis* MTCC. Fang et al. (2012) reported decolorization of reactive azo such as Reactive Deep Blue M-26GE dye by Lac21 with the mediator and without a mediator.

Artificial phenolic compounds were degraded (90%) through laccase from *T. thermophillus* in the absence of costly intermediators in the first few hours. Congo Red dye was decolorized with high efficiency by LacTT in alkaline condition having optimum activity after 24 h in the presence of NaCl. It is assumed that at high concentration of chloride at which majority of the effluents are treated, fungal laccase may lose their activity. Hence, the above laccase should be an ideal candidate for the cleaning of textile effluent (Liu et al. 2015).

Liu et al. (2017) isolated salt-tolerant strain *Bacillus circulans* BWL1061 to remove 50 mg/L methyl orange and 50 mg/L Cr(VI) under anaerobic condition with 60 g/L NaCl. During the decolorization process, the Cr(VI) reduction occurred preferentially over the dye decolorization due to the dominant utilization of electron by Cr(VI). The analysis of enzyme activities suggested that azoreductase, NADH-DCIP reductase and laccase were associated with decolorization of methyl orange.

Role of laccase in pulp and paper industry

Paper manufacturing and recycling companies face major problems in the eradication of phenolic compound such as lignin and development in the visible characteristics of pulp. This can be achieved using various chemicals based methods, but they are highly hazardous and lead to increased environment pollution. This trigger the use of ligninolytic and hemicellulolytic enzymes which satisfies the entire requirement. The enzymatic deinking improves brightness, whiteness, remaining ink, etc., which indirectly saves energy and overall costs (Virk et al. 2013; Saxena and Chauhan 2016). Enzyme-mediated bleaching of old newsprint pulp is helpful in the enhancement of brightness by removing the lignin component (Hakala 2011; Xu et al. 2007, 2009) (Fig. 3).

Till date, most of the laccases have been isolated and characterized from fungi that are unable to degrade lignin, whereas bacterial laccase has not been much explored (Sharma et al. 2007). The individual enzyme can adequately degrade phenolic compound because of its high redox potential. The incorporation of mediator increases the availability and dimension of the enzyme against non-aromatic ring-containing compounds. Researchers have hypothesized that in the non-availability of intermediator compounds, enzyme molecules are unable to arrive inside the cell wall of wood because of its large size and, therefore, unable to degrade phenolic compounds (Saxena and Chauhan 2016).

Singh et al. (2008) explored the application of laccase produced from γ-proteobacterium JB to perform biobleaching of soda pulp using the statistical method. Results show that enzyme treatment enhances brightness, tear index and burst index and decrease kappa number by 5.89, 8, 18 and 21.1%, respectively. Enzyme treatment significantly decreases the chlorine consumption up to 10% to achieve the same brightness of pulp sheets.

Sondhi et al. (2015) explored the use of extracellular thermo-alkali stable laccase from *Bacillus tequilensis* SN4 for pulp biobleaching. There were 7.6% enhancement in brightness and 28% decrease in lignin content retained in the absence of *N*-hydroxy-benzotriazole mediator, as well as 12% enhancement in brightness and 47% decrease in lignin content in the presence of a mediator.

Researchers showed that laccase can work more efficiently in combination with hemicellulolytic enzymes for efficient deinking and biobleaching of pulp. The combination of enzymes, i.e., xylanase and laccase, could be an effective tool for decreasing the content of lignin and related compound from the pulp (Valls and Roncero 2009; Saxena and Chauhan 2016). Virk et al. (2013) showed that old newsprint can be recycled through a combination of the physical method (sonication and microwaving) and enzymatic method (laccase and xylanase), i.e., (S–MW–XL) that leads to 28.8% increase in brightness and 73.9% reduction in ERIC content.

Gupta et al. (2015) co-produced thermo-alkali stable ligninolytic and hemicellulolytic enzyme by growing two different *Bacillus* sp. in the same medium in solid-state fermentation for deinking and biobleaching.The combination of xylanase and laccase revealed a synergistic effect for the enhancement of pulp properties. With dual cultivation, there are many advantages like better substrates utilization, enhanced enzyme yield as well as the inhibitory effect on the growth of non-desirable microorganism.

Role of laccase in the textile industry

Laccases are able to degrade phenolic, aromatic amine, their substituted compounds having various functional groups as well as non-phenolic compounds (Sondhi et al. 2015) (Fig. 3). Therefore, it is possible to use laccase enzyme in the textile industry for the removal of textile dyes and phenols and waste detoxification. Till date, laccases produced by fungi have been widely employed for the degradation of dyes present in textile effluents due to their greater redox potential (Couto and Herrera 2006). Moreover, nowadays researchers have explored the use of bacteria laccase for the degradation of textile dye due to their interesting properties such as production in short time, inexpensive media and stable nature.

Textile dyes, especially Bromophenol blue and Congo red, were successfully decolorized by laccase from *Geobacillus thermocatenulatus* MS5 (Verma and Shirkot 2014), whereas commercially available dyes used for textile were also decolorized satisfactorily by *B. safensis* DSKK5 in different carbon sources (Singh et al. 2014).

Wang and Zhao (2016) showed that the color removal of simulated textile effluent (STE) through a recombinant laccase enzyme was 77.0% after 48 h. The decolorization rates of purified and crude CotA laccase were much higher when STE was buffered at neutral pH.

Role of laccase in pollutant degradation

Polycyclic aromatic hydrocarbons (PAHs) are the main pollutant distributed evenly in a natural environment like soil, air or aquatic environment (Fig. 3). They consist of a benzene ring arranged linearly, angularly or in clusters (Zeng et al. 2011; Li et al. 2010). Most of these pollutants and their intermediates are hazardous for humans as well as carcinogenic to living beings. These aromatic hydrocarbons are xenobiotic in nature due to their low water solubility and poor degradation rate (Ihssen et al. 2015). Till date, few reports are available which show the ability of bacterial sp. to degrade xenobiotic compounds (Zeng et al. 2011; Menaka et al. 2015). It is hypothesized that laccase enzyme converts polycyclic aromatic hydrocarbons to their quinines form and thereafter carbon dioxide. When an enzyme is employed along with mediator HBT, it converts acenaphthylene and acenapthylene to 1,2-acenapthalenedione and 1,8-napthelic acid (Madhavi and Lele 2009).

Rajeshwari and Bhuvaneswari (2016) showed that purified laccase from *Bacillus* sp. PK4 converts 92% Bisphenol A (BPA) into 4-ethyl-2- methoxy phenol as an end product. Similarly, degradation of benzo[a]pyrene (BaP) by laccase leads to the formation of methyl 3-hydroxy-8-methoxy-9,10-dioxo-1-propylanthracene-2-carboxylate, benzene acetic acid methyl ester as well as polymeric/multiple oxidized products detected by GC–MS analysis.

Menaka et al. (2015) identified. 13 among 2400 isolates, which have the ability to degrade 2, 4-dichlorophenol. Out of them, the most promising isolate was identified as *Bacillus subtilis*. Laccase-mediated removal of chlorophenols is a low-cost, environmentally friendly and highly efficient biochemical process.

Margot et al. (2013) showed that laccase from *Streptomyces cyaneus* are capable of oxidizing three micro-pollutants (BPA [bisphenol A], inflammatory drug DFC [diclofenac] and MFA [mefenamic acid] in acidic pH.

Laccase and biosensor technology

Laccase act on a wide range of substrates and it is capable to react with phenolic compunds therefore it can be useful in biosensor technology (Fig. 3). Oxygen and various reducing substrates (especially phenols and anilines) which are catalyzed by laccase are easily detected when combined with a different physical instrument that acts as biosensor. Generally, biosensors based on laccase are of two types: the first type monitors spectrum variation (at an absorbance of 600 nm) of enzyme, whereas the second type monitors voltage changes from a modified oxygen electrode (Madhavi and Lele 2009). Singh et al. (2010) immobilized alkali-tolerant laccase on nitrocellulose membrane which reacted linearly to various substrates like syringaldazine, catechol, catechin and L- DOPA even at low concentrations.

Role of omics techniques in various industrial applications

The inherent difficulty of lignocellulose and phenolic compounds degradation due to their recalcitrance and biological toxicity of products will require an engineered organism or a community of organisms to improve the efficiency and stability of the process (Zuroff and Curtis 2012). To gain a better understanding on how lignocellulose or phenolic compounds breakdown occurs, different omic techniques (genomics, transcriptomics, proteomics, chemoproteomics and metabolomics) are used to measure or sequence any molecule in isolated cultures or microbial communities. Multi-omic measurements use a system biology-based approach by merging both traditional molecular and biological techniques, paired with high-resolution and high-throughput instrumentation, to collect mass quantities of gene, protein and cellular data, optimizing the architecture of discovery and validation methods in science. Altogether, these multi-omic measurements allow a detailed analysis of the biological processes and the identification of key microbial pathways for successful progress in various industrial applications (Rosnow et al. 2016).

Bacterial candidates able to degrade lignocellulosic polysaccharides have been identified by omics techniques. The genomic analysis of endophyte *Pantoea ananatis* Sd-1 cultured in rice straw revealed four putative laccases, Lac1 to Lac4. However, only Lac4 contains the complete signature sequence of laccase and shares 64% sequence with other characterized bacterial multi-copper oxidases. Lac4 could decolorize various synthetic dyes and exhibit the degradation rate of 38% for lignin (Shi et al. 2015a, b). Furthermore, proteomic analysis of *P. ananatis* Sd-1 confirmed that considerable amounts of proteins involved in lignocellulose degradation were only detected in rice straw cultures. Rice straw saccharification levels in the secretome

of *P. ananatis* Sd-1 reached 129.11 ± 2.7 mg/gds (Ma et al. 2016).

NG et al. (2013) carried out the proteomic approach to identify the gene and enzyme which play important roles of bioelectricity generation and dye-decolorization from the bacterium *Proteus hauseri* ZMd44. Using peptide sequences from tandem mass spectroscopy and the whole genomics annotation of the closely associated strain, two full length genes of 543 bp (laccase; role in oxidation and reduction reaction) and 1086 bp (Omp F, porin; role in providing channel for related proteins) were cloned, which played the crucial role for azo dye decolorization.

Thermophilic bacteria are a potential source of enzymes for the deconstruction of lignocellulosic biomass. In an interesting study carried out related to metagenomic and proteogenomic analyses of bacterial consortium, switchgrass was degraded at high temperature with high levels of glycoside hydrolase and ligninolytic activities. Major abundant bacterial community members from the genera *Thermus*, *Rhodothermus*1, *Gemmatimonadetes*, *Paenibacillus*, *Rhodothermus*2, *Thermobaculum*, *Sphaerobacter*, and *Thermomicrobium* exhibit two, two, five, three, two, two, nine and three types of putative laccases involved in lignocellulose deconstruction (Dhaeseleer et al. 2013). Moreover, using omic approach a designer cellulosomes were constructed (able to degrade cellulose, hemicelluloses and lignin simultaneously) by combining dockerin-fused laccase (from aerobic bacteria *Thermobifida fusca*) into cellulosome (from anaerobic bacteria). The resultant chimera yielded a twofold increase in amount of reducing sugars released from wheat straw compared with the control, giving the route to alternative fuels production (Davidia et al. 2016).

Taking natural coal as a "seed bank" of new bacterial strains which are able to degrade lignin, 393 and 483 bacterial strains were isolated from a meager lean coal sample from Hancheng coalbed and a brown coal sample from Bayannaoer coalbed, respectively. Of the 876 strains, 612 were positive for lignin degradation function, including 218 strains belonging to 35 species in Hancheng and 394 strains belonging to 19 species in Zhongqi. Among them, the dominant lignin-degrading strains were *Thauera* (Hancheng), *Arthrobacter* (Zhongqi) and *Rhizobium* (both) including *Massila* for the first time, which was in high expression by real time PCR detection, confirming coal as a good seed bank (Wang et al. 2016).

Conclusion and future scope

In conclusion, the present review provides comprehensive information of the occurrence as well as molecular, biochemical and structural properties of different bacterial laccases reported till date. Strategies for further improvements of laccase such as genetic engineering, cloning in suitable heterologous hosts for enzyme overproduction, protein engineering to enhance enzyme kinetics and substrate binding and directed evolution to improve enzyme activity and stability have also been discussed. Laccase enzyme has the property to act on a range of substrates and to detoxify a range of pollutants as well as oxidation of harmful products, which have made them useful in paper, pulp and textile industries, etc. However, one of the limitations for the large-scale application of laccase is the lack of capacity to produce large volumes of the highly active enzyme at an affordable cost. The use of inexpensive sources for laccase production is being explored in recent times. In this regard, an emerging field in the management of industrial wastewater is exploiting its nutritive potential for the production of laccase. Besides solid wastes, wastewater from the food processing industry is particularly promising. Secondly, laccase plays an important role in the carbon cycle and could help in degrading a wide range of xenobiotic or phenolic compounds. The problem with laccase is its low substrate specificity and a very wide range of reactions that it can potentially catalyze. The enzymatic oxidation of aromatic compounds can generate by-products that convert the blue laccase into yellow laccase (YL), which does not require any mediator to degrade pollutants unlike blue laccase, according to some authors. Thus, there is a need for more research in this area in the near future. Moreover, despite many efforts to address the involvement of laccase in the transformation of lignocelluloses, it is still not completely clear how important a role laccase plays in lignin degradation, because in plant biomass it could be exploited as an enzymatic pretreatment method in cellulosic ethanol production.

Hopefully, these questions will attract more attention of researchers in the future. Therefore, it is not surprising that this enzyme has been studied intensively and yet remains a topic of research today and will remain in future.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Human and animal rights and informed consent Research involving human participants and/or animals/informed consent: not applicable for this study.

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