Edible Mushroom: A Potent Producer of Industrial Enzymes

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Abstract: **Edible mushrooms are hugely appreciated in every part of the world because of their nutritive value, ease of production as well as non-toxicity. In recent years we are getting more inquisitive about these culinary wonders as they are showcasing a wide array of secondary metabolites with numerous potential applications. These nutritionally rich food supplements are capable of producing a number of enzymes having prospects in industries like brewery, dairy, food & feed processing, textile, paper, leather, agrochemical, photography and pharmaceuticals etc. This article reviews quite a few of the reported enzymes available from wild and cultured edible mushrooms for their production media, production rates and functional attributes. Recent reports of parameters affecting their production are noted as well. The article has also discussed application prospects and current omics approaches exploring intricate roles of mushroom enzymes in development and metabolic pathways of these edible fruiting bodies. Cumulative treatment makes this article one uniquely up-to-date and comprehensive narrative of edible mushroom enzymes.**

Index Terms: **cellulolytic edible mushroom, industrial enzymes, ligninolytic, peroxidase**

I. INTRODUCTION

Edible mushrooms are the delicious fruiting bodies of filamentous fungi from Ascomycota and Basidiomycota phylum. Mushrooms are good source of carbohydrates, proteins, fats, vitamins, minerals, enzymes and other bioactive compounds with considerable amount of water and fiber but low in calorie (Tripathy & Gupta, 2016). Nutrient content of any edible mushroom depends on the substrate on which they grow, environmental condition and their age. Carbohydrates in mushrooms are mainly polysaccharides in form of glycogen and other indigestible forms like dietary fiber, cellulose, chitin, mannan and glucans. Homo and hetero glucans with β (1 $\rightarrow$ 3), β (1 $\rightarrow$ 4) and β (1 $\rightarrow$ 6) glycosidic bonds available in mushrooms are considered as healthy constituents (Bernas & Lisiewska, 2006; Ghosh, 2020). Prominent sugar is mannitol although glucose, galactose, trehalose, mannose and fructose are also present in mushrooms (Cruz & Pintado, 2016). Mushroom proteins are composed of all the essential amino acids along with

alanine, arginine, glycine, histidine, glutamic acid, aspartic acid, proline and serine (Cruz & Pintado, 2016). As mushroom proteins are rich in lysine, they can better supplement cereal-based diets which are poor in lysine (Ghosh, 2020).

Fat content of edible mushroom is fortunately low and 70% of fatty acids are unsaturated in nature. Mushrooms are very rich in minerals like copper, iron, potassium, magnesium, calcium, phosphorous, zinc and sodium (Ghosh, 2020). In addition to them, some mushrooms also possess iodine, fluorine, mercury, manganese and sulphur etc. These edible varieties possess abundant group B vitamins like thiamine, riboflavin, pyridoxine, pantothenic acid, nicotinic acid, nicotinamide, folic acid and cobalamin (Ho & Tan, 2020; Ghosh, 2020). Other than B vitamins, ergosterols, biotin, phytochinon and tocopherols are also present in mushrooms. Characteristic flavor and aroma of mushroom dishes comes from a wide range of octavalent carbonate alcohols and carbonyl compounds like 1-octanol, 3-octanol, 3-octanon, 1-caprynol-3-ol, 1-octynol-3-ol, 2-octynol-3-ol and 1-caprynol-3-on etc. (Bernas & Lisiewska, 2006). Nitrogenous compounds, minerals and oxidation of unsaturated fatty acids also contribute to aroma generation.

These edible creatures also possess a large group of enzymes including oxidases, lipases, cellulases, lignin degrading enzymes, invertase and proteolytic enzymes (Ghorai & Khowala, 2009; Sherief & Temraz, 2010; Montoya & Levin, 2011; Pandit & Maheshwari, 2012; Rodrigues da Luz & Kasuaya, 2012; Lim & Kang, 2013; Adebayo & Martinez-Carrera, 2015; Nadim & Shamekh, 2015; Majumder & Khowala, 2016; Karnan & Panneerselvam, 2016; Hermosilla & Diez, 2018; Murniati & Nurhanifah, 2018; Gomathi & Ramalakshmi, 2019; Benmrad & Jaouadi, 2019; Ding & Li, 2019; Hock & Shing, 2020; Karittapattawan & Benchawattanon, 2021).

Edible mushrooms *Pleurotus florida, Pleurotus ostreatus, Ganoderma lucidum, Pleurotus cyststidiosus, Agaricus brasiliensis, Flammulina velutipes, Pleurotus eous, Auricularia polytricha, Hericium erinaceus*, *Agrocybe aegerita, Hypsizygus marmoreus, Lepista luscina, Lyophyllum schimeji, Pleurotus*

djamor, Schizophyllum commune, Coprinus comatus, Inonotus obliquus, Ganoderma applanatum, Grifola fondosa, Lentinus edodes, Lepista luscina, Piptoporus betulinus, Pleurotus eryngii, Cordiceps militaris, Cordyceps sinensis, Morchella esculenta and many others were grown on various synthetic and complex media to study their intracellular and extracellular hydrolytic and oxidative enzyme pools (Krupodorova & Barshteyn, 2014; Zaidi & Ali, 2015; Kumla & Lumyong, 2020). Wild edible macrofungi collected from the forests and markets of different parts of India were also explored for their bioprospection potential (Khaund & Joshi, 2014).

Different classes of enzymes reported from edible mushrooms are extensively utilized in various industries such as dairy, food & feed processing, brewery, leather, textile, paper, agrochemicals, and pharmaceuticals etc. Peroxidases are utilized in various industrial sectors. These enzymes are used to treat textile dyes in textile industry, to degrade herbicides and other wastes in waste treatment plant and to remove lignin from lignocellulosic biomass to prepare animal feed or compost. In food and brewing industry, these enzymes improve quality of animal feed and help in development of flavor, color and nutritional quality of the food (Hock & Shing, 2020).

Laccases play crucial roles in bioremediation, beverage stabilization (like fruit juice, wine, beer etc.), bakery industry and overall improvement of food quality. Laccases are widely used in textile, waste management, paper and pulp industry, food and brewing industry, green biotechnology as well as in health and personal care products (Chukwuma & Ismail, 2020). These enzymes are essential for detoxification and decontamination of waste, decolorizing dyes and degrading polyaromatic hydrocarbons in waste management. In paper industry, laccases are used for removing lignin from wood and bio-bleaching of wood pulp. In food industry, laccases help in stabilization of wine, processing of fruit juices and improvement of texture of dough while baking. These enzymes are also required during pretreatment of lignocellulose, bioremediation of food industry waste water, composting of lignocellulose material, and chemical synthesis of biofuel cells and sensors etc. Laccases are utilized in diagnosis, enzymatic and immunological assays and tests, hair dying and also in reducing effects of poison ivy dermatitis (Chukwuma & Ismail, 2020).

Cellulases are essential for breaking cellulose polymer and utilizing the end products in various industries (Ghorai & Khowala, 2009, Roy & Banik, 2021). In textile industry, these enzymes are required for biostoning of denim garments, improving the efficiency of detergents and cleaning tiles. Cellulase can be used as a potent antitumor agent. In paper and pulp industry, cellulases are used for biochemical pulping, paper recycling and deinking, deinking recycled fibers and improving drainage and runnability of paper mills. These enzymes are also vital for preparing easily degradable soft paper and cardboard, improved lignocellulosic biomass for animal feed, residues for

improvement of soil fertility and for preparing formulations to remove industrial slime. In food and brewing industry, cellulases are utilized to extract and clarify fruit and vegetable juices, produce fruit nectars and purees, extract olive oil used in carotenoid extractions for production of food coloring agents and prepare additives for the food industry as thickener (Chukwuma & Ismail, 2020).

Xylanases mediate desizing of yarn before weaving and bioscouring or removal of waxy material from plant fibre. These enzymes are also essential for complete breakdown of plant biomass comprising of lignin, cellulose and hemicellulose to produce biofuels and other value-added products (Bhardwaj & Verma, 2019). In paper and pulp industry, xylanases are required for bleaching kraft pulp and deinking printed papers. These enzymes are also essential for synthesizing pharmaceutically important xylo-oligosaccharides such as probiotics, anti-inflammatory, anti-hyperlipidemic, anti-oxidant, anti-allergic, anti-cancerous and anti-microbial agents (Bhardwaj & Verma, 2019). In food and feed industry, xylanases are used to prepare animal feed for cattle, poultry and fish. Xylanases are also important for clarification of fruit juices and improving rheological property of bread (Ghorai & Khowala, 2009).

Pectinases are widely used in fruit juice clarification, juice extraction, manufacture of pectin free starch, deguming of natural fibres, treatment of waste water or sewage and in cocoa and tobacco industry. Pectinase treatment increases the rate of fermentation of tea and removes its foaming tendency and the enzyme also removes mucilaginous coat from coffe beans (Ghorai & Khowala, 2016; Pereira & Regina, 2017). Proteases hold major share of the industrial enzyme market. Since long these enzymes are used in laundry detergents (Benmrad & Jaouadi, 2019). Esterase enzymes are involved in ester formation and transesterification with potential application in food, pharmaceuticals and cosmetic industries (Shivashankar & Premkumari, 2014). Flavor acetates produced from primary alcohols have huge application for their characteristic fragrance. Antioxidant property of edible mushrooms are eminent because of their free radical scavenging ability coming from the antioxidative stress enzymes such as superoxide dismutase, peroxidase and catalase etc (Kaushal & Bhatt, 2018).

Enzymes are highly attractive option for industrial applications because of their specificity and biodegradable nature. Enzymes from microbial sources are preferred over animal or plant sources due to their ease of preparation, short generation time, ease of manipulation of related genes and large availability in nature. All these may attribute to the huge rise in global industrial enzymes market share in 2020 to reach USD 5.93 billion and expected to generate revenue of USD 9.14 billion in 2027 (www.grandviewresearch.com). Present article reviews several industrially sort after enzymes from wild and cultured edible mushroom species for their production and applications emphasizing recent developments in various roles. Novelty of the

article can be attributed to its up-to-date and exhaustive description regarding production media, production rate, functions and developments involving edible mushroom enzymes.

II. ENZYMES FROM EDIBLE MUSHROOMS

Mushroom cultivation starts with spore germination followed by mycelial colonization, spawn production and then development of fruiting bodies. During these stages of mushroom development, mycelia usually secrete various enzymes depending on the growth condition and substrate utilization. Released enzymes breakdown substrates to simpler organic components which can be taken up via the hyphal network for further growth and development of the mushrooms. Enzymes are necessary for all the metabolic activities of the mushrooms like hydrolysis, oxidation, reduction and transfer etc. Presence of various enzymes in the mushrooms also contribute to their nutritive value, flavor and shelf-life (Jonathan & Adeoyo, 2011). Growth of edible mushrooms on substrates and development of fruiting body thereafter are highly dependent on the level of hydrolytic and oxidative enzymes secreted by the mushroom to cleave the organic polymeric constituents of the substrates (Gomathi & Ramalakshmi, 2019). Edible mushrooms are reportedly rich sources of various ligninolytic, cellulolytic, proteolytic, lipolytic and stress enzymes as listed in Table I.

Table I. Enzymes from Edible Mushroom

Enzymes	Class of enzyme	Application	Reference
Lignolytic			
Lignin peroxidase	E.C.1.11.1.14	Biodegradation of lignin	Fernandez-Fueyo & Martinez, 2014; Gomathi & Ramalakshmi, 2019
Manganese peroxidase	E.C.1.11.1.13	Bioremediation, Biopulping, Biobleaching	Hock & Shing, 2020
Versatile peroxidase	EC 1.11.1.16	Dual ability to oxidise Mn(II) and phenolic and non-phenolic compounds, Superior to both lignin peroxidase and manganese peroxidase	Adebayo & Martinez-Carrera, 2015; Weng & Han, 2021
Tyrosinase	E.C.1.14.18.1	Food industry, biosensor, bioremediation	Sharma & Thakrele, 2016; Weng & Han, 2021
Laccase	E.C. 1.10.3.2	Paper pulp bleaching, textile dyes, synthetic dye decolouration,	Khaund & Joshi, 2014 Karittapattawan &
		biosensors, detoxification of polluted water, bioremediation, chemical synthesis	Benchawattanan on, 2021
Cellulolytic			
Endo-β-1,4-glucanase and Exo-β-1,4-glucanase	EC 3.2.1.74 and EC 3.2.1.91	Textile industry, food and feed industry, pulp and paper industry, bioethanol production	Ghorai & Khowala, 2011; Roy & Banik, 2021
β-glucosidase or Cellobiase	E.C. 3.2.1.21	Food processing industry, pharmaceuitical industry(agrochemicals and drugs), biofuel	Ghorai & Khowala, 2010; Roy & Banik, 2021
Xylanase	EC 3.2.1.8	Food and feed industry, paper and fibre industry, biofuel	Simair & Zhong, 2015; Bhardwaj & Verma, 2019
Amylase	EC 3.2.1.1	Food, detergents, textile, drink, animal feed, paper production, fermentation	Ghorai & Khowala, 2009; Jonathan & Adeoyo, 2011
Invertase (sucrase)	E.C. 3.2.1.26	Food industry, alcohol industry	Chowdhury & Khowala, 2009
Pectinase	EC 3.2.1.15	Extraction, clarification, filtration and depectinization of fruit juices, wines Maceration of fruits, vegetables and removal of inner wall of lotus seed, garlic, almond and peanut	Ghorai & Khowala, 2011; Pereira & Regina, 2017
Others			
Protease	many under EC 3.4.21.	Brewing, dairy, meat, detergent, leather and photographic industries	Majumder & Khowala, 2016; Benmrad & Jaouadi, 2019
Esterase	E.C. 3.1.1.1	Soft and pro drug design, Synthesis of short chain esters, Metabolism and detoxification of agrochemicals and pharmaceuticals	Shivashankar & Premkumari, 2014

A. Ligninolytic enzymes: Oxidoreductases

Annually a large amount of plant residues is produced from agricultural, forest and agro-industrial sources which are non-food materials. Majority of them are not utilized to generate energy or value-added products. This biomass is readily available and cheap in nature and has drawn quite interest for some time to

exploit as a substrate for generating biofuel, compost and feed stocks etc. Plant biomass is mainly composed of three different polymeric compounds – cellulose, hemicellulose and lignin. Plant biomass composition also differs depending on the type of plant (Baruah & Kalita, 2018; Yadav & Vivekanand, 2018). Complete degradation of lignocellulosic biomass to simple carbohydrates is achieved by the help of two categories of enzymes namely oxidative enzymes and hydrolytic enzymes. Oxidative enzymes are ligninases which act on recalcitrant lignins such as phenol oxidase or laccases and peroxidases like lignin peroxidase, manganese peroxidase and versatile peroxidase and dye - decolorizing peroxidases etc. Hydrolytic enzymes act on cellulose and hemicellulose (Weng & Han, 2021). Among cellulose, hemicellulose and lignin, cellulose is the most abundant as it constitutes around 40-50% of the total biomass. It is a fibrous, insoluble and crystalline linear homopolysaccharide of repeating (1,4)-D-glucopyranose units linked via β-1,4 glycosidic linkages having an average molecular weight of around 100,000 (Himmel & Foust, 2007). Hemicellulose is a heteropolymer of xylans, mannans, glucans, glucomanans or galactans with side chains. This heterogeneous polysaccharide of average molecular weight <30,000 is degraded without much ado due to its amorphous nature (Hamelinck & Faaji, 2005). On the other hand, lignin even being the smallest fraction representing 10-25% of the biomass, is the most complex part of the plant material. This long chain aromatic polymer of phenyl propane (major), methoxy groups and non-carbohydrate polyphenolic substances seals the gaps between cellulose and hemicellulose (Hamelinck & Faaji, 2005). Endo 1,4 beta xylanase, beta xylosidase, alpha-L-arabinofuranosidase, alpha glucouronidase and acetyl xylan esterase are required for hemicellulose degradation.

Lignin structure varies greatly with the plant source. The basic constituents of lignin are guaiacyl alcohol, p-coumaryl alcohol, syringyl alcohol linked via aryl ether (β-O-4), phenyl coumaran (β-5), resinol (β-β), biphenyl ether (5-O-4) and dibenzodioxocin (Weng & Han, 2021). Lignin is degraded to heterogeneous aromatics which enters into central carbon metabolisms of the mushroom. Recalcitrant lignin can be depolymerized by the help of different oxidases like lignin peroxidase, manganese peroxidase, versatile peroxidase, dye-decolorizing peroxidase and laccase. Degraded lignin can be a versatile source of value-added products like polyhydroxyalkanoates (bioplastics), lipids (as biofuel), animal feed additive, pesticides, compost/biofertilizer, vanillin and muconic acid etc. (Weng & Han, 2021). Ligninolytic enzymes are extracellular, oxidative and non-specific enzymes which produce unstable products via oxidative reactions. Table II and III represent various oxidoreductases and hydrolytic enzymes produced from different edible mushrooms.

1) Lignin peroxidase

Lignin peroxidases (diaryl propane: oxygen, hydrogen peroxide oxidoreductase EC 1.11.1.14) possess heme containing iron atom in its active site. They catalyze hydrogen peroxide dependent oxidation of non-phenolic aromatic compounds into cation radicals to decompose them. Lignin depolymerization via lignin peroxidase is quite efficient because of its high reduction potential (Weng & Han, 2021).

Pleurotus sajor-caju grown on coir pith showed maximum lignin peroxidase and manganese peroxidase activity of about 16.25 U/ml and 20.2 U/ml respectively on 20th day of fermentation with Azolla and Soya hulls as supplement (Radhakrishnan & Jayakumaran, 2012). Growth of fungi in supplemented media resulted in reduction of organic carbon and lignin content steadily during the fermentation. Degradation started from fifth day of inoculation and reached to a maximum between fifteenth and twenty fourth day with gradual decrease thereafter. Within 25 to 30 days, lignin content was reduced from 38.5% to 16.15%.

2) Manganese Peroxidase

This is the main oxidizing enzyme of ligninolytic peroxidases. Manganese peroxidase (Mn II: hydrogen peroxide oxidoreductase, EC 1.11.1.13 are again heme containing peroxidases that oxidise phenolic compounds to phenoxy radical by oxidation of Mn (II) to Mn (III) ion in the presence of hydrogen peroxide (H_2O_2) as a cofactor. Initial depolymerization of lignin requires lignin peroxidase and manganese peroxidase, so presence of both the enzymes in reaction mixture will speed up the depolymerization process (Weng & Han, 2021).

Plastic degrading potential of edible mushrooms was checked for *Pleurotus ostreatus*, *Pleurotus eryngii, Lentinula edodes* and *Agaricus bisporus* in presence of Bisphenol A (2.5-10µl/L) and di-(2-ethylhexyl)-phthalate(250-1000µg/L) (Hock & Shing, 2020). The enzymes involved in degradation of di-(2-ethyhexyl)-phthalate were laccase, esterase and manganese peroxidase. As phthalates are hydrophobic in nature, their absorption in fungal mycelia or parts will be facilitated by hydrphobin producing mushrooms like *Pleurotus sp.* In presence of Bisphenol A, mushroom growth was limited as evident from biomass estimation but di-(2-ethyhexyl)-phthalate induced growth and enzyme production in all the edible mushrooms. Highest manganese peroxidase production was reported from *Pleurotus eryngii* against di-(2-ethyhexyl)-phthalate (750 µg/L) (Table II).

Effect of nutrient nitrogen and Mn on production of manganese peroxidase were analysed in *Pleutorus sajor-caju* PI-27 (Fu & Buswell, 1997). Ammonium nitrate (2.6 mM-N) and L-asparagine (26mM-N) were used as low and high nitrogen sources respectively with glucose as the sole carbon source. In low nitrogen medium, maximum manganese peroxidase activity of 66U/ml was reached after 12 days and in high nitrogen medium

maximum activity of 47U/ml was achieved after 14 days. In low nitrogen medium a second peak of activity although much lower was observed after 18days of growth. Manganese peroxidase production in low nitrogen medium was maximum when Mn concentration was around 15 to 30ppm. two manganese peroxidase peaks were detected in FPLC analysis of culture fluid of the mushroom indicating isoforms of the enzymes. This was also confirmed by PAGE. Enzyme isoforms are commonly found in lignocellulolytic fungi.

Mushrooms of 37 white rot fungi were collected from different forest areas of Andhra Pradesh, India and analysed for their ligninolytic abilities. 12 of them produced manganese peroxidase in malt extract agar in presence of 0.05% guaiacol and then transferred to Treveror's medium (peptone 1 gm, malt extract 20gm and dextrose 20 gm in 1L distilled water) with 10% Black liquor from a factory containing 90% lignin. Among the investigated mushrooms *Tremates versicolour* produced highest manganese peroxidase activity of 56.13 U/L. Another edible mushroom *Tremella fondosa* produced 29.12 U/L of manganese peroxidase and 5.95 U/L of lignin peroxidase (Seshikala & Charya, 2012).

3) Versatile peroxidase

This broad substrate preferring unique enzyme has a heme access channel, a catalytic tryptophan and Mn oxidation site. Versatile peroxidase demonstrates similar catalytic mechanisms to that of both lignin peroxidase and manganese peroxidase, so this is called as hybrid peroxidase. Only difference is that, versatile peroxidase is capable of directly degrading high reduction potential substrates without the presence of veratryl alcohol and oxidizing Mn^{2+} independently. It's bifunctional nature has made it an attractive choice for biotechnological applications (Weng & Han, 2021).

Edible mushroom *Pleurotus ostreatus* is a well-known white rot of wood and other lignocellulosic material for its selective lignin degrading ability. Degradation of lignin was possible because of a variety of heme peroxidases secreted by the mushroom (Table II) belonging to non-animal Class II superfamily (Fernández-Fueyo & Martinez, 2014). Among them, three versatile peroxidases and six manganese peroxidases were characterized for their catalytic activities, pH stability, temperature stability and molecular structures. Characterized enzymes were able to oxidise Mn^{2+} at a conserved site. For versatile peroxidases the site was composed of E36, E40 and D175 whereas for manganese peroxidases it was composed of E36, E 40 and D181. Versatile peroxidases also possess one lignin oxidation site containing tryptophan (w) at 164/170/164 (depending on the enzyme 1/2/3) which was connected to the heme group. The indolic side chain of the W164 of versatile peroxidase 1 was exposed facilitating the collection of electrons from the bulky lignin molecule. On the other hand, lignin-related substrates were not oxidised by manganese peroxidases where the active tryptophan was substituted by alanine or aspartic acid. Peroxidase pool of *Pleurotus ostreatus* was able to degrade non-phenolic lignin model dimer and synthetic lignin although it lacked lignin peroxidase (Fernández-Fueyo & Martinez, 2014). Versatile peroxidase is the main enzyme involved in lignin modification in absence of Mn^{2+} (Feldman & Hadar, 2017).

4) Laccase

Laccases (benzenediol: oxygen oxidoreductases, EC 1.10.3.2) are blue multicopper oxidases that catalyze the oxidation of various aromatic substrates along with the reduction of molecular oxygen to water. Laccase from fungal source usually have higher reduction potential. This enzyme can degrade both phenolic and non-phenolic compounds with oxygen as final electron acceptor (Weng & Han, 2021). A broad substrate range including polyphenols, methoxy-substituted phenols, aromatic diamines and others with low substrate specificity make them quite suitable for industrial applications (Karittapattawan & Benchawattananon, 2021).

Wild edible mushrooms *Lentinus sajor-caju*, *Pleurotus giganticus* and *Panus sp.* from Tripura were identified as laccase producers using 0.02% guaiacol as substrate. Several local and commercial strains of edible mushroom from Khon Kaen Province, Thailand were explored for laccase activity (Debnath & Saha, 2018). *Agrocybe aegerita, Agaricus bisporus, Hypsizygus marmoreus, Lentinula edodes, Pleurotus eryngii, Pleurotus ostreatus* and *Pleurotus sajors-caju* were found to be potent producer of laccase in extracellular medium (Karittapattawan & Benchawattananon, 2021) as noted in Table II. It may be noted that copper sulphate along with Tween 80 and 4,6-dimethyl-2-mercaptopyrimidine induced laccase production in all mushrooms.

Volvariella volvaceae, strain 14, grown on cotton waste produced multiple forms of laccase in submerged culture at 30°C, 85% humidity and alternate 12 hours illumination (499 lux) and darkness before fruiting (Chen & Buswell, 2003). $CuSO_4$ and various aromatic compounds induced enzyme synthesis. Enzyme activity was low during vegetative growth but increased significantly during fruiting body and sporophore development. In low nitrogen medium maximum 7.2 U/l of laccase was detected over a growth period of 16 days. In high nitrogen medium highest laccase activity of 31.8 U/l was achieved on 14th day. In presence of ferulic acid, 2,5-xylidine, veratric acid and 4-hydroxybenzoic acid laccase activity was induced to 52.2 U/l, 43.5 U/l, 43.2 U/l and 33.6 U/l respectively. 4-hydroxybenzaldehyde also induced laccase production but to a lower extent at 12.3 U/l. However, in syringic acid, vanillic acid, p-coumaric acid, homovanillin or catechollux supplemeted media no enzyme activity was observed.

Table II. Ligninolytic enzymes of Edible Mushroom

Enzyme (s)	Mushroom (s)	Substrate(s) and Culture conditions	Activity/ Properties of the enzyme	Reference (s)
Peroxidase	*Lentinus edodes*	Basal liquid medium, Glucose 10g/L, yeast extract- 3g/L, peptone -1g/L, MgSO$_4$.7H$_2$O- 1g/L, KH$_2$PO$_4$.3H$_2$O – 1g/L, 25°C, pH 6.5±0.5	117.96± 2.88 IU/L	Sudarson & Venkatesan, 2014
Polyphenol oxidase	*Termitomyces sp.* (Tm7)	malt extract agar, pH 5.5, temperature 27°C,	3.8 OD change/min/mg of protein on 12th day of incubation	Gomathi & Ramalakshmi, 2019
Peroxidase	*Termitomyces sp.* (Tm4)	malt extract agar, pH 5.5, temperature 27°C	3.87 OD change/min/mg of protein on 12th day of incubation	do
Recombinant Versatile peroxidase 1	*Pleurotus ostreatus*	--	K_m 5.4±0.2µM, K_{cat} 12.9±0.3 s^{-1} [against reactive black 5]	Fernandez-Fueyo & Martinez, 2014
Recombinant Manganese peroxidase 2	*Pleurotus ostreatus*	--	K_m 92±5 µM, K_{cat} 159±3 s^{-1} [against Mn^{2+}]	do
Manganese peroxidase	*Pleurotus ostreatus*	Potato dextrose broth supplemented with Bisphenol A and di-(2-ethyhexyl)-phthalate, 25°C	26.61U/L [di-(2-ethylhexyl)-phthalate], 2.69 U/L [Bisphenol A]	Hock & Shing, 2020
Manganese peroxidase	*Pleurotus eryngii*	do	54.11U/L [di-(2-ethylhexyl)-phthalate], 2.88 U/L [Bisphenol A]	do
Manganese peroxidase	*Lentinula edodes*	do	31.69 U/L [di-(2-ethylhexyl)-phthalate], 5.6 U/L [Bisphenol A]	do
Manganese peroxidase	*Agaricus bisporus*	do	22.09 U/L [di-(2-ethylhexyl)-phthalate], 5.4 U/L [7.5µl/L Bisphenol A]	do
Versatile peroxidase	*Pleurotus eringii*	Purified through ammonium sulfate precipitation, ion exchange and gel filtration chromatography	40 kDa, PI 4.1, Km 203.09 mol/L [against ABTS], Vmax 188.68 U/mg, Temp optima 50°C, pH 3	Chen & Liang, 2010
Manganese peroxidase	*Hypsizygus ulmarius*	Potato dextrose agar plates, 28±2°C	6.11x10^{-4} IU/ml	Yogachitra 2019
Lignin peroxidase	*Pleurotus florida*	do	4.64x10^{-4} IU/ml	Yogachitra 2019
Laccase	*Agrocybe aegerita*	Potato dextrose agar, Solid state fermentation in mixed leaf litter, 31±2°C for 6-12 days	Kk26 93.75 U/ml [2, 6 Dimethoxyphenol] 87.15 U/ml [guaiacol]	Karittapattawan & Benchawattanon, 2021
Laccase	*Agaricus bisporus*	do	Kk1 81.15 U/ml [2,6 Dimethoxyphenol], 73.99 U/ml [guaiacol]	do
Laccase	*Hypsizygus marmoreus*	do	Kk23 108.57 U/ml [2,6 Dimethoxyphenol], 93.27 U/ml [guaiacol]	do
Laccase	*Hypsizygus marmoreus*	do	Kk5 101.51 U/ml [2,6 Dimethoxyphenol], 119.66 U/ml [guaiacol]	do
Laccase	*Lentinula edodes*	do	Kk8 74.09 U/ml [2,6 Dimethoxyphenol], 75.20 U/ml [guaiacol]	do
Laccase	*Lentinus squarrosulus*	do	Kk25 433.27 U/ml [2,6 Dimethoxyphenol], 411.66 U/ml [guaiacol]	do
Laccase	*Pleurotus ostreatus*	do	Kk24 432.76 U/ml [2,6 Dimethoxyphenol], 418.55 U/ml [guaiacol]	do
Laccase	*Pleurotus Ostreatus* Yang 1	Tomato juice Syringic acid and Cu^{2+} added after 3 days, 28°C, 180 rpm	29753.09 U/L (inducer for 5 days), 55.6kDa, K_m 0.15mM, V_{max} 4.41x10^{-7}mM/s [against ABTS], pH optima 3, Temp optima 50°C, Stable pH 9-11	Liu & Yang, 2021
Laccase	*Volvariella volvacea*	Paddy straw, 30-35°C	0.355U/ml	Karnan & Panneerselvam, 2016
Laccase	*Pleurotus nebrodensis*	Guiacol with micronuteients, 26°C one week	489.17 U/L on the 16th day	Fen & Haiping, 2014
Laccase	*Agrocybe sp.*	Basal liquid medium, Glucose 10g/L, yeast extract- 3g/L, peptone -1g/L, MgSO$_4$.7H$_2$O- 1g/L, KH$_2$PO$_4$.3H$_2$O – 1g/L, 25°C, pH 6.5±0.5	13.23± 1.45 IU/L	Sudarson & Venkatesan, 2014
Laccase	*Oudemansiella radicata*	Potato dextrose agar plates, 28±2°C	6.5x10^{-4}IU/ml	Yogachitra 2019
Tyrosinase	*Agaricus bisporus*	Wheat straw, Temp 18-22°C, Humidity 60-70% Light 10-20 lux	6.112 U/mg	Sharma & Thakrele, 2016
Tyrosinase	*Pleurotus florida, P. dyjamore and P.oysterus*	do	7.74 U/mg, 5.81 U/mg and 3.69 U/mg respectively	do

Highly active laccase, LAC-Yang 1 was isolated and purified from *Pleurotus ostreatus* strain yang1. Different chlorophenols such as 2,6-dichlorophenol, 2,3,6-trichlorophenol and chlorophenol mixtures were used as substrates to investigate the degradative efficiency of the pure enzyme (Liu & Yang, 2021). Pure enzyme showed lowest substrate affinity (K_m) of 0.12 mM against 2,6-DMP and highest V_{max} of 4.41 x 1^{-7} mM/s was achieved against ABTS (Table II). Interestingly the enzyme was very stable at the pH range of 9 to 11 and demonstrated 71.57%, 67.58% and 64.50% of activity when incubated at pH 9, 10 and 11 for 7 days. Pure enzyme showed strong tolerance towards SDS and EDTA whereas DTT, sodium azide, mercaptoethanol strongly inhibited the enzyme activity. Enzyme activity was not affected in presence of Mn^{2+}, Cu^{2+}, Mg^{2+}, Na^+, K^+, Zn^{2+}, Al^{3+} and Cd^{2+}. However, Fe^{2+} inhibited enzyme activity. Different organic solvents such as acetonitrile, isopropanol and DMF strongly inhibited enzyme activity whereas the enzyme was insensitive towards glycerol and propylene glycol. The enzyme showed stability in presence of Mn^{2+}, Mg^{2+} and glycerol. With 4 U/ml activity the enzyme degraded 91% of 800mg/L 2,6-dichlorophenol during 12 hours but degradation rate of 2,3,6 - trichlorophenol was slower compare to it. The enzyme however, rapidly degraded the chlorophenol mixture. The enzyme tolerated metal ion mixtures during degradation of 2,6-dichlorophenol and 2,3,6-trichlorophenol but acetonitrile and isopropanol strongly inhibited the enzymatic degradation process. The enzyme ameliorated toxic effects of different concentrations of 2,6-dichlorophenol on the germination of *Oryza sativa*, *Triticum aestivum* and *Mung bean* seeds effectively.

Fresh fruit body extracts of 21 wild mushroom species were collected from Noun division in the western region of Cameron to screen for their laccase, manganese peroxidase and lignin peroxidase activities (Ematou & Moundipa, 2020). Among the edible mushrooms such as *Afroboletus luteolus*, *Amanita rubescens*, *Lactifluus gymnocarpus*, *Lactifluus rubroviolascens*, *Xerocomas sp.*, *Coriolopsis polyzona*, *Echinochaete brachypora*, *Genoderma lucidum*, *Neonothopanus hygrophanus*, *Polyporus tenuiculus*, *Schizophyllum commune*, *Termitomyces aurantiacus*, *Termitomyces clypeatus*, *Termitomyces letestui*, *Termitomyces mboudaiena*, *Termitomyces schimperi*, *Lentinus cladopus*, *Lentinus squarrosulus* and *Pleurotus pulmonarius* etc. only *Xerocomas sp.* was not able to produce lignin peroxidase. Specific activities of the enzyme lignin peroxidase was 0005±0.0004 U/mg in *Lactifluus gymnocarpus* whereas in *Lentinus cladopus* the value was 0.0278±0.0017 U/mg. Manganese peroxidase activity was recorded from all the edible mushrooms except from *Termitomyces schimperi* and *Schizophyllum commune*. However, highest enzyme activity of 0.1992±0.005 U/mg was noted in *Lactifluus gymnocarpus.* Laccase titre was higher in all mushroom species compare to other enzymes. Maximum laccase activity of 17.5994 U/mg was achieved from *Coriolopsis polyzona* extract. So, the mushroom demonstrated highest

ligninolytic enzyme activities. Production of laccase was induced by xylidine addition in *Pleurotus ostreatus*.

Recombinant laccase which formed via Lac-2 gene of *Pleurotus ostreatus* expression in *Pichia pastoris* X33 yeast strain, was efficient in degrading corn stover lignin. Optimum pH values of the recombinant enzyme against 2,2'-Azinobis-3-ethylbenzothiazoline-6-sulfonic acid, 2,6-dimethoxyphenol and 2-methoxyphenol were 3.0, 3.0 and 3.5 respectively (Song & Song, 2020). Optimum temperature for the reaction was determined at 50°C. The enzyme was thermostable and resistant to acid or alkali. Lignin degradation rate from corn stover by the recombinant enzyme was 18.36% while for the native strain degradation rate was 14.05%.

Production of laccase from fungi are regulated by several factors such as carbon limitation, nitrogen source, method of cultivation, concentration of microelements, physical factors (pH, temperature etc.) and presence of inducers. Addition of laccase and proteolytic enzymes to oat flour resulted in significant improvement of loaf specific volume and lowering crumb hardness and chewiness leading to improved texture quality of oat bread (Brijwani & Vadlani, 2010). Food and beverage industry waste water containing heavy amounts of phenols, polyphenols, amines and other aromatic compounds were also treated with laccase for removal of those compounds (Brijwani & Vadlani, 2010).

5) Tyrosinase

Tyrosinase (EC 1.14.18.1) belongs to a group of type-3 copper proteins which are involved in melanin synthesis. It performs monophenolase or cresolase activity by o-hydroxylation of monophenols using molecular oxygen. Subsequent oxidation and other nonenzymatic reactions lead to the formation of dark brown pigments (Halaouli & Lomascolo, 2006). In Basidiomycotina, melanins are synthesized from L-tyrosine, c-glutaminyl-3,4-dihydroxybenzene (GDHB), or catechol whereas in Ascomycotina, it is synthesized from 1,8-dihydroxynaphthalene (DHN) during browning and pigmentation. These pigments build a defense system against certain stress factors like UV radiation, gamma rays, free radicals, extreme temperatures and dehydration and prevents cell wall lysis by hydrolytic enzymes. They also play significant roles in spore formation, defense and virulence mechanism. Tyrosinase available from edible mushroom is low in amount and intracellular.

Agaricus bisporus, *Pleurotus florida*, *Pleaurotus dyjamore* and *Pleurotus oysterus* grown on wheat straw were investigated for distribution and production of tyrosinase during growth (Sharma & Thakrele, 2016). Amongst different stages of growth, maximum tyrosinase was accumulated during premature stage of those edible mushrooms (Table II). Enzyme was not uniformly distributed in the fruiting body. Maximum tyrosinase activity of 9U/mg was obtained from the part of the stem connected to the cap.

Tyrosinase from button mushroom *Agaricus bisporus* was isolated via ammonium sulphate precipitation, Sephadex G-100 gel filtration column and then DEAE-cellulose ion exchanger (Zaidi & Ali, 2014). Pure enzyme was obtained after rerunning the eluted fraction through the ion exchanger DEAE-cellulose column. It was a single protein of approximately 95KDa in SDS-PAGE. Temperature optima of the enzyme was 35°C although the pure enzyme was active in the temperature range from 30°C to 65°C. pH optima of the enzyme was 7.0 and the enzyme retained 65% of its activity at that pH after 24hours. Substrate affinity or Km of the enzyme was 0.933mM against L-DOPA signified its therapeutic effectiveness against melanogenesis as the enzyme was characteristically similar to human tyrosinase.

Tyrosinases are also known as polyphenol oxidase, phenolase, catechol oxidase, o-diphenyl oxidase, monophenol oxidase or cresolase etc. Rejected *Pleurots ostreatus* was used prepare a crude extract to check its phenol oxidizing ability (Murniati & Nurhanifah, 2018). Highest specific activity was recorded at 25.15 U/mg against 0.3mM phenol and 15.60 U/mg against 0.2 mM catechol at pH 7. Maximum polyphenol oxidase activity was calculated at 20°C and pH 7 as 79.23 U/ml against 0.3mM phenol and 49.11 U/ml against 0.2 mM catechol. 10 to 15 ml of crude extract containing 79.23 U/ml polyphenol oxidase activity added to phenol solution showed more than 50% effective oxidation of phenol to quinone and 20-50ml of the same extract removed more than 90% of phenol via oxidation. Moreover, crude extract with 1800 U/ml activity effectively removed 100% of phenol from 50mg/L phenol in 50mM phosphate buffer at pH 8.0.

14 heterokaryotic strains of the edible and medicinally important mushroom *Hericium erinaceus* were cultivated for production of laccase and tyrosinase in the growth medium prepared by malt extract and peptone (Gryganski & Molitoris, 2000). Strains producing white to yellow, yellow to brown or brown colored fruit bodies are found to be better laccase producers compare to strains having white fruit bodies. Similar trend was observed in case of tyrosinase enzyme as well.

B. Hydrolases

1) Cellulase

Cellulase is a multienzyme complex composed of endo-β-1,4-glucanase, exo-β-1,4-glucanase I and II and β-glucosidase or cellobiase. The enzymes act sequentially to break the linear polymer into monosaccharide glucose unit. The endo enzyme creates random cleavage of internal bonds of the cellulose linear chain. Then exo-β-1,4-glucanase II targets the non-reducing ends of the chain and exo-β-1,4-glucanase II attacks at the reducing ends to produce disaccharide cellobiose. β-glucosidase acts on cellobiose to generate monomeric units of glucose. The last stage of the total hydrolysis process is the rate limiting step (Ghorai & Khowala, 2011; Roy & Banik, 2021).

Enzyme production from edible mushrooms vary greatly depending on the nature of the lignocellulosic materials. When *Pleurotus ostreatus* was grown on some solid wastes, lignin biodegradation was double in case of sawdust compare to rice straw (Sherief & Temraz, 2010). On the other hand, hemicellulose and cellulose degradation were greater in case of rice straw than saw dust. However, fruiting event was earlier in rice straw. At both mycelial and fruiting stage, exoglucanase, endoglucanase, carboxoxymethyl cellulase (CMCase) titer were higher in saw dust medium. In *Pleurotus eryngii* grown on ramie stalks, kenaf stalks, bulrush stalks and cottonseed hull showed ramie stalks and kenaf stalks were best suitable to cultivate the mushroom with biological efficiency of 55% and 57% respectively (Xie & Peng, 2016). Both the substrates induced cellulase, hemicellulase and lignin depolymerization enzymes. Growth and development pattern indicated lignin preference of the mushroom rather than cellulose or hemicellulose.

Table III lists some of the hydrolytic enzymes produced from edible mushrooms. Most popular and palatable mushrooms from Orissa such as *Russula lepida, Russula brevipes, Russula nigricans, Volvariella volvaceae, Lentinus tuberregium, Macrolepiota procera* and *Calocybe indica* were collected from tropical moist deciduous and semi ever green forest of the state (Rajoriya & Gupta, 2016). Among the species studied, highest L-asparaginase activity was recorded in *Russula nigricans* and *Russula brevipes* whereas *Macrolepiota procera* and *Russula lepida* were moderate producers. *Russula brevipes*, *Russula nigricans, Russula lepida* and *Calocybe indica* demonstrated more cellulase activity compared to amylase.

Several commercial strains of *Lentinula edodes* namely IE-40, IE -105, IE-124, IE-171, IE-242 (cross of IE-244 and IE-245), IE-243, IE-244, IE-245 and IE-246 were grown in coffee beans at 25±2°C (Mata & Perez-Merlo, 2016). Samples were estimated for cellulase activity after 7, 14, 21, 28 and 35 days of incubation. During fruiting period, samples were taken after primordia formation, first harvest and one week after first harvest. Strains showed similar patterns in terms of secretion of hydrolytic enzymes. During early stages of adaptation to the substrate enzyme activity was lower which increased later on during formation and development of the fruiting bodies. Maximum cellulase activity over 2.35mU/g was detected during the fifth week of incubation (Table III).

Lignocellulytic genes were studied in edible mushrooms *Lentinula edodes, Ganoderma lucidum, Pleurotus ostreatus, Coprinus cinereus, Volvariella volvaceae, Laccaria bicolor, Agaricus bisporus* and others (Chen & Bian, 2016). White rot fungi like *Lentinula edodes, Pleurotus ostreatus, Ganoderma lucidum* (35-61) and straw rot fungi like *Volvariella volvaceae, Coprinus cinereus* (54-55) have large number of cellulolytic genes compare to *Laccaria bicolor* and *Agaricus bisporus.* Similar trend was observed in case of hemicellulolytic enzyme genes, lignin degrading auxiliary enzyme genes and lignin

oxidase genes. Saccharification of the pulp from straw forage sorghum pre-treated by acid and delignification by edible mushroom's multienzyme complex was higher in *Trametes versicolor* TRAM01 and *Pleurotus ostreatus* PLO06 compare to the commercial enzyme (Table III) (Cardosos & de Queiroz, 2018).

Termitomyces sp. are famous for their association with termites. These edible mushrooms are efficient degraders of cell wall polymers like cellulose, hemicellulose and lignin. Various hydrolytic enzymes like cellulase, amylase, xylanase, β-glucosidase or cellobiase, sucrase and alkaline phosphatase etc. have been isolated and purified from *Termitomyces clypeatus* (Ghorai & Khowala, 2009; Chowdhury & Khowala, 2009; Ghorai & Khowala, 2010; Ghorai & Khowala, 2011; Ghorai & Khowala, 2016; Majumder & Khowala, 2016). Culture filtrate enzymes from *Termitomyces clypeatus* containing β-glucosidase showed comparable efficiency with commercial cellulase during saccharification of carboxymethyl cellulose (Table III) (Ghorai & Khowala, 2011). *Termitomyces albuminosus* and other species are also noted producers of lignocellulolytic enzymes of industrial importance as mentioned in Table III (Gomathi & Ramalakshmi, 2019). G*enoderma lucidum* strain G0119 grown on potato dextrose agar showed increased endoglucanase activity gradually during growth phases but maximum cellobiohydrolase and β-glucosidase activities were observed during phase 4 (Zhou & Zhang, 2018). Enzyme activities in different layers of growth varied and the upper layers contained relatively higher enzyme activities compared to the other two layers. Gene expression, protein abundance and enzymatic activity analysis revealed that overall expression of cellulase was higher than that of hemicellulose and lignin modifying enzymes specially during fruiting body development. Most abundant extracellular lignocellulolytic enzyme produced by the mushroom strain was type I cellobiohydrolase. Lignin modifying enzymes were mainly AA2 family heme peroxidases and laccases.

2) Xylanase

The principal component of hemicellulose is xylan which is composed of α-1,4-linked d-xylosyl backbone branched with pentoses, hexoses and uronic acids. Xylanases are debranching enzymes responsible for hydrolysing xylobiose of hemicellulose polymer. Xylanase production was estimated in *Pleurotus eryngii* grown in presence of different concentrations of glucose, xylose, sucrose, starch, xylan, wood straw and rice husk powder as carbon source (Simair & Lu, 2016). Potassium nitrate, sodium nitrate, diammonium hydrogen phosphate, urea and corn steep liquor etc. were utilized as nitrogen source (Table III). Crude xylanase was thermostable as it retained more than 40% of its activity within 10 minutes at 100°C. It also showed stability in between pH 5 to 7. When incubated for longer times (60 minutes) the crude enzyme lost only 20% and 25% of its activity at 60°C and 70°C

respectively in presence of $ZnCl_2$ making it suitable for use in pulp and paper industries.

3) Amylase and others

Amylases are complex group of enzymes that hydrolyses polysaccharides like starch to glucose, thus play a wide range of biotechnological applications in food industry, fermentation, textile and paper industry (Ghorai & Khowala, 2009). Starch is composed of two types of polymeric units of glucose namely amylose and amylopectin. Amylose is a linear polymer of glucose having maximum of 6000 units of the monosaccharide linked via α-1, 4 glycosidic bond whereas amylopectin is composed of α-1, 4 glycosidic bonded chains of 10-60 glucose monomers with α-1,6 glycosidic linked side chains of 15-45 glucose units (Gopinath & Chinni, 2017). Amylases are broadly classified into α, β and γ subtypes. Amylases may act as endoenzymes which catalyze hydrolysis in a random manner within the starch molecule resulting in linear or branched oligosaccharides of various chain length. However, the exoenzymes hydrolyze the substrate from the nonreducing end yielding successively shorter end products. Alpha-amylases or 1,4-α-D-glucan glucanohydrolase (EC 3.2.1.1) are calcium metalloenzymes and act on α-1, 4 glycosidic bonds of large alpha linked polysaccharides like starch and glycogen at random locations yielding either maltotriose and maltose from amylose or maltose, glucose and 'limit dextrin' from amylopectin (Gopinath & Chinni, 2017). They are also called the endoenzymes as they cleave the bonds present in the interior of the molecule at random fashion. Pectin is a complex plant polysaccharide composed of esterified D-galactouronic acid residues in an α-(1-4) chain. Pectinases act on pectin to break them down to α-(1-4)-polygalactouronic acid residues. Rate of hydrolysis is dependent on the chain length and higher the chain length, rate of hydrolysis is also high (Bharadwaj & Udupa, 2019).

Pleurotus sajor-caju grown on onion waste orduced a thermostable pectinase through solid state fermentation (Pereira & Regina, 2017). The yield and biological efficiency of the fermentation in water immersion state were 45.73% and 4.66% respectively. The crude enzyme activity was 4.82U/ml which demonstrated optimum pH at 3.0 and 6.0 and temperature at 80°C. Substrate affinity of the enzyme was low at 243.83mM and maximum reaction rate was 6.99mM/min.

Table III. Cellulolytic enzymes from edible mushrooms

Enzyme (s)	Mushroom (s)	Substrate(s) and Culture conditions	Activity/ Properties of the enzyme	Reference(s)
cellulase and amylase	*Volvariella volvacea*	Paddy straw, 30-35°C	0.024U/ml and 0.076 U/ml respectively	Karnan & Panneerselvam, 2016
cellulase	*Pleorotus ostreatus*	Citrous Limonium and Carica Papaya wastes, Double papaya waste with rice straw, 20-25°C	4.2-7U/g of fresh fruit bodies, 14.2 U/ g of fresh fruit bodies	Rashad & Nooman, 2009
invertase	*Pleorotus ostreatus*	Lemon pulp, 20-25°C	2-2.5 times than control	do
polygalacturonase	*Pleorotus ostreatus*	Lemon pulp, 20-25°C, Lemon pulp + rice straw, 20-25°C	9.8 U/g of fresh fruit bodies, 373.5 U/g of fresh fruit bodies	do
amylase	*Pleorotus ostreatus*	Lemon pulp, 20-25°C, Papaya fruit waste, 20-25°C	32.45 U/g of fresh fruit bodies, 31.88 U/g of fresh fruit bodies	do
cellulase	*Lentinus edodes, Hypsizygus ulmarius and Pleorotus florida*	Basal liquid medium, Glucose 10g/L, yeast extract- 3g/L, peptone -1g/L, MgSO$_4$.7H$_2$O- 1g/L, KH$_2$PO$_4$.3H$_2$O – 1g/L, 25°C, pH 6.5±0.5	294.14± 2.08 IU/L, 98.41±1.45 IU/L and 93.78± 2.6 IU/L respectively	Sudarson & Venkatesan, 2014
cellulase	*Termitomyces sp.* (Tm3)	malt extract agar, pH 5.5, temperature 27°C, (optimum)	10.27μmol of glucose released/min/mg of protein at 12th day of incubation	Gomathi & Ramalakshmi, 2019
xylanase	*Termitomyces sp.* (Tm4)	malt extract agar, pH 5.5, temperature 27°C, (optimum)	9.87μmol of xylose released/min/mg of protein at 12th day of incubation	do
amylase	*Termitomyces sp.* (Tm6)	malt extract agar, pH 5.5, temperature 27°C,	14.5 μmol of glucose released/min/mg of protein on 12th day of incubation	do
β-glucosidase	*Termitomyces clypeatus*	Cellobiose 1%, Succinate 0.05%, 2-Deoxy glucose (2DG), other micronutrients, pH 5, 30°C, shaking	K$_m$ 0.092 mM, V$_{max}$ 35.54 U/mg, 143.8 U/ml (at 500μg/ml 2DG on 6th day), Comparable saccharification ability with respect to commercial cellulase	Ghorai & Khowala, 2011
cellulase and laminarinase	*Lentinula edodes*	Coffee pulp, 25°C	2.35mU/g after fifth week of incubation, 8.00mU/g at the beginning of week 1 or 2	Mata & Perez-Merlo, 2016
cellulase	*Coriolus versicolor*	yeast extract supplemented medium	0.68 unit/ml	Jonathan & Adeovo, 2011
amylase	*Agaricus blazei*	Carboxymethyl cellulose	0.6 unit/ml	do
xylanase	*Pleurotus eryngii*	Glucose 6.0g, Yeast extract 0.2 g,, Peptone 0.5g, KH$_2$PO$_4$ 1.0g, MgSO$_4$.7H$_2$O 0.5 g, pH 5.5, 120 rpm and 27 ± 2°C	pH optima 5, Temp optima 60°C, Activator Zn^{2+}, Ca^{2+}, 6.068 IU/ml against 0.6% xylose 7.185 IU/ml against 1% corn steep liquor	Simair & Lu, 2016
endoglucanase and exoglucanase	*Schizophyllum commune*	malt extract medium, 37°C and at pH 5.5	100 REA and 220mg/ml respectively after 7days, Temp optima 45°C and 55°C respectively, pH optima 6 and 5 respectively, inhibitors Cu and veratryl alcohol	Vijaya & Reddy, 2011
carboxymethyl cellulase	*Pleurotus ostreatus* PLO06 and *Trametes versicolor* TRAM01	natural and pretreated pulps of sorghum straw, 70% humidity at 28°C	2.25 U/mg	Cardosos & de Queiroz, 2018
cellulase and avicellulase	*Pleurotus ostreatus* PLO06	natural and pretreated pulps of sorghum straw, 70% humidity at 28°C	1.32 U/mg and 4.12 U/mg	do
β-glucosidase	*Trametes versicolor* TRAM01	natural and pretreated pulps of sorghum straw, 70% humidity at 28°C	1.88 U/mg	do
amylase and pectinase	*Lentinula boryana*	wheat straw dextrose agar,25°C for 7 days	1554 U/gX and 1657 U/gX (International unit per gram dry biomass of mushroom)	Diaz-Godinez & Tellez-Tellez, 2016
amylase and pectinase	*Pleurotus djamor* var. *roseus*	potato dextrose agar, 25°C for 7 days	700 to 2000 U/gX	do
carboxymethyl cellulase	*Hericium erinaceus*	Carboxymethyl cellulose micronutrients, 26°C, 120 rpm	22.58 U/L on the 10th day	Fen & Haiping, 2014

4) Protease

Proteases are indispensable in various industries like dairy, leather, detergent, brewing, meat and photographic industries due its hydrolytic capabilities of amide linkage. Mushrooms are rich in proteases *Lepista nuda*, *Termitomyces clypeatus* etc. Many metaloproteases are currently famous for other bioactivity like proteases from *Lepista nuda* had shown antiproliferative activity on human hepatoma HepG2 cells. Serine protease from *Termitomyces clypeatus* was capable of killing cancer cells, restoring p53 level and cleaving surface proteoglycans (Majumder & Khowala, 2016). Some proteases from edible mushroom are listed in Table IV. Metalloprotease from *Oudemansiella radicata* was purified from the mushroom extract through DEAE-cellulose column equilibrated with sodium acetate buffer at pH5.6 (Geng & Ng, 2017). The pure enzyme was characterized for its activator, inhibitors, Km, Vax, temp and pH optima etc. (Table IV).

A novel alkaline and detergent stable protease (SPPS) was isolated from *Pleurotus sajor-caju* strain CTM10057 (Benmrad & Jaouadi, 2019). The pure enzyme was not inhibited by trypsin-like or chymotrypsin competitive reagents (Table IV). Metalloprotease inhibitors like EDTA and EGTA affected the enzyme activity insignificantly whereas serine protease inhibitors strongly inhibited the pure enzyme suggesting the proteolytic nature of the pure enzyme. It was highly stable at a pH range of 6-11 and was also heat stable as it showed half-life of 8, 3 and 1 hour at 80, 90 and 100°C respectively. Thermostability of the pure enzyme was increased in presence of Ca^{2+} and sorbitol. It exhibited esterase and amidase activity on some substrates. Interestingly it showed preference towards aromatic and hydrophobic amino acid residues such as Ala, Phe, Met, Leu and Tyr attached to the carboxyl side of the cleavage sites of the chromogenic substrates. The protease showed higher efficiency in comparison to other enzymes and

elevated tolerance to organic solvents. So, this enzyme can be a potential biocatalyst for peptide synthesis in aqueous and non-aqueous (or low water activity) systems. As the enzyme is active in alkaline pH and high temperature, it can also be used as an effective additive in detergent formulations. It was quite effective in removing blood stains from cotton fabrics when mixed with Dixan and performed better compare to Flavourzyme 500 L. Edible mushroom *Lentinus citrinus* DPUA 1535 and *Pleurotus ostreatoroseus* DPUA 1720 were investigated for protease

Table IV. Proteases from Edible Mushroom

Enzyme (s)	Mushroom (s)	Culture condition	Enzyme properties	References
Neutral protease	*Cordyceps militaris*	Glucose - 40g/L, Yeast extract - 10g/L, KH_2PO_4 - 0.5g/L, $K_2HPO_4.3H_2O$ – 0.5g/L, $MgSO_4.7H_2O$ – 0.5g/L, Temp 25°C, 110rpm, Grown mycelia	Optimum pH 7.4, Optimum temp 37°C, Hydrolyse fribin α, β, γ chains, Activator Ca^{2+}, Mg^{2+}, Inhibitor Cu^{2+}, Co^{2+}	Kim & Kim, 2006
		incubated with silk worm larvae		
Cysteine protease	*Pleurotus ostreatoroseus* DPUA 1720	Biocomposite made of amazonic tuber *Dioscorea alata*	144.22 U/ml, Optimum temp 40°C, pH Optima 7	Machado & Teixeira, 2017
Metalloprotease	*Armillariella mellea*	--	18.54KDa, pH optima 7, Temp optima 55°C, Hydrolyse Aα and Bβ subunits of human fibrinogen, Activator Mg^{2+}, Zn^{2+}, Co^{2+}, Inhibitor Hg^{2+}, EDTA and 1,10-phenanthroline	Kim & Kim, 1999
Alkaline protease	*Pleurotus sajor-caju* strain CTM10057	g/L lentil flower 15, yeast extract 3, glucose 10, KH_2PO_4 1, K_2HPO_4 1 pH 5.6, in PD Broth PDA 3 days at 28°C and 180rpm	65KDa, Activator Ca^{2+}, Mg^{2+}, Fe^{2+}, Inhibitor Cd^{2+}, Ni^{2+}, Hg^{2+}, pH optima 9.5, Temp optima 60°C, K_m 0.275mg/ml, V_{max} 79000µmole/mg.min^{-1}	Benmrad & Jaouadi, 2019
Metalloprotease	*Oudemansiella radicata*	--	39 KDa, specific activity 2.42 U/mg, Km 0.65mg/ml (against casein), Vmax 125.85µg/ml/min, pH optima 7.0 Temp optima 50°C, Inhibitors Cd^{2+}, Hg^{2+}, Cu^{2+}, Pb^{2+} and Fe^{3+}, Activator K^+, Mn^{2+} and Fe^2	Geng & Ng, 2017

production in presence of amazonic tubers *Dioscorea trifida*, *Manihot esculenta* and *Dioscorea alata* supplemented with rice bran or manioc flour residue in varied proportions (Machado & Teixeira, 2017). Each combination was positive for protease but highest titre was achieved from *Pleurotus ostreatoroseus* DPUA 1720 cultivated in *Dioscorea alata* (Table IV). Lowest proteolytic activity of 24.88 U/ml was found from *Pleurotus ostreatoroseus* DPUA 1720 grown in *Manihot esculenta* supplemented with 10% manioc residue. Highest proteolytic acitivity of 52.40 U/ml was achieved from *Lentinus citrinus* DPUA 1535 grown in *Dioscorea trifida* with 20% rice bran. Minimum enzyme activity was 10.73 U/ml in presence of *Dioscorea alata* supplemented with 10% rice bran. Enzyme from *Pleurotus ostreatoroseus* was stable between pH 7-8 and temperature 40-50°C for one hour with relative activity of 94-100%. It was strongly inhibited by iodine acetic acid, PMSF and EDTA suggesting the presence of cysteine and serine protease. Similar reduction in activity was observed in presence of Cu^{2+} and Zn^{2+} whereas K^+, Mg^{2+} and Ca^{2+} were weak effectors.

5) Fibrinolytic activity

Formation of fibrin through clotting of blood from fibrinogen by thrombin causes thrombosis leading to myocardial infarction and other cardiovascular diseases in the blood vessel. Blood clot can be dissolved by the help of plasmin which degrades fibrins via hydrolysis of insoluble fibrin fibres. Plasmin is generated from plasminogen by plasminogen activators such as blood plasminogen activator, tissue plasminogen activator, vascular plasminogen activator, streptokinase-plasminogen complex and urokinase etc (Kim & Kim, 1999). These thrombolytic agents used for clinical purpose also impart some side effects such as resistance to reperfusion, incident of acute coronary reocclusion and bleeding complications. In the search of a safe and effective thrombolytic agent, fermented fish, beans and edible mushrooms were explored since long.

Proteases from *Pleurotus ostreatus*, *Armillariella mellea*, *Grifola fondosa*, *Flamulina valutipes* (Fr) Sing, *Cordyceps militaris* and many other edible mushrooms were characterised for their fibrinolytic efficiency against human fibrinogen as potential candidates for oral fibrinolytic therapy. Kim & Kim (1999) isolated and characterized one fibrinolytic protease from *Armillariella mellea* having twice activity of plasmin (1.5U/ml) after screening 65 species of mushroom from Mt. Chiak, Korea (Table IV). The pure enzyme isolated from fruit body extract behaved as plasmin like enzyme rather than a plasminogen activator as it directly hydrolysed fibrin plate without plasminogen. Quantitative analysis by ICP-MS showed 0.92 mole of Zn per mole of the enzyme indicating one atom of zinc (ion) may be associated with one molecule of enzyme. The enzyme was stable upto 60°C and was insensitive to trans epoxysuccinyl leucylamide 4-guanidinobutane (cysteine protease inhibitor), PMSF (serine protease inhibitor), pepstatin (aspartic protease

inhibitor) and 2-mercaptoethanol (indicating S-S bond was not responsible for structure and function). However Hg^{2+}, EDTA and 1,10-phenanthroline significantly inhibited fibrinolytic activity indicating the enzyme is a metalloprotease and Zn is essential for enzymatic activity (as per ICP-MS data). Pure enzyme showed broad substrate specificity as it hydrolysed a range of synthetic nitroanilide peptides. Although the enzyme hydrolysed fibrin and fibrinogen but other blood proteins such as thrombin, human albumin, bovine albumin, urokinase, haemoglobin and human immunoglobulin G (IgG) were not hydrolysed by the enzyme.

One neutral protease was isolated from crude extract of *Cordyceps militaris* rapidly hydrolysed the α-chain of fibrin followed by γ-y chain although the β-chain was hydrolysed more slowly (Kim & Kim, 2006). The hydrolysis pattern was not similar to that of plasmin. The pure enzyme also showed fibrinogenolytic activity as it hydrolyzed fibrinogen Aα, Bβ and β chains (Table IV). The enzyme was stable in the pH range of 7 to 8 at 37°C for 1 hour and it was able to retain more than 80% of its activity at pH 10. Interestingly, the enzyme showed high degree of specificity towards chymotrypsin substrate Meo-Suc-Arg-Pro-Tyr-pNA.HCl (S-2586) suggesting its amidolytic acitivity can be utilized as a chymotrypsin-like serine protease.

6) Esterase

These enzymes are associated with metabolism of a number of therapeutics such as cholesterol lowering drug (lovastatin), anti-infuenza drug (Oseltamivir), narcotic analgesic meperidine (Demerol), cocaine and heroin (Shivashankar & Premkumari, 2014). This enzyme is also crucial for the enantioselective hydrolysis of esters to produce optically pure compounds or resolution of racemic mixtures by transesterification. Fruiting body of *Hypsizygus ulmarius* produced 2.25µmole/ml of esterase (Shivashankar & Premkumari, 2014). pH optima of the enzyme was 6 but the enzyme was stable over the pH range of 3-9. The enzyme was stable in the temperature range of 20-40°C with optima at 30°C. The enzyme activity was strongly inhibited by $FeSO_4$ and slightly inhibited by $MgCl_2$, $NiSO_4$ and NaCl but presence of $CuSO_4$ induced the enzyme activity. Substrate affinity and maximum reaction velocity of the purified esterase was found to be 0.33mM and 0.47mM/sec respectively.

7) Stress Enzymes

Accumulation of minerals in higher amount in different parts of the fruiting body of the edible mushrooms in wild may often lead to stress response in the system inducing reactive oxygen species. This in turn induce mushroom antioxidant defense system to produce antioxidant enzymes such as superoxide dismutase, peroxidase and catalase (Georgescu & Chelarescue, 2016). Superoxide dismutase converts superoxide anions to hydrogen peroxide and molecular oxygen. Catalase and peroxidase eliminate hydrogen peroxide via formation of water and oxygen.

Pleurotus ostreatus, *Pleurotus djamor* var. roseus and *Pleurotus florida* were investigated for their antioxidative stress enzyme titre (Kaushal & Bhatt, 2018). *Pleurotus djamor* var. roseus showed maximum 23.17 IU/mg activity in ethanolic extract whereas *Pleurotus florida* showed maximum 22.09 IU/mg activity in methanolic extract. Free radical scavenging potential of ethanolic extract of *Pleurotus djamor* var. roseus was 90.74%. 0.47 U/ml and 0.35 U/ml of peroxidase activity was obtained from ethanolic extract of *Pleurotus djamor* var. roseus and methanolic extract of *Pleurotus florida* respectively. Methanolic extract of *Pleurotus florida* demonstrated 84.97% superoxide radical scavenging activity. Maximum antioxidant potential of the mushroom enzymes was achieved at a pH of 6-6.5. Temperature and pH optima of superoxide dismutase from *Pleurotus djamor* var. roseus were 40°C and 6 respectively. The same enzyme from *Pleurotus florida* showed optimum temperature and pH at 40°C and 6.5 respectively. Peroxidase from *Pleurotus djamor* var. roseus and *Pleurotus florida* showed optimum pH at 6 and 6.5 respectively and their temperature optima was at 37°C.

Edible mushrooms *Pleurotus sajor-kaju*, *Volvariella volvaceae*, *Agaricus bisporus* and *Pleurotus ostreatus* were tested for their antioxidant, peroxidase, ascorbate oxidase and catalase activity (Surekha & Haseena, 2011). Antioxidant activity was calculated as equivalents of α-tocopherol (µg/gm wt). 1.7 units were availavle from *Agaricus bisporus* and *Pleurotus ostreatus* but in *Volvariella volvaceae and Pleurotus sajor-kaju* 1.1 and o.3 units were available respectively. *Agaricus bisporus* contained highest peroxidase and catalase activity compare to others. Ascorbate oxidate activity was maximum in *Agaricus bisporus* (16 U) followed by *Volvariella volvaceae* with 7U. Ethyl acetate extract of *Agaricus bisporus* and *Pleurotus ostreatus* showed broad spectrum of antibiotic activity.

Ageing is characterized by decreased levels of ascorbate and ascorbate peroxidase activity. Extra-mitochondrial system like microsomal electron transport and other enzyme systems such as xanthine oxidase, aldehyde oxidase, dihydroorotic dehydrogenase and a group of flavoproteins dehydrogenase etc. are responsible for oxidative stress, O_2^- and reactive oxygen species. Stress amelioration is achieved by a set of scavenging enzymes such as glutathione reductase, ascorbate synthase, catalase and superoxide dismutase etc.

Pleurotus ostreatus treated aged Wistar rats showed significant lowering in the level of xanthine dehydrogenase in the kidneys, heart and brain compare to untreated aged rats (Thomas & Jayakumar, 2014). Extract treated aged rats showed significantly increased levels of glucose-6-phosphate dehydrogenase in all the above-mentioned organs including lever. Similar observation was noted in case of ascorbate peroxidase enzyme when the aged rats were treated with the mushroom extract. Analyzing the isoforms of the enzymes present in different organs of treated and untreated animals, differential patterns were observed. Lower number of ascorbate peroxidase isozyme was found in the brain tissues of

aged untreated animals indicating more susceptible nature of that organ to stress condition. Thus, mushroom extract was effective as therapeutic supplement in reducing age related oxidative stress in aged rats by increasing secondary antioxidant enzymes like glucose-6-phosphate dehydrogenase, ascorbate peroxidase while reducing oxidative marker xanthine dehydrogenase in major organs such as liver, kidney, heart and brain (Thomas & Jayakumar, 2014).

III. FACTORS AFFECTING ENZYME PRODUCTION

Edible mushrooms show substrate preference and depending on the substrates on which they grow enzyme expression may vary.

A. *Substrates*

In *Pleurotus ostreatus* grown on wood or sawdust lignin depolymerizing enzymes such as manganese peroxidase and laccase were produced whereas in *Volvariella volvacea* grown on its preferable substrate containing high cellulose and low lignin cellulolytic enzymes such as endoglucanases (five), cellobiohydrolases (five) and two β-glucosidases were dominant (Buswell & Yu, 1996). *Pleurotus ostreatus* is well known for their ligninolytic non specific oxidative enzymatic systems. This system comprises of laccases, versatile peroxidases, short manganese peroxidases, dye-decolorizing peroxidases and heme-thiolate peroxidases etc. The production of these enzymes is dependent on growth media composition, pH, temperature as well as growth phase of the edible mushroom. However, Mn^{2+} concentration was found to affect the expression of different enzyme genes as it serves as a preferred substrate for these enzymes (Knop & Hadar, 2015).

B. *Small Secreted Proteins (SSPs)*

Cre 1 gene was found to behave as a regulator for expression of carbohydrate metabolizing enzymes in many fungi. In *Pleurotus ostreatus PC9,* one genetically modified edible mushroom, overexpression of cre 1 lead to lower level of secreted cellulolytic enzymes and cre 1 deleted strains were associated with increased levels of cellulolytic activity. Cre 1 overexpression affected different enzymes involved in lignocellulose hydrolysis differently indicating other factors might be involved in the overall expression of the enzymes (Yoav & Hadar, 2018). In *Pleurotus ostreatus,* SSPs were found to be associated with the regulatory expression of some lignin degrading enzymes. Studies indicated SSPs may function as regulators, at least in part, of the ligninolytic system in *Pleurotus ostreatus* as manipulation of SSP expression affected transcriptional, translational and enzyme activity responses of several key ligninolytic enzymes such as aryl-alcohol oxidase, aryl-alcohol dehydrogenase and versatile peroxidase 1 (Feldman & Hadar, 2019).

Function of SSP was elucidated via reverse genetics using RNAi to overexpress or knockdown the members in *Pleurotus*

ostreatus. Analysis of the phenotypes revealed the involvement of ssp1 in the transition from tropophase to iodophase, aging and metabolism along with regulating ligninolytic enzyme production. These proteins also function as fruiting body effectors as their overexpression negatively affected fruiting body initiation. SSPs are produced under diverse conditions such as ssp1-3 are available in rich peptone-glucose media followed by exposure with 5-hydroxymethylfurfural whereas ssp6 is produced in cellulose supplemented media (Feldman & Hadar, 2020).

C.   *Mycovirus*

Some mycoviruses are latent as they do not express characteristic symptoms after infection but many of them are responsible for producing several morphological and physiological changes in the infected host. Along with enzyme activities, growth rate, colony morphology, spore production and pigmentation etc. are affected in presence of the pathogen (Song & Kim, 2020). In *Pleurotus ostreatus,* several disease causing mycoviral agents have been identified so far like oyster mushroom spherical virus (OMSV), oyster mushroom isomeric virus (OMIV), *P. ostreatus* spherical virus (POSV), oyster mushroom dsRNA virus (OMDV), *P. ostreatus* virus 1 (PoV1) and *P. ostreatus* ASI2792 virus (PoV-ASI2792; PoV) (Song & Kim, 2020).

P. ostreatus at mycelial stage accumulated 13times more viral RNA compared to the fruiting body stage. POVF10 and POVF12 cured strains of *P. ostreatus* secreted 86.5% more phenol oxidase than the PoV infected mushrooms. After infection, 337 times reduced expression of lignin degrading enzyme manganese peroxidase gene, mnp2 was noted in the mycelium of POV strains than cured POVF12 strains (Song & Kim, 2020). In case of chitinase gene also, 132-fold reduced expression was observed in POV strain. Glycoside hydrolases (GH) related to cellulose, hemicellulose, chitin, pectin and starch degradation like cellulase, xylanase, chitinase, polygalactouronase, amylase and β-glucosidase etc. were down regulated in the POV strain during the vegetative mycelial stage. Similar trend was observed in case of genes involved in lignin degradation like manganese peroxide and laccase genes. Two other genes involved in mushroom growth namely lipase and aspartic protease were also found to be down regulated. In the fruiting body stage of the infected PoV strain, down regulated expression was observed in case of laccase (2), cellulase, chitinase, amylase and β-glucosidase genes (Song & Kim, 2020).

IV.   FUTURE PROSPECTS

Industrial enzymes must have a preferable cost to benefit ratio which has led to introduction of various treatments to the enzymes to make them more stable and effective. In the last few decades, we have come through several options like i) optimization of production media, ii) formation of aggregates for enhanced stability and catalysis, iii) cross-linking or immobilization of enzymes on various support materials, iv) genetic engineering for improvement of production and catalytic activity of enzyme and v) use of nanoparticles to form different conjugates with enzyme etc. (Roy & Banik, 2021).

In recent times, many mushroom enzymes were identified with not so usual activities. Crude enzymes from *Hericium* strain from Japan showed milk clotting ability with ultra-high temperature pasteurized milk indicating its applicability in cheese production (Kishimoto & Tanimoto, 2018). Edible and medicinal mushrooms *Ganoderma lucidum*, *Hericium erinaceus*, *Pleurotus ostreatus*, *Grifola frondose* and *Flammulina velutiper* were found to be capable of biotransformation of ginsenosides (Liu & Yuan, 2019). These ginsenosides are pharmacologically important as they have anti-inflammatory, antidiabetic, antifatigue, antioxidant, antiobesity and antitumor activities (Liu & Yuan, 2019). They are used in preparation of functional food, traditional medicine and cosmetics with high economic potential.

Ding & Li proposed (2019) a low-cost pretreatment method applying edible mushroom *Pleurotus sajor-caju* for value added products such as enzymes, sugars and ethanol via green technology (Ding & Li, 2019). Fungal co-culture of white rot and brown rot was found to be more effective for pretreatment of lignocellulosic biomass compare to single culture because white rot and brown rot fungi are known to selectively degrade lignin and holocellulose respectively. Sequential inoculation of *Ganoderma lobatum* for 10 days followed by *Gloeophyllum trabeum* for next 10 days resulted improved glucose yield compare to the single cultures of *Ganoderma lobatum* and *Gloeophyllum trabeum* respectively (Hermosilla & Diez, 2018).

Brown film formation during development of primordia and fruiting body of *Lentinula edodes* is known to be induced by blue light (Huang & Gu, 2020). Transcriptome comparison and validation of the expression profile via qRTPCR of the edible mushroom grown under that light revealed that blue light stimulated content of polysaccharides by enhancing the activities of enzymes. Most of the 730 differentially expressed genes were of the oxidoreductase activity group. Amongst them, 433 genes were found to be upregulated while 297 were down-regulated. Carbohydrate metabolism genes involved in the brown film formation were found to be contributing mostly in pentose and glucuronic acid conversion as well as starch and sucrose metabolism. 51 genes were identified as up-regulated amongst 79 carbohydrate-active enzyme genes engaged in that event suggesting that those enzymes play significant roles in brown film formation to ensure enough nutrition to be supplied during development of the edible fruiting bodies (Huang & Gu, 2020).

Green synthesis of nanoparticles (NPs) has become popular nowadays for many reasons such as low cost, easy synthesis methods, high water solubility and eco-friendly nature. Mushrooms *Agaricus bisporus, Pleurotus spp., Lentinus spp., and Ganoderma spp* etc. are wellknown machineries for green NPs production (Bhardwaj & Kuca, 2020). In mushrooms, two modes

of synthesis are operating namely intracellular and extracellular. Among them, intracellular method involves transportation of ions in presence of the enzymes which is more suitable for making composite films. *Pleurotus ostreatus* is found to be capable of synthesizing NPs intracellularly compare to other *Pleurotus* species. Ag (4, 28 and 50 nm), Au (22.9 nm), ZnS (2-5nm) and Zn (15nm) etc are reportedly synthesized by *Pleurotus ostreatus.* Those NPs have antibacterial, antifungal, anticandidal, antioxidant, anticancer, photocatalytic and other activities (Bhardwaj & Kuca, 2020).

Very recent reports of gene editing with CRISPER/Cas9 in edible mushroom *Pleurotus ostreatus* could be applicable to molecular breeding, fruiting development and lignin degradation (Boontawon & Honda, 2021). While classical breeding would have taken a lot amount of time and labor, this plasmid-based CRISPER/Cas9 mediated precise gene disruption could be able to deliver improved strains with desirable traits as well as heterologous gene expression (Boontawon & Honda, 2021. Cytochrome P450 monooxygenase (gene cyp5150l8) responsible for a three-step biotransformation of lanosterol at C-26 to ganoderic acid 3-hydroxy-laosta-8, 24-dien-26-oic acid, was edited in *Ganoderma lucidum* via CRISPR/Cas9 assisted gene editing platform (Wang & Zhong, 2020). Evidently, this editing tool will help in strain molecular breeding and biotechnological application of mushrooms in future. Different omics tools like proteomics, transcriptomics, genomics and metabolomics tools are essential to analyze molecular function and role of various gene products in cellular processes of the mushroom strains (Tellez-Tellez & Diaz-Godinez, 2019). Still, a lot of questions remain unanswered in the above-mentioned studies which need introduction of available tools for further research. With technological advancement we may look forward to hitherto unknown avenues of applications using enzymes from edible mushrooms.

CONCLUSION

Edible mushrooms are catering us in numerous ways since ages. These colorful toadstools flattered our tastebuds with their distinctive flavors and established their therapeutic character in traditional medicine and treatment. The rich pool of intracellular and extracellular enzymes available from those edible varieties contribute significantly in food & feed, brewery, dairy, textile, paper, agrochemical, leather, photography and pharmaceutical industries. These enzymes ameliorate the waste materials in our environment via myco-remediation, act on agrowastes to generate fuels with less carbon emission and promote synthesis of nanoparticles in eco-friendly way. Gaining insights of these enzymes from edible mushrooms not only benefit us from diet or health perspective but also in reaching overall sustainable development goals for our environment and life on this planet. With recent advances in omics approaches we are gradually uncovering the pathways involving various metabolic activities of

mushroom enzymes and their true potential. Still many edible mushrooms remain undiscovered in wild and potential roles of their treasure trove of enzymes are yet to be harnessed industrially.

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