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Review Article

An Overview of Production and Industrial Exploitation of Bacterial Laccases

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FA reviewed the literature and wrote the manuscript. MI supervised the study. HAS helped in manuscript writing. SA did literature survey. MK critically reviewed the dinal draft.

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Abstract | Laccases (p-diphenol: oxygen oxidoreductase, EC 1.10.3.2) are multi-copper polyphenolic oxidases that oxidize many phenolic and non-phenolic aromatic compounds such as amino or methoxy monophenols, syringaldazine, ABTS and amino or methoxy monophenols. They have been depicted in various species of bacteria, plants and in different genera of fungi. Laccases have been purified by various methods. It involves in di-oxygen to water reduction and 1e- oxidation of phenolic and its allied parts. Laccases are mostly used in different industries like food, paper and pulp, pharmaceutical and textile etc. Both laccases and mediators have been used in different process like delignification of pulp. Laccases from bacterial species are used in dye decolouration and biobleaching processes. This review article describes the whole overview of laccases.

Novelty Statement | This paper reported the updated knowledge about bacterial laccases.

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Introduction

Laccases (p-diphenol: oxygen oxidoreductase, EC 1.10.3.2) are the top abundant adherents of multi-copper protein family that also encompass monoxygenases, dioxygenases, tyrosinases. Their phylogenetic development is from microbial blue copper proteins azurins to ceruloplasmin, the plasma proteins of eukaryotes (Mayer and Harrel, 1979; Harvey and Walker, 1999; Solomon *et al*., 1996; Claus, 2003). Yoshida firstly discovered laccase enzyme in *Rhus vernicifera* (Japanese tree) sap in 1883. Whereas, in 1985 laccase was characterized as metal -containing oxidase by Bertrand (Solomon *et al*., 1996; Mayer and Harrel, 1979; Harvey and Walker, 1999; Giardina *et al*., 2010).

Enzymes comprise about 15% to 30% of carbohydrates and 60 to 90 kDa molecular mass. These coppers containing laccase molecules are EC 1.10.3.2 (1,4-benzenediol: oxygen oxidoreductases) and are reported in micro-organisms as well as in higher plants. These are the glycosylated poly-phenols oxidases that hold four Cu^{2+} (copper ions) per molecule and execute one electron (e^-) of the phenolic oxidation and its allied compound as well as oxygen reduction to water. (Couto and Herrera, 2006; Gianfreda *et al*., 1999). Mediators (e^- shuttle) support the laccase enzyme to oxidize the non-phenolic substrates (Baiocco *et al*., 2003).

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Laccase enzymes are described based on having three prosthetic groups of copper categorized on electron paramagnetic resonance ((EPR) signals and light absorbance (Claus, 2003). T1 (Type-1) copper is the site of first oxidation and exhibit absorption band at about 600 nm. The intense electronic absorption via covalent bond of cysteine-copper resulted in blue shade (color) of T1 copper. Whereas, T2 (Type-2) copper and T3 (Type-3) copper jointly form trinuclear center of laccases and appear as a site of dioxygen reduction (Roberts *et al.*, 2003). T2 copper exhibit paramagnetic attributes in EPR but unable to show absorption band in visible range. T3 copper exhibit band at 330nm (Decker and Terwilliger, 2000). Reduction of oxygen molecule resulted in water liberation. Two histidines show linkage with T2 copper and similarly six histidines show linkage with T3 copper. Hydroxyl bridge amid two copper (Cu) atoms of T3 upholds the robust anti-ferromagnetical connection (Kumar *et al.*, 2003) Figure 1.

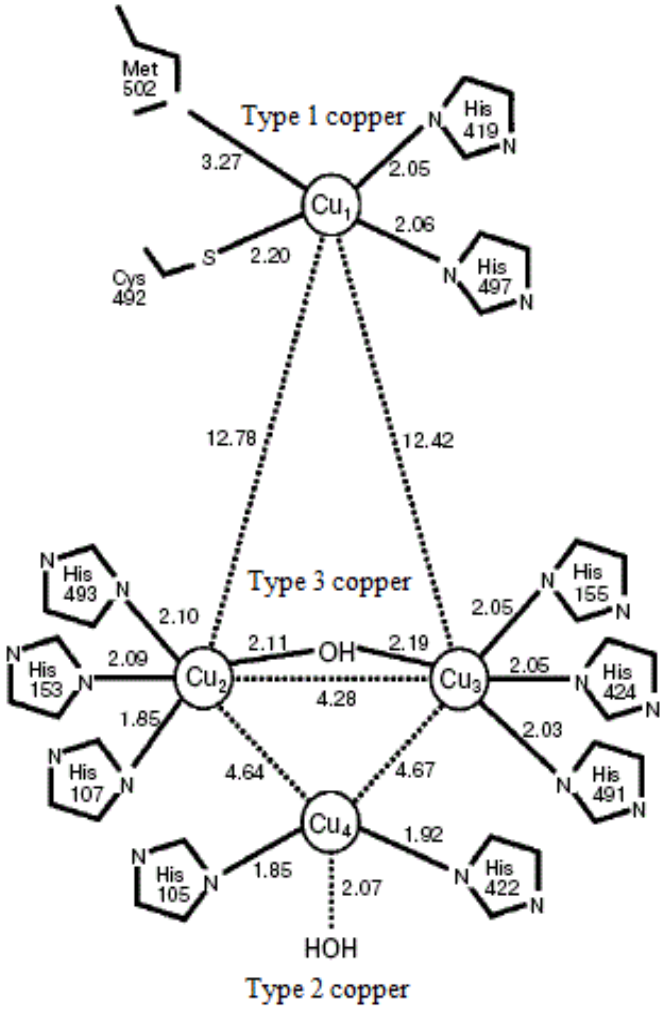

Figure 1: Scheme of T1 and T2/T3 copper sites of laccase (CotA) from *Bacillus subtilis* (modified from Enguita *et al.*, 2003).

Laccase enzymes show catalytic action on phenolic components of lignin by oxidizing Cα and hence cleaving Cα- Cβ as well as aryl-alkyl. It is supposed that laccase catalyze the following: firstly, reducing substrate leads T1 copper reduction, secondly; internal electron shifts from T1 Cu to T2 Cu and T3 Cu, Thirdly, at T2 Cu and T3 Cu molecular oxygen reduces to water. Reducing substrate oxidizes by laccase enzyme resulted in loss of solo electron and free unstable radical formation. The radical further undergoes enzymatic (phenol to quinone, oxidation) or non-enzymatic like polymerization, disproportion or hydration reactions (Xu, 1999).

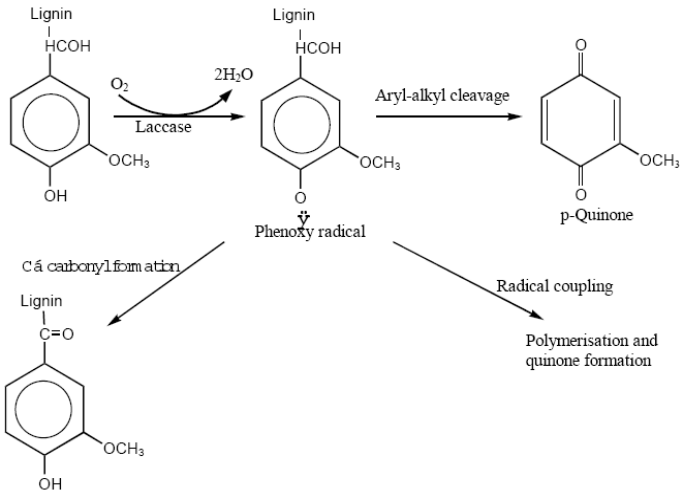

Figure 2: Laccase action on lignin, phenolic sub-units oxidation (adapted from Archibald *et al.*, 1997).

Distribution of laccase enzyme was reported in insects, bacteria, higher plants and fungi. Plants containing turnips, potatoes, apples, pears, cabbages and many other vegetables have laccases. Deuteromycetes, Basidiomycetes and Ascomycetes as well as 60 other fungi have laccase enzyme. (Gianfreda *et al.*, 1999). Laccase based bacterial strains were found such as *Bacillus sp*. HR03, *B. subtilis* SF, *B. halodurans*, *B. subtilis* WP1, *B. pumilus*, *P. desmolyticum* NCIM 2112, *P. putida* and *Azospirillum lipoferum* etc (Narayanan and Murugan, 2014).

Sources

The first microbial laccase was reported in rhizospheric bacterial strain, *Azospirillum lipoferum* accompanying plant root (Givaudan *et al.*, 1993; Sharma *et al.*, 2007; Sharma and Kuhad, 2008). Where its function was found to be melanin pigment formation (Sharma and Kuhad, 2008; Faure *et al.*, 1994, 1995). *Yersinia pestis, Pseudomonas maltophila, Xanthomonas campesteris* (copA), *Thermus thermophilus* HB27, *Streptomyces psammoticus* MTCC 7334, *S. laven dulae, Streptomyces griseus* (epoA), *S. cyaneus, Streptomyces antibioticus, Pseudomona flourescens GB-1, Bacillus subtilis, Pseudomonas syringae, Pseudomonas putida* GB1(cumA), *Caulobacter crescentus, Pseudomonas aeruginosa, Mycobacterium tuberculosum, Pseudomonas aerophilum* (pae1888), *Bordetella compestris, Oceano bacillusiheyensis* (cotA), *Marinomonas mediterranea, Escherichia coli, Alpha-proteobacterium* SD21 and *Aquifex aceolicus* are some bacterial strains in which

laccase enzyme has been reported (Alexandre and Zulin, 2000; Enguita *et al*., 2003; Sharma *et al*., 2007; Arora and Sharma, 2010). Laccase enzyme that was obtained from Marinomonas mediterranea, a marine bacterium had six Cu binding sites but no functional assignment (Amat *et al*., 2001; Sharma and Kuhad, 2008). Laccase obtained from CotA (constituent of endospore coat) of *Bacillus subtilus* is best studied. CotA takes part in bio-generation of brown coloured spore pigment (Driks, 2004). This pigment act as protective cover against harmful hydrogen peroxide (H_2O_2) and Ultra violet (UV) rays (Martins *et al*., 2002).

Production

Solid state fermentation (SSF)

The process occurring in near absence or absence of free-flowing water is denoted as solid-state fermentation (SSF). Bacterial laccase synthesis under SSF appeared as economical (Couto and Herrera, 2006). To run SSF about 15% moisture or wetness is indispensable. The following substrates are mostly utilized in SSF such as wheat bran, wood shavings, cereal grains, sawdust and various other materials of animal and plant too (Galzer and Nikaido, 2007). Murugesan *et al*. (2007) studied that in SSF, the conditions for growth of microorganisms are almost compatible to their natural habitation. By employing SSF conditions, phenol oxidase (a laccase-type) was derived from *Streptomyces cyaneus* bacterium and was proposed that enzyme phenol oxidase would be suitable for solubilization as well as mineralization of the lignin contents from wheat straw (Berrocal *et al*., 2000).

Submerged fermentation (SMF) /liquid fermentation (LF)

Fermentation taking place in excessive water or liquid is denoted as submerged fermentation and it came in strong focus in 1940s (Singhania *et al*., 2010). By employing SmF, a significant amount of laccase can be achieved because of having set configurations of bioreactor and ease in controlling parameters (Thiruchelvam and Ramsay, 2007). The SmF established procedures that have been optimized and cultivated for decades for enzymes synthesis by bacterial strains or others cannot be substituted by SSF (Hölker, 2005). According to Téllez-Jurado *et al*. (2005) liquid batch culture in SmF presented more growth and synthesis of laccase than that of SSF Agricultural wastes appeared as cheap substrates for laccase synthesis and acted as ligninolytic enzymes inducers because of having cellulose, hemicellulose and lignin contents. Wheat bran has been considered the most suitable substrate for laccase enzyme synthesis with SmF and SSF as well (Papinutti *et al*., 2003; Marques de Souza *et al*., 2002).

Factors affecting laccase production

Influence of nitrogen and carbon source

An ideal and defined growth medium for organism comprises 0.1% and 1% (w/v) of yeast extract (nitrogen source) and many other sources (carbon and nitrogen) respectively. Sources of carbon such as mannose, fructose, lactose, maltose and glucose are usually used. Superfluous concentration of sucrose as well as glucose act as inhibitors for initiation thus lessens the laccase synthesis. Polymeric substrates just like cellulose are capable enough to tackle such problems (Lee *et al*., 2004). Peptone, (NH4)2SO4, NaNO3, yeast extract and urea are sources of nitrogen and are usually used. However, exhaustion of nitrogen leads to trigger of production of laccase (Keyser *et al*., 1978).

Influence of incubation time and temperature

On laccase synthesis, there is a narrow effect of temperature but optimum or ideal temperature changes from strain to stain. Optimal temperature for laccase synthesis changes with correspondence to the presence of dark (30°C) and light (25°C) (Thurston, 1994; Pointing *et al*., 2000). Activity of laccase enzyme significantly augmented by pre-incubating at the temperatures of 40°C and then 50°C (Farnet *et al*., 2000). According to Palmieri *et al*. (1993), an unchanged in activity was observed even after such a long incubation period beyond 4 hours at 40 °C. The spore-coat of strain *Bacillus subtilis* has CotA component that is a gene product. CotA is a bacterial laccase is best studied enzyme (Hullo *et al*., 2001). The exception of CotA is its thermo-stability with half-life of 2 hours at 80°C and 75°C optimal temperature (Martins *et al*., 2002).

Influence of pH

Thurston (1994) observed the limited or narrow effect of pH on laccase synthesis. However, reactions of substrate for laccase enzyme cause effect on variation of optimal pH. Reactions of substrate for laccase enzyme cause effect on variation of optimal pH. According to several reports, laccase activity exhibits its profile as bell-shaped. At optimal pH, the enhancement in substrate oxidation occurs because of potency difference amid T1 Cu and phenolic substrate whereas, hydroxyl anion (OH^-) makes bond to T2/T3 Cu centre of laccase (Kunamneni *et al*., 2007). For syringaldazine substrate, the activity of enzyme was observed in 3.0–8.0 pH range. Optimal pH 4.0 and 5.0 was determined for L1 (laccase isozyme) and L2 respectively (Cordi *et al*., 2007).

Influence of inducer

Inducers such as guaiacol, ferulic acid, veratryl alcohol, ethanol and gallic acid enhance the synthesis of laccase enzyme. On attaining the growth phase, synthesis of laccase enzyme in ɣ-proteobacterium JB augmented 13 times after adding $CuSO_4$ to media. Malachite green, Ethidium bromide, Thymol blue and phenol red have also stimulated the synthesis of laccase by 19, 17, 2 and 4 folds respectively (Kanam *et al*., 2004). Alcohol boosted laccase activity comparatively to xylidine. Boost of laccase by alcohol appeared costly method (Lee *et al*., 1999).

Influence of metal ions

From alkaline medium, the obtainable laccase lessens 50 times than that of cultivation media having low copper ion concentration (Palmieri *et al.*, 2000; Assavanig *et al.*, 1992). Zhang *et al.* (2010) studied that EDTA, Mg^{2+}, Cu^{2+} and Zn^{2+} at 6.25-50mM proved to be un-affecting agents for the activity of laccase enzyme. However, a decline in laccase activity was observed due to Fe^{2+} and Ca^{2+} ions at 6.25-50mM and 25-50mM concentrations respectively. Molecular and Biochemical approaches were employed for identification of soil bacterial strain *Stenotrophomonas maltophilia* AAP56. Without any substrate, the influence of Zn^{2+}, Mn^{2+}, Cu^{2+}, Mg^{2+}, Ca^{2+}, Fe^{2+}, urea, EDTA and sodium azide by 5 minutes incubation period at 4°C was studied. A significant increase in enzyme synthesis about 2.6 folds with 275UL-1 activity of laccase enzyme was noted Galai *et al.* (2009).

Purification of laccase

Enzymes purification employing ammonium sulphate has been carried out for several years. However, protein precipitation via buffer/desalt exchange of protein, ammonium sulphate, gel filtration and anion-exchange chromatography proved to be more effectual methods (Grotewold *et al.*, 1998). Purification of bacterial laccase derived from soil bacterial strain *Pseudomonas putida* F6 had done by employing the coalition of gel filtration and anion-exchange chromatography and consequently observed an escalation in activity of laccase enzyme by 518 and 747 Umg^{-1} experimented by McMahon *et al.*, 2007. Partial purification of laccase derived from cell of *Streptomyces psammoticus* strain was done by applying an ordinary method ammonium sulphate for precipitation whereas, copper and calcium alginate beads were applied for immobilization of laccase in entrapment method. However, alginate beads using calcium-based laccase immobilization hold just 42.5% of the activity of laccase whereas in contrast, alginate bead utilizing copper substantiated better for immobilization of laccase by holding 61% of the laccase activity (Niladevi and Prema, 2008). Purification of bacterial laccase from a strain Azospirillum lipoferum was carried out by dialysis method in which ammonium sulphate was expended for precipitation of protein from supernatant (Diamantidis *et al.*, 2000). Purified bacterial laccase derived from strain Streptomyces lavendulae REN-7 exhibited 73kDa molecular mass and solo band of protein after applying 10% of SDS-PAGE (Suzuki *et al.*, 2003).

Catalytic activity

Catalytic activity of laccase enzyme upswings by the grouping of laccase enzyme and mediators. These mediators are very tiny (little molecular weight) and act as electron carrier amid laccase enzyme and substrate (Duran *et al.*, 2002; Galli and Gentili, 2004) Laccase enzymes have been widely used to oxidize or catalyze substrates for many years. The following phenolic and non-phenolic substrates have been oxidized or catalyzed are methoxy- or amino-monophenols, and non-phenols such as ABTS, hydroxyindoles, syringaldazine, aromatic diamines etc. (Mayer, 1987; Cai *et al.*, 1993). The efficiency of laccase along with ABTS rises many folds, so it oxidizes laccase substrates and non-laccase substrates both (Bourbonnais and Paice, 1992). Bacterial laccase with broader pH appears more effective as compared to other laccases like fungal laccase when employed industrially such as bio-bleaching of textiles stuffs, paper pulp processing etc. (Singh *et al.*, 2009b). Singh *et al.* (2007) and Ye *et al.* (2010) reported the activity and stability of bacterial laccases at extensive pH range probably 6.0 to 8.5. As the laccase derivative of Metagenomec worked best at 9.0 pH for a non-phenolic substrate "syringaldazine" (Ye *et al.*, 2010). Singh *et al.* (2007) and Ye *et al.* (2010) reported the activity and stability of bacterial laccases at extensive pH range probably 6.0 to 8.5. As laccase derivative of Metagenomec worked best at 9.0 pH with a non-phenolic substrate "syringaldazine" Ye *et al.* (2010). Whereas, *Bacillus halodurans* C-125 derived alkaline bacterial laccase Lbh1 activity at optimum pH range 7.5–8.0 was observed with syringaldazine as confirmed by Ruijssenaars and Hartmans, 2004. Bacterial strain c-proteobacterium JB laccase showed 70% stability at both acidic 3.0 pH and alkaline 10.6 pH and 80% stability at broad 4.0 to 9.0 pH range with 48 hours incubation period at normal 37°C temperature. The absence of protease production may be a reason of stability (Singh *et al.*, 2007).

Applications

Laccases are used biotechnologically because they have capability to oxidize a variety of phenolic compounds as well as non-phenolic compounds (Figure 3) (Mohammadian *et al.*, 2010). Laccases are exploited in the following industries including textile, petrochemical, paper, pulp, food, wood, pharmaceutical (medicines) etc. (Arora and Sharma, 2010). Couto and Herrera (2006) found that Laccases are not only confine to water distillation systems but they are also being involved in anticancer medicines (drugs) preparation as well as reducing the harmfulness of cosmetics. Now researchers are trying to work for the enzymatically organic compounds production and utility of laccases for the development of biosensor, biotransformation and bio-oxidation. (Arora and Sharma, 2010).

Pulp and paper industry

Formation of paper at industrial level is acquired by following conventional method by using chemical oxidants having oxygen or chlorine for pre-treatment e.g. separation of lignin and delignification (Luisa *et al.*, 1996). In last few years, industrially the traditional and polluting methods of pre-treatment i.e. chlorine-based chemical methods have changed into oxygen-based chemical methods.

However, use of laccase is safer method for pre-treatment or delignification of wood pulp along with protection of cellulose integrity. (Barreca *et al.*, 2003; Gamelas *et al.*, 2005; Shi, 2006). Mediators are the chief chemical agents that support laccases in the process of delignification of wood pulp (Bourbonnais *et al.*, 1997). Laccases cannot oxidize lignin directly. Mediator (e^- shuttle) plays an important and intermediate role in delignification. The oxidation of mediator is done by laccases whereas it (mediator) then oxidizes lignin in wood (Bourbonnais *et al.*, 1997; Svendsen and Xu, 2001). This indirect delignification is supposed to be impossible because of huge structure of laccase and its access towards lignin present in plant cell (Sharma *et al.*, 2007; Kandioller and Christov, 2001; Singh *et al.*, 2008). Laccases obtaining from two bacterial strains *P. stutzeri* (soil bacterium) (Kumar *et al.*, 2005) and *S. cyaneus* (Arias *et al.*, 2003) along with mediators HOBT and ABTS have been used in the process of bio-bleaching of eucalyptus kraft pulps (Held *et al.*, 2005). Laccases have competency to functionalize and cross-link the lignocellulosic fibers (Call, 2005; Guebitz and Cavaco, 2003; Xu *et al.*, 2006).

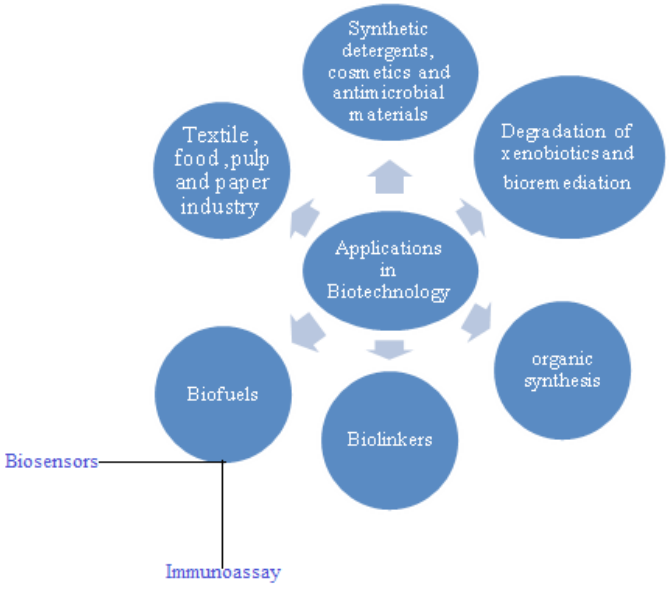

Figure 3: Scheme of applications of laccase (adapted from Morozova *et al.*, 2007).

Textile industry

Artificial dyes are being used extensively in industries, most probably in textile, food, paper printing, leather and cosmetic industries for coloration purposes (Forgacsa *et al.*, 2004). Tavares *et al.* (2009) found that dyes are actually dyed or shaded molecules and give colour to cellulose fibers. These dyes become responsible for the assembly of large amount of stained effluent. As a result, the synthetic colours cause hindrance in biodegrading process (Wesenberg *et al.*, 2003; Moilanen *et al.*, 2010). Problem in using artificial dyes is its carcinogenicity because of having aromatic compounds (Baughman and Perenich, 1988). Laccases exploitation is rising rapidly, to decolourize wastewater as well as bleaching of textiles and artificial dyes (Setti *et al.*, 1999). Microbial laccases from bacterial strains *Stenotrophomonas maltophilia* and *Streptomyces psammoticus* are competent enough to decolorize numerous synthetic dyes (Romero *et al.*, 2006; Niladevi *et al.*, 2007). Paszczynski *et al.* (1991) has worked on the improvement of degradation of azo dyes by the application of Streptomyces (*bacterial* sp.). These azo dyes are approximately half of total synthetic dyes (Selvam and Swaminathan, 2003).

Food industry

In food processing industry, laccases are being employing in different areas i.e. juice processing, wine stabilization, baking as well as bioremediation of industrial effluents because of its capability to remove unwanted phenolic compounds (Couto and Herrera, 2006). Yague *et al.* (2000) found that the effluents of beer factory are somehow hazardous for environment because of its black colour (dark brown) and holding polyphenolic compounds. Laccase plays role in removing these phenols and bond between enzyme-substrate by using membrane filter method (Minussi, 2002). Phenolic contents and oxidative products already existing in juices provide flavor or taste, aroma and colour to it. Enzymatic darkening is a condition in which polymerization and phenolic as well as polyphenolic oxidation cause change in odor and colour of juice. So, in order to keep juices in original colour and taste or high quality, laccases are used in food processing industries (Ribeiro *et al.*, 2010). Laccases are used in bakery products too. Laccases are supplemented to dough to enhance or improve gluten structure of dough, product volume, crumb structure and baked products softness (Minussi *et al.*, 2002).

Immobilization of laccases

Glass ceramic was taken as decolourizing agent in textile industry after modified by chemicals aminopropropyltriethoxysilane/ glutaraldehyde as well as carbodiimide/glutaraldehyde. Besides this montmorillonite was also used to decolourize textiles after modification by aminopropyltriethoxysilane/ glutaraldehyde chemicals (Peralta-Zamora *et al.*, 2003). Laccases immobilized on various substrates i.e. ceramics support and the best one pyrolytic graphite (Minussi *et al.*, 2007). Alumina pellet substrates were employed for immobilization of laccase-based spores of bacterial strain "Bacillus SF". Immobilized spores as well as free spores had ability to decolourize the common dyes used in textile industry like Acid Blue 74, Mordant Black 9, Mordant Brown 15, Mordant Brown 96. The immobilization took about 90 minutes. However, at 60°C half-life increased by 66-80 hours after immobilization of laccase-based "Bacillus SF" on alumina pellet substrates (Held *et al.*, 2005).

Pharmaceutical industry

In pharmaceutical or medicine industry, laccase molecules have been employed in generation of detoxifying agent and antimicrobial agent. Anti-inflamatory, sedatives, anesthetics and antibiotics are also synthesized with the use of laccases (Arora and Sharma, 2010; Nicotra *et al*., 2004; Haught *et al*., 2001; Juelich *et al*., 2001; Johansen, 1996). By the expense of laccases, anticancer drug "actinocin" has been made from a chemical 4-methyl-3-hydroxyanthranilic acid. The drug "actinocin" cures the cancer by causing hindrance in DNA transcription from tumor (cancer) cell (Burton, 2003). The oxidative conversion of both aromatic compounds and aliphatic amines into acid "3-(3, 4-dihydroxyphenyl)-propionic" can be done by laccases and the resultants act as anti-viral agents (Ncanana *et al*., 2007). Laccases also show inhibitory action for the reverse transcriptase of HIV-1 reported by Wang and Ng (2004). Roggen *et al*. (2001) found another function of laccase that is to lessen the allergenicity.

Conclusion

Laccases are not only present in bacteria but also in plants and fungi. Laccases of bacteria (bacterial Laccases) are enzymes secreted by different bacterial strains such as *Streptomyces sp., Pseudomonas sp., Bacillus* sp. etc. These catalyze redox reactions. Bacterial laccases have different biotechnological applications like food industry, textile industry, dye decolouration, pharmaceuticals. These are also involved in biodegradation/ detoxification the industrial effluents as well as in bioremediation. In paper and pulp industry it is used as biobleaching agent.

Conflict of interest

The authors have declared no conflict of interest.

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