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REVIEW ARTICLE

Diverse Metabolic Capacities of Fungi for Bioremediation

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Abstract Bioremediation refers to cost-effective and environment-friendly method for converting the toxic, recalcitrant pollutants into environmentally benign products through the action of various biological treatments. Fungi play a major role in bioremediation owing to their robust morphology and diverse metabolic capacity. The review focuses on different fungal groups from a variety of habitats with their role in bioremediation of different toxic and recalcitrant compounds; persistent organic pollutants, textile dyes, effluents from textile, bleached kraft pulp, leather tanning industries, petroleum, polyaromatic hydrocarbons, pharmaceuticals and personal care products, and pesticides. Bioremediation of toxic organics by fungi is the most sustainable and green route for cleanup of contaminated sites and we discuss the multiple modes employed by fungi for detoxification of different toxic and recalcitrant compounds including prominent fungal enzymes viz., catalases, laccases, peroxidases and cyrochrome P450 monooxygeneses. We have also discussed the recent advances in enzyme engineering and genomics and research being carried out to trace the less understood bioremediation pathways.

Keywords Bioremediation · Recalcitrant compounds · Ligninolytic enzymes · White-rot fungi · Laccase

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Abbreviations

AM	Arbuscular mycorrhiza
AMF	Arbuscular mycorrhizal fungi
APs	Alkylphenols
BPS	Biopurification system
DyPs	Dye-decolorizing peroxidases
DDT	Dichlorodiphenyltrichloroethane
DTAB	Dodecyl trimethyl ammonium bromide
ECHO	Extra-heavy crude oil
EDCs	Endocrine disrupting chemicals
ESI	Electron spray ionization
ESTs	Expressed sequence tags
ETPs	Effluent treatment plants
HMW-PAHs	High molecular weight PAHs
LiP	Lignin peroxidases
MnP	Manganese peroxidases
MSW	Municipal solid waste
M-TRFLP	Multiplex terminal restriction fragment length polymorphism
OFMSW	Organic fraction of MSW
PAHs	Polyaromatic hydrocarbons
PCBs	Polychlorinated biphenyls
PCDDs	Polychlorinated dibenzo-*p*-dioxins
PCDFs	Polychlorinated dibenzofurans
PCS	Phytochelatin synthase
POPs	Persistent organic pollutants
PPCPs	Pharmaceuticals and personal care products
ROS	Reactive oxygen species
SSF	Solid-state fermentation
SSH	Suppression subtractive hybridization
TALEN	TAL effector nuclease (TALEN)
TNT	Tri-nitro toluene
TOC	Total organic carbon
TrOCs	Trace organic contaminants

TCP	3,5,6-Trichloro-2-pyridinol
UPO	Unspecific peroxygenases
VFAs	Volatile fatty acids
VP	Versatile peroxidase

Introduction

Industrialization and growing affluence in the developed world along with population explosion and rapid development in the developing countries has resulted in accelerated environmental degradation on a large-scale. Owing to the above reasons, chemical and solid waste management has become a major cause of concern today since environment is being loaded with a large quantum of contaminants and recalcitrant compounds like polyaromatic hydrocarbons (PAHs), polychlorinated biphenyls (PCBs), polychlorinated dibenzo-*p*-dioxins (PCDDs), polychlorinated dibenzofurans (PCDFs) and, heavy metals etc. Many conventional physico-chemical methods of treatment/removal of these compounds, though effective, are not feasible for application on large scale [1]. However bioremediation has been recognized to be environment-friendly and economical for the efficient conversion of toxic, recalcitrant compounds into non-toxic products by applying natural biological processes especially in case of contaminated land and water. This technique involves application of suitable microbes in the polluted system which perform various physical and chemical reactions as a part of their metabolism resulting in degradation and removal of pollutants [2, 3]. Bioremediation of pollutants can be carried out by applying any one of the following processes such as natural attenuation, biostimulation and bioaugmentation or a combination thereof. This has been aptly demonstrated during the bioremediation of atrazine [4], petroleum hydrocarbons [5, 6], and tri-nitro toluene (TNT) [7, 8] in soil microcosms.

Though bioremediation technologies for industrial chemicals based on activated sludge microorganisms are well-established [9, 10], their performance has been found to be relatively less efficient for removing persistent trace organic contaminants (TrOCs) [11, 12]. Fungi play a major role as decomposers and symbionts in all ecosystems including soil and aquatic habitats owing to their robust morphology and diverse metabolic capacity due to which they are specially suited for the purpose of bioremediation. Mycoremediation is a form of bioremediation in which fungi are used to decontaminate contaminated areas. There has been growing interest in the unique capacity of fungi to degrade such pollutants by employing a variety of extracellular and intracellular enzyme systems including peroxidases and cytochrome P450 respectively for detoxification and biodegradation [13–15].

Figure 1 shows the different mechanisms adopted by fungi for bioremediation of toxic, recalcitrant compounds and this review assesses the multifaceted role of fungi in the bioremediation of xenobiotic compounds with reference to features employed by the fungi for detoxification and subsequent bioremediation of toxic waste. Though a lot of work is done in the area of mycoremediation, there are still some areas like degradation pathways which are not totally understood. Development of molecular biology techniques is helping to understand the mechanisms better and to design better expression systems for bioremediation. This review aims at highlighting the broad-spectrum bioremediation potential of fungi, and advances in the area of genomics and proteomics with respect to mycoremediation.

Fungi as Agents of Bioremediation

Fungi can survive in a variety of habitats with complex soil matrix serving as the major location for fungal colonization along with freshwater as well as marine habitats which also show stable colonization of fungi. Fungi can largely thrive in the soils of different climatic conditions including the extreme ones and propagate through the dispersal of spores in the air and also help in maintaining the balance of ecosystem [16]. They have also been reported to survive in effluent treatment plants (ETPs) treating various waste waters [17, 18]. The diversity of habitats and ability for secreting multitude of enzymes makes fungi potential candidates for bioremediation at various sites.

White-Rot Fungi

White-rot fungi are chief agents of biodegradation of lignininous material in nature which contribute in the global carbon recycling. Endocrine disrupting chemicals (EDCs) and TrOCs such as pharmaceuticals and personal care products (PPCPs) which can result in effects such as bioaccumulation, acute and chronic toxicity to aquatic organisms, and possible adverse effects on human health have generated a lot of interest with reference to their degradation by white-rot fungi. Majority of the studies have demonstrated the bioremediation potential of white-rot fungi; *Phanerochaete chysosporium*, *Trametes versicolor*, *Bjerkandera adjusta* and *Pleurotus* sp., by virtue of producing different ligninolytic enzymes such as laccases and peroxidases [19]. The ligninolytic enzymes from white-rot fungi have been applied for transformation of variety of organic pollutants such as pesticides from contaminated wastewaters by promoting

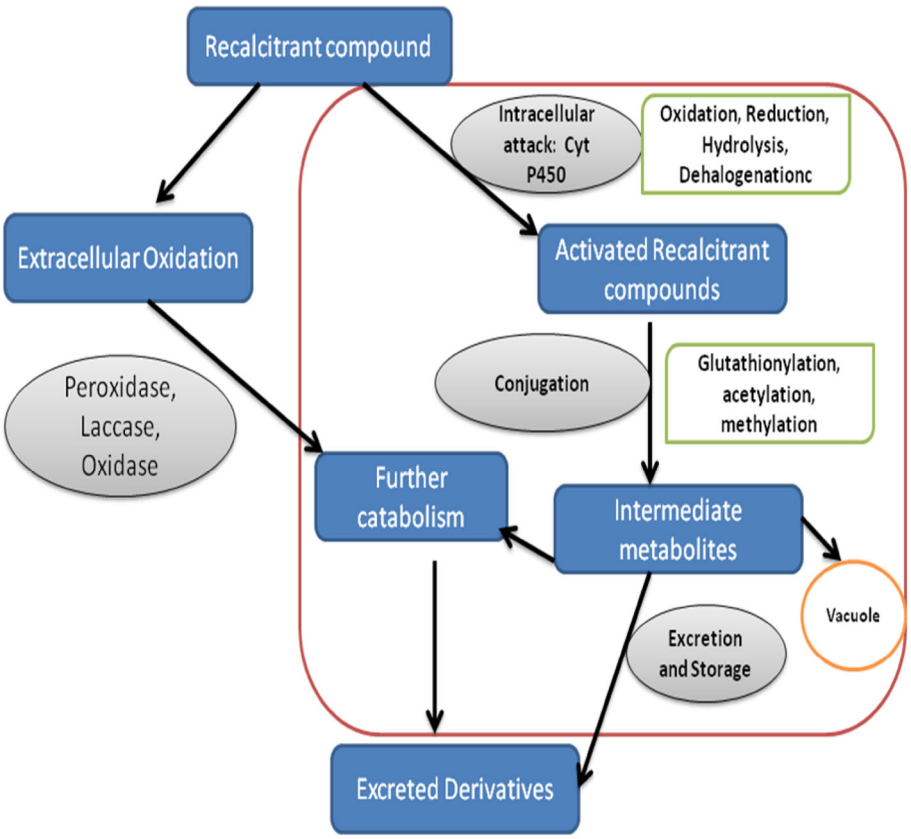

Fig. 1 Mechanisms adopted by fungi for bioremediation of toxic, recalcitrant compounds

microbial activity using a biopurification system (BPS) [20]. Owing to restricted access of ligninolytic enzymes to lignin granules which are deposited on the surface of lignocellulosic fibres, pressure refining was applied for separation of fibres of lignocellulosic materials. This strategy enhanced the accessibility of ligninolytic enzymes from white-rot fungus *Ceriporiopsis subvermispora* which showed higher delignification from pressure refined *Miscanthus* than milled *Miscanthus* [21]. Extracellular ligninolytic enzymes also have capacity for adsorption of dyes which has made white-rot fungi, a dominating force in the area of dye degradation or decolourization as demonstrated in case of decolorization of Direct Blue 14 by various species of *Pleurotus* [22] and Remazol Brilliant Blue-R by *Agaricomycete*, a white-rot fungus from Amazon forest [23]. Diverse fungal groups such as *Coriolus versicolor*, *Hirschioporus larincinus*, *Inonotus hispidus*, *Phanerochaete chrysosporium*, *Phlebia tremellosa* have been reported for decolourization of dye effluent [14] while 38 species of white-rot fungi were shown to cause reduction in total phenolics (>60 %) and color (≤70 %) from olive-mill wastewater [24]. Similarly, white-rot fungi have been applied for remediation of cresolate contaminated soil with bioaugmentation of two strains—*T. versicolor* and *Lentinus tigrinus* [25]. The cresolate-polluted soil was contaminated with residual recalcitrant petroleum hydrocarbons and high molecular weight PAH fraction remaining after a biopiling treatment. Significant degradation of the residues could be achieved by biostimulation with lignocellulosic substrate along with bioaugmentation of fungi. However, there was always a possibility that this type of treatment could promote the growth of local microbes which might subsequently dominate the augmented organism thereby stressing the need for validating such types of studies at a small scale before field applications. In addition to above applications of ligninolytic enzymes for bioremediation of variety of compounds, other features such as laccasses have also been employed by white-rot fungi for degradation of substituted organic compounds at enhanced removal efficiencies [26–28]. Considering the significance of such features in bioremediation, attempts have been made for increasing the laccase production in white-rot fungi, *T. versicolor* and *P. ostreatus* by solid state fermentation on orange peels followed by further testing of its capacity for bioremediation of PAHs such as phenanthrene and pyrene [29]. Laccase production from *T. versicolor* cultures was 3000 U/ L and though, *P. ostreatus* produced 2700 U/ L laccase, it showed better removal of phenanthrene and pyrene. For a better understanding and exploitation of bioremediation

potential of fungi to the fullest, there is a need for studying these fungi at genomic level.

Marine Fungi

The potential of marine fungi for production of secondary metabolites, biosurfactants, novel enzymes, polysaccharides and polyunsaturated fatty acids in addition to their application in bioremediation of hydrocarbons and heavy metals has been well documented [30]. Their ability to adapt to high saline conditions and pH extremes provides a biological advantage to these fungi over terrestrial fungi. The efficiency of marine microbes for metal ion removal points towards the promising nature of extremophilic organisms for bioremediation as well as in nanotechnology. With the different potential applications in view, role of marine fungi from mangrove areas has been reviewed by Thatoi et al. [31] with special focus on their diversity, immense ecological role, and biotechnological potential as a source of novel drugs, enzymes, biodiesel, biopesticides, and bioremediation. Recently, Bonugli-Santos et al. [32] have documented the significant role of enzymes from marine-derived fungi and their biotechnological relevance. Marine fungi have even been found to tolerate high concentrations of heavy metals such as lead and copper [33] and their interaction with metal ions in marine ecosystems can be used for synthesis of metal nanoparticles of desired properties [34]. Fungi possess the ability to synthesize nanoparticles both extra and intracellularly which are being used for diverse applications in areas ranging from textile industries, food preservations, to medicines and clinical microbiology etc. [35–37].

Several factors have been proposed for enhancing the bioremediation of toxic and persistent organic pollutants by applying fungi. The attribute of marine fungi for producing laccase tolerant to high salinity and phenolics was aptly exploited by Divya et al. [38] in case of *Trichoderma viride* Pers NFCCI-2745 isolated from an estuary polluted with phenolics. Similar applications of enzyme mediated bioremediation was demonstrated for decolorizing Remazol Brilliant Blue-R dye using three basidiomycetes isolated from marine sponges [39], and anthraquinone dye Reactive Blue 4 by *C. unicolor*, a marine white-rot basidiomycete. Gao et al. [40] proposed that biostimulation and bioaugmentation could affect the biotransformation of persistent organic pollutants (POPs) such as PCB 118 by two marine fungi belonging to genus *Penicillium* in presence of maifanite [41]. Another POP, pentachlorophenol was shown to be biotransformed at high concentrations by marine-derived fungus, *Trichoderma harzianum* [42]. while other marine derived fungi including *Mucor*, *Aspergillus*, *Penicillium* and slime mold demonstrated bioremediation potential for water soluble crude oil fractions between 0.01 and 0.25 mg/mL though higher concentrations resulted in toxicity to the organisms [43].

Extremophilic Fungi

Fungi from extreme environments are very important from industrial point of view owing to their extremophilic enzymes which posses several special characteristics such as thermotolerance, pH tolerance, and tolerance to other harsh conditions [44]. Amongst the extreme environments, effluent treatment plant represents one such potential niche which could be targeted for fungi with capacity for diverse bioremediation applications, owing to their exposure to high levels of pollutants from industrial effluents.

The above properties make them ideal candidates for economical and environment-friendly processing and bio-conversions of raw materials such as in food industries, leather processing, textiles manufacture, animal feed preparation, and bio-remediation [45]. Recently, Sinha et al. [46] described the potential applications of metallophilic microbes in bioremediation of problematic heavy metals from the environment and achieved nanoparticle synthesis with their usage which can be helpful for bioremediation. A psychrophilic fungus, *Cryptococcus* sp. isolated from deep-sea sediments showed tolerance and growth in presence of high levels of heavy metals (upto 100 mg/L) $ZnSO_4$, $CuSO_4$, $Pb(CH_3COO)_2$ and $CdCl_2$ [47] which could provide insight into their mode of adaptation under such conditions. Many hydrolytic enzymes which are known to show activity under extremophilic conditions have been reported to be involved in remediation processes under extreme conditions such as high salinity and extra-heavy crude oil (ECHO) contamination due to drilling waste from oil belts. Extreme acting laccases were observed to be responsible for bioremediation activity in *Pestalotiopsis palmarum* when wheat bran was present and lignin peroxidases were produced when extra heavy crude oil was the only carbon and energy source [48, 49]. Other enzymes such as chitinases produced by a psychrophilic fungus, *Lecanicillium muscarium*, could be applied for enhancing the activity of insecticides owing to their ability for acting on insect chitin exoskeleton [50, 51]. Not only can the extremophilic fungi be used in bioremediation studies, but their isolation from extreme environments such as a deep biosphere habitat represented by fumarolic ice caves on Antartica's Mt. Erebus can also be applied for identifying unique fungi capable of utilizing energy sources other than photosynthesis in addition to providing information about possible human contamination of such extreme regions [52].

Symbiotic Fungi with Plants and Bacteria

Fungi are known to forge close association with plants and bacteria in order to overcome the barrier of restricted growth under different environmental conditions. Arbuscular mycorrhizal fungi (AMF) represent the most common symbiotic relationship between fungi and plants wherein, fungal partner promotes pollutant removal by providing higher surface area for absorption of pollutants through its hyphae and spores by mobilizing the pollutants and binding to the root. AMF colonization was observed in root samples from plants used for phytoremediation of groundwater contaminated with various pollutants in a constructed wetland [53]. Certain plant-associated fungi (*A. nidulans*, *Bjerkandera adusta*, *Trametes hirsuta*, *T. viride*, *Funalia trogii*, *Irpex lacteus*, *P. ostreatus*) could survive in presence of and decolorize textile industry effluents [54]. Similar colonization of AM fungus *Rhizophagus custos* under root-organ cultures was responsible for high levels of tolerance to PAHs especially anthracene with lower formation of toxic by-product anthraquinone [55]. Enhanced ^{137}Cs uptake by quinoa plants on loamy soil after inoculation with a commercial AM product was also shown to be associated with mycorrhizal effect due to root colonization [56]. Recently, ectomycorrhizal fungi, *Suillus bovinus* and *Rhizopogon roseolus* in association with *Pinus* have been shown to be helpful for cadmium removal which was also subject to the effect of other environmental factors like the type of nutrients and pH [57]. Other applications of such fungi have been targeted at overcoming technical barriers of algal bio-fuels and photosynthetic biorefineries by co-cultivation of microalgae and fungi for the complete removal of single algal cells from fermentation medium. This allowed their extraction and harvest by simple filtration, in addition to resulting in increased biomass, lipid, and bio-product yields [58]. In spite of the benefits of co-culture studies for bioremediation, their applications are difficult and require deeper understanding about the interaction between multitude of metabolic pathways from different organisms.

Bioremediation Potential of Fungi

Fungi have been shown to play a significant role in bioremediation of variety of pollutants such as POPs, textile dyes, petroleum hydrocarbons, pulp and paper industry effluents, leather tanning effluents, PAHs, pesticides, PPCPs (Table 1). Filamentous fungi like *Aspergillus*, *Curvularia*, *Acrimonium* and *Pithium* have been studied for their metal tolerance ability [59]. Members of the basidiomycota, such as *T. versicolor* and white-rot fungi *Pleurotus ostreatus* have been reported to degrade model PAHs in solid-state fermentation (SSF) during growth on agro-industrial wastes, such as orange peels [29]. Bioremediation/decolourization of coloured effluents from sugar industry, textile dye, bleached kraft pulp mill, leather tanning effluents has been reported in case of fungi belonging to various groups including *Aspergillus*, *Penicillium* and alkalophilic white-rot fungi indicating diverse substrate preference of these fungi [14, 60–64]. Coffee pulp could be decaffeinated in presence of fungi under controlled conditions with extra nutrients for applications in animal feed preparation or for bioethanol production as was studied in case of fungi such as *Aspergillus restrictus*, *Chrysosporium keratinophilum*, *Fusarium solani*, *Gliocladium roseum*, *Penicillium* and *Stemphylium* [65]. Bioremediation in presence of fungi *A. niger* and *P. chrysosporium* exhibited substantial removal of petroleum hydrocarbons from soil contaminated with petrol and diesel at short incubation periods as indicated by enhanced total organic carbon (TOC) removal [66]. Silambarasan and Abraham [67] studied the removal of chloropyriphos and its metabolite 3,5,6-trichloro-2-pyridinol (TCP) by fungal strain *A. niger* JAS1 from contaminated soils even in absence of additional nutrients with complete removal of both the metabolites. The degradion of TCP by chlorpyrifos-degrading strain was a significant finding considering the antimicrobial nature and catabolite repression property exhibited by TCP.

Bioremediation of Toxic Recalcitrant Compounds

Bioremediation of many toxic, organic compounds from industrial effluents is an essential pre-requisite for release of such effluents into the environment owing to their persistence in soil, water, and air, and carcinogenic and mutagenic properties which are associated with their biomagnification potential. Amongst the various toxic pollutants, PAHs are complex organic compounds with fused, highly stable, polycondensed aromatic rings, which have been reported to be efficiently bioremediated by fungi on account of high lipase production as observed in case of 21 PAH degrading fungi including *Aspergillus*, *Curvularia*, *Drechslera*, *Fusarium*, *Lasiodiplodia*, *Mucor*, *Penicillium*, *Rhizopus*, *Trichoderma* isolated from PAH contaminated soil [25, 68, 69]. Action of other nonspecific extracellular enzymes was responsible for providing degradation ability to several fungi for explosives such as TNT in presence of co-substrates including cellulose and lignin [8]. Conventionally, many toxic chemicals are used in agro-industrial operations such as in bleaching of agro-residual pulp in paper mills resulting in toxic effluent. Dhiman et al. [70] developed a green technology for pulp and paper industry consisting of enzymatic pre-treatment using bacterial xylanase and fungal laccase-mediator system which

Table 1 Overview of the bioremediation potential of fungi

SN	Compound	Fungi	References
1	POPs		
	Polychlorinated biphenyls	*Doratomyces nanus*, *D. purpureofuscus*, *D. verrucisporus*, *Myceliophthora thermophila*, *Phoma eupyrena*, and *Thermoascus crustaceus*	Mouhamadou et al. [160]
		Aspergillus niger	Marco-Urrea et al. [161]
	Polychlorinated dibenzofurans	White rot fungi	Wu et al. [162]
		Phanerochaete sordida	Turlo [163]
	Phenylurea herbicide diuron	*Mortierella*	Ellegaard-Jensen et al. [164]
2	Textile dye decolourization	*Aspergillus niger*, *A. foetidus*, *T. viride*,	Jebapriya and Gnanadoss [14]
		A. sojae, *Geotrichum candidium*,	
		Penicillium sp., *Pycnoporus cinnabarinus*	
		Trichoderma sp.	
		White rot fungi	Ma et al. [165]
		Bjerkandera adusta, *Ceriporia metamorphosa*,	
		Ganoderma sp.	
3	Petroleum products		
	Crude oil	*A. niger*, *Rhizopus* sp., *Candida* sp.,	Damisa et al. [166]
		Penicillium sp., *Mucor* sp.	
	Gasoline	*Exophiala xenobiotica*	Isola et al. [167]
4	Bleached kraft pulp mill effluent	*Rhizopus oryzae or Pleurotus sajor caju*	Duarte et al. [63]
5	Effluent from leather tanning	*Aspergillus flavus*, *Aspergillus* sp. *and A. niger*	Bennet et al. [62]
		Aspergillus jegita	Reya et al. [64]
6	PAH		
	Diphenyl ether	White rot fungi	Wu et al. [162]
		Pleurotus ostreatus	Rosales et al. [29]
		Trametes versicolor	
	Anthracene	*Armillaria* sp.	Hadibarata et al. [155]
	Naphthalene	White rot fungi	Hadibarata et al. [168]
		Pleurotus eryngii	
7	PPCP		
	Caffiene	*Chrysosporium keratinophilum*, *Gliocladium roseum*, *Fusarium solani*, *A. restrictus*, *Penicillium and Stemphylium*	Nayak et al. [65]
	Citalopram, fluoxetine, sulfamethoxazole	*Bjerkandera* sp. R1, *Bjerkandera adusta* *and Phanerochaete chrysosporium*	Rodarte-Morales et al. [169]
8	Fungicide		
	Metalaxyl and Folpet	*Gongronella* sp. and *R. stolonifer*	Martins et al. [170]
9	Pesticide		
	Chlorinated hydrocarbons: Heptaclor	*P. ostreatus*	Purnomo et al. [28]
	Chloropyriphos	*Aspergillus terreus*	Silambarasan and Abraham [67]
10	Heavy Metals	*Aspergillus*, *Curvularia*, *Acrimonium*, *Pythyme*	Akhtar et al. [59]
		Aspergillus flavus	Kurniati et al. [82]

resulted in significant reduction in toxicity of the paper mill effluent.

The toxicity of chemicals used in dyeing industries is manifested in the form of decreased carbohydrate, protein and chlorophyll and increased proline content in exposed plants in addition to reduction in the rate of seed germination and growth of crop plants [71, 72]. Basic and acid dyes are the most toxic for aquatic organisms including algae and fishes and have the tendency to pass through food chain and ultimately reach human body resulting in various

physiological disorders [73, 74]. White-rot fungi are extensively studied for their variable degradative capacities [14] which have been exploited to achieve optimum dye degradation in co-culture or sequential degradation studies. 89.4 % removal of Reactive Remazol Blue at pH 6 and 69.23 % at pH 3 at 100 mg/L dye concentration was achieved in 6 days by co-culture of *Aspergillus versicolor* and *Rhizopus arrhizus* which was facilitated by dodecyl trimethyl ammonium bromide (DTAB) [75]. *Schizophyllum commune* IBL-06, a white-rot fungus, was able to completely decolorize direct dye Solar Brilliant Red 80 [76] while, *C. versicolor* was shown to degrade an azo dye, Acid Orange 7 [77].

Among the other toxic compounds, pesticide chlorpyrifos and its major metabolites were completely degraded within 24 h of incubation in mineral medium by *Aspergillus terreus* [67]. Gene expression studies for degradation of similar pesticide dichlorvos (2,2-dichlorovinyl dimethyl phosphate) by *Trichoderma atroviride* revelaed that the tolerance was associated with functioning of ABC transporters and alteration in expression of 5382 genes [78]. A *Mucor racemosus* strain DDF was found to show diverse substrate specificity and could degrade dieldrin in 10 days with 9 % aldrin *trans*-diol generation in addition to other pesticides such as heptachlor (94 %), heptachlor epoxide (67.5 %), endosulfan (80 %), endosulfan sulfate (95 %) [79].

Bioremediation of Heavy Metals

The wide-scale distribution of heavy metals in the environment owing to their application in multiple areas is a cause for concern due to their systemic toxicity to human health even at low concentrations. Due to high degree of toxicity leading to health effects such as multiple organ failure and carcinogenic effects, heavy metals; arsenic, cadmium, chromium, lead, and mercury are considered as priority metals which need to be removed from environment in order to reduce their impact on public health and environment. Tchounwou et al. [80] have analyzed the role and production of different heavy metals and their environmental occurrence and its relation to the potential human exposure with special focus on molecular mechanisms of the toxic effects. Different microbes show the ability to tolerate the presence of heavy metals and possess different mechanisms for their removal from environment. High tolerance and remediation capacity of filamentous fungi towards heavy metals like Cd, Cu and Ni (up to 1500 mg/L) assumes significance for bioremediation of these metals from contaminated soil and waste water [59]. Members of genus *Aspergillus* are known for their versatility to degrade a diversity of toxic compounds ranging from heavy metals, textile dyes, aromatic compounds, pesticides etc. *A. flavus* and *A. niger* have been reported for their capacity to reduce heavy metals such as Cr^{6+} to Cr^{3+} [62]. Another species, *A. foetidus* isolated from a wastewater treatment plant was found to be tolerant to high concentrations of lead (Pb) up to 200 mg/L which was removed through biosorption [81] as was also observed in bioremediation of aqueous substrates containing mercury (II) by *A. flavus* strain which was able to remove about 98 % mercury in presence of 10 mg/L mercury in the medium [82]. Mumtaz et al. [83] demonstrated the potential of fungi like *Aspergillus*, *Cryptococcus*, *Penicillium* and *Curvularia* for bioremediation of uranium contaminated soils which was attributed to their uranium binding ability. Symbiotic association of AM fungi with the roots of plants promoted immobilization of heavy metals and hence provided ability to plants to grow in metal-contaminated soils as observed in case of enhanced Cd tolerance of plants [84, 85]. Further enhancement in remediation potential of toxic compounds by fungi could be achieved by certain pre-treatments. In a study, Das et al. [86] exposed *Aspergillus* sp. to gamma rays (20–100 Gy) in Cd supplemented media which resulted in an increase in growth and higher Cd removal in comparison to un-irradiated controls.

Bioremediation of Municipal Solid Waste (MSW)

The generation of tons of municipal solid waste (MSW) in developing countries has led to creation of most of public health and environmental problems [87, 88]. Though incineration and land-filling are commonly used methods for disposal of MSW, incineration is an expensive process, while, land filling sites are a main source of secondary environmental pollution including fouling of air, bad odour, and increased pathogen content in soil. On the other hand, composting and land-filling require vast areas of land and hence are not suitable for countries with limited land availability [89]. Pandit et al. [90] have discussed about various technological advances for treating this misplaced resource. The authors have proposed composting and biomethanation by anaerobic digestion to be the desirable solution for managing MSW due to two benefits, management of MSW and production of value added products such as volatile fatty acids (VFAs), biogas, and organic residue/compost for application as a soil conditioner or fertilizer. In order to enhance the efficiency and rates of these processes, treatment of MSW by fungi and their hydrolytic enzymes such as cellulases, proteases, amylases, and lipases could be applied for the conversion of complex polymeric substances to simple compounds which are precursors for VFA and biogas production. This was demonstrated by Janveja et al. [91] who evaluated the potential of steam, acid, and base pretreated kitchen waste residues to serve as substrate for solid-state fermentation of cellulolytic, hemicellulolytic, pectinolytic, amylolytic

enzymes by a locally isolated strain of *Aspergillus niger*. The benefit of these enzymes in pre-treatment and their effect on enhanced efficiency for hydrolysis and saccharification of selected biomasses i.e. willow and rice straw was demonstrated by application of a fungal consortium composed of two fungi *Armilleria gemina* and *Pholiota adipose* [92]. Composting of other residual biomass may be enhanced in the presence of white–rot fungi, followed by utilization of spent biomass for soil application [93]. The tolerance of wood-rotting fungi *Antrodia xanthan* and *Fomitopsis palustris* to copper was exploited in bioremediation of copper deposited wood [94].

Features Employed by Fungi for Detoxification and Bioremediation of Toxic Waste

Fungal Enzymes in Bioremediation

Fungal enzymes of industrial importance include cellulases, xylanases, amylases, proteases, lipases, laccases, peroxidases, catalases etc. which can find potential applications in managing organic waste such as organic fraction of MSW (OFMSW) [93]. These enzymes can be used for hydrolyzing the polymeric substances such as cellulose, xylan, starch, protein, and lipid present in wastes including food, kitchen, vegetable market, leaf litter etc. which could be further subjected to composting, or used for production of value added products such as VFAs and biogas [89, 94]. Depending on the species and the environmental conditions, white-rot fungi produce one or more types of ligninolytic enzymes whose role is not only limited to the degradation of lignin in natural lingo-cellulosic substrates, but also in the degradation of various xenobiotic compounds including dyes and thus can find application in bioremediation studies. These enzymes modify azo dye structure by destruction of chromophoric assemblies leading to formation of phenoxyl radicals in the reactions [75]. Ligninolytic enzymes secreted by white rot fungi for oxidation of lignin in the extracellular environment of the fungal cell, have been categorized into two groups: peroxidases-manganese and lignin peroxidases (MnP and LiP) and laccases [14, 95]. Laccases and some fungal class II peroxidases from white-rot basidiomycetes are well established in degradation of persistent organic pollutants [96]. Such enzymes from extremophilic fungi can be helpful for remediation under extremes of high salinity and extra-heavy crude oil contamination such as the drilling waste from oil belts. Much interest is currently focused on developing tailor-made enzymes through protein engineering techniques and recombinant expression of genes from white-rot fungi which are effective tools for eco-friendly treatment of toxic wastes [10, 97–99].

Laccase

Laccases are copper containing extracellular enzymes belonging to group of blue oxidases which use copper as co-factor and molecular oxygen as co-substrate. Laccases are capable of oxidizing most of the phenolic and non-phenolic compounds, and their activity has been observed to be more than 20 times greater in fungi such as *T. versicolor* than other organisms [100]. The non-specific nature of their activity on a variety of substrates makes them ideal catalyst for different industrial applications of which these enzymes have been extensively explored for their efficient bioremediation potential [101]. One such application was its demonstration in recycled paper industry for deinking of offset printed paper wherein laccases from three basdiomycetes (*Trametes villosa*, *Coriolopsis rigida*, *Pycnoporus coccineus*) and one ascomycete (*Myceliopthora thermophila*) were assayed for decolourization of flexographic inks in presence of synthetic and artificial mediators [102]. The resistance of textile dyes to fading on exposure to sunlight, water, and their persistence in environment due to synthetic origin is a cause for concern owing to their toxicity Verma et al. [41] and Vishwanath et al. [101] for the first time reported the marine fungal laccase mediated decolourization, detoxification, and mineralization of Reactive Blue 4 at relatively high concentrations of 1000 mg/L. Studies on degradation of Bisphenol A, an endocrine disrupting chemical by laccase purified from *Fusarium incarnatum* showed that 91.43 % of 200 mg/L Bisphenol A was eliminated when incubated with laccase [103]. Some extremophilic fungi like *Penicillium pinophilum* isolated from Himalayan region was demonstrated to produce laccase at low temperatures [104]. However the mechanism of action of laccases under extreme conditions is less explored, with crystal structure of only a few laccases being fully known including those from ascomycetes *Melanocarpus albomyces* (MaL) and *Thielavia arenaria* (TaLcc1) which differ from other laccases by the presence of a conserved 'C-terminal plug' probably in proton transfer processes [105]. In spite of their tremendous potential in bioremediation, the utility of laccases is restricted by their low shelf life. This drawback can be overcome by immobilization of the enzyme on nanoparticles thus providing high residual activities over a broad range of pH and temperature [106]. Other innovations include tailoring of these enzymes through application of tools such as directed evolution for making mutants with enzymes showing activity over broader substrate ranges and environmental factors [107, 108]. The essential requirement for tailoring enzymes through above tools is the availability of high-throughput assays for screening. Pardo et al. [109] developed new colorimetric assays for screening of activities for engineered laccases, which were based on oxidation of syringyl compounds. Fungal laccases can not only be exploited for their catabolic

potential, but are also known for other reactions such as dimerization, oligomerization and polymerization reactions of numerous aromatic compounds. This makes them ideal candidates for use as biocatalysts in synthesis of various dyes and colourants including those with phenolic, non-phenolic, phenoxazinone, and azo dyes with improved selectivity thereby providing the benefit of reduced material and energy waste associated with chemical and fermentation route for such syntheses [110].

Catalase

As observed in other biological systems, reactive oxygen species (ROS) accumulation results in damage to cellular macromolecules, which is deleterious for cellular integrity. Primary defense mechanism to ROS generation in fungi consists of monofunctional catalases and bifunctional peroxidase/catalase enzymes. Inhibition of catalase in presence of pesticide lindane has been reported to manifest in the form of increased ROS generation and hence in ROS-mediated damage resulting in inhibition of growth of *Saccharomyces cerevisiae* [111]. Heavy metals such as lead (Pb), copper (Cu), cadmium (Cd), zinc (Zn) have been reported to be among the major reasons for ROS induction in microbial cells. All studies on effect of heavy metals on ROS generation have indicated a concomitant increase in anti-oxidative enzymes. Chakraborty et al. [81] achieved good growth and tolerance of *Aspergillus foetidus* in presence of 200 mg/L Pb(II) which was associated with simultaneous increase in levels of anti-oxidative enzymes including catalase for detoxifying malondialdehyde and H_2O_2. Similar observations on enhancement of *Aspergillus* spp. tolerance to oxidative stress induced by heavy metals-100 mg/L Cu(II) and 750 mg/L Zn(II) were made by Mitra et al. [112]. The authors confirmed the increase in ROS generation from increased expression of enzyme copper–amine oxidase while the ability of the fungal culture to withstand heavy metal induced oxidative stress was demonstrated by increased activities of catalase among other enzymes. Though, not much is known about the effect of heavy metals on the fungal physiology, exposure of *P. chrysosporium* to cadmium or lead (50–100 μM) has been shown to result in inhibition of catalase and peroxidase and increase in cytochrome P450 (CYP450) activity [113]. In contrast to this study, higher catalase activity was observed when Pb^{2+}, Cu^{2+} were added individually or in combination to the fungal consortia consisting of *A. niger*, *Penicillium* sp. and *Rhizopus* sp. at about 50 mg/L [114]. Lin et al. [115] suggested that catalase activity could be used as monitoring tool for monitoring bioremediation efficiency since their study revealed that catalase activity decreased with increasing oil concentration during bioremediation of oil contaminated soil. Thus, considering the significance of catalases in providing heavy metal tolerance capacity to fungi, fungi producing this enzyme can be promising candidates for bioremediation of metal contaminated sites.

Peroxidase

Peroxidases are classified into lignin peroxidase (LiP), manganese peroxidase (MnP) and versatile peroxidase (VP) depending on their source and activity. Of these, LiP and MnP are heme peroxidases which require the presence of hydrogen peroxidase and manganese for activity and are mostly reported for degradation of toxic compounds by white-rot and basidiomycetes fungi. On the other hand, VP enzymes are broad substrate specific enzymes capable of oxidizing both phenolic and non-phenolic compounds and are highly valued for biotechnological processes such as bioremediation [116]. Additionally, dye-decolorizing peroxidases (DyPs) and unspecific peroxygenases (UPO) are other heme peroxidases using hydrogen peroxide to catalyze oxidations of various non-phenolic lignin model compounds along with other organic compounds but do not fit in the above classification system [117–119]. One such peroxidase produced by *B. adusta* was shown to disrupt the phthalocyaninic ring in phthalocyanine dyes by cleavage of azo bond thus leading to decolorization of azo and phthalocyanine dye. The mineralization capacity of the fungal enzyme for dye was validated by identification of the transformation products by EPR spectroscopy and mass spectrometry [120]. Recently, a MnP enzyme from *C. subvermispora* was engineered for enhancing the acidic stability even at pH 2. The acid stability and high Mn^{2+} oxidizing activity was incorporated by studying its crystal structure as a scaffold, and a stable enzyme was engineered which could oxidize Reactive Black 5 as well as veratryl alcohol [121]. Liers et al. [118] demonstrated the occurrence of five fungal DyPs which possessed catalytic properties of both LiP and VP (high-redox peroxidases) as seen from their ability to oxidize non-phenolic aromatic compounds along with Reactive Black B and also low-redox potential peroxidases as seen from oxidation of phenolic substrates. The study highlighted the need for carefully classifying peroxidase activities in crude enzyme mixtures of fungi owing to the difficulty in distinguishing the DyPs from LiP and VP and suggested that such classification based on catalytic specificity was possible only after purification of the different enzymes.

Fungal Cytochromes in Bioremediation

Fungi possess complex oxidative and hydrolytic enzymatic systems for detoxifying toxic compounds in the environment. Besides these systems, certain fungi possess intracellular networks which constitute the xenome, consisting

of cytochrome (CYP) P450 monooxygenases and the glutathione transferases for dealing with diverse range of pollutants. The members of the detoxification pathways which generally belong to multigenic families such as cytochrome P450 monooxygenases and glutathione transferases together constitute the xenome [15]. The fungal cytochrome P450 system can serve as versatile catalyst for region- and stereospecific oxidation of non-activated hydrocarbons, and can be ideal substitutes for chemical catalysts [122]. Ichinose [123] has highlighted the significance of cytochrome P450 systems in metabolism of series of endogenous and exogenous compounds. Separate cytosolic and mitochondrial iso-forms of P450 found in *Fusarium oxysporum* and other fungi are employed by fungi in degradation of dioxins [10, 124]. CYP63A2 P450 monooxygenase from white-rot fungus *P. chrysosporium* oxidized crude oil aliphatic hydrocarbon *n*-alkanes, endocrine-disrupting long-chain alkylphenols (APs), mutagenic/carcinogenic fused-ring high molecular weight PAHs (HMW-PAHs) [98]. *F. oxysporum* CYP monooxygenases were promising catalysts in significant production of ω-hydroxy fatty acids [13]. Pre-induction of the P450 monooxygenase before application in degradation studies could result in enhanced PAH removal [125]. Enhanced removal of pollutants also achieved by molecular tools aimed at rapid and over production of cytochrome P450 monooxygenase such as the use of a broad-range yeast expression system with a viral vector (*Arxula adeninivorans*) [126].

Technological Advances in Fungal Bioremediation

Bioremediation of toxic organics is the most sustainable and green route for cleanup of contaminated sites and fungi happen to be an important constituent of this ecosystem owing to presence of multiple modes for tackling the problem of contamination. However, their applications are dependent on environmental factors and long lag phase, high sludge generation, difficult process control which may impact direct application of fungal biomass in bioremediation. Several technological advances have been made in area of fungal bioremediation to overcome the associated shortcomings. One such advance involves the preference of enzymes over that of the fungal biomass on account of reduced bioremediation time, no lag phase, minimal sludge generation and easy process control. Though enzymes themselves present other problems of high cost and low shelf life due to lower stability, developments in whole cell and enzyme immobilization have extended their stability thereby increasing shelf life and hence leading to enzyme reuse and reduced costs. Recent developments in various bioreactors like fluidized beds and rotating biological contactors have been applied for bioremediation with immobilized fungi [14]. Novel bioreactor systems are continuously being designed for the removal of dyes like Reactive Green 19 by white-rot fungi [127]. A two stage reactor was successful in degradation azo dye Reactive Blue 222 through combination of Photo-Fenton's and aerobic treatment with two white-rot fungi *P. ostreatus* IBL-02 and *P. chrysosporium* IBL-03 [128]. A white-rot fungus, *T. versicolor* showed significant removal of two TrOCs (80–90 % bisphenol-A removal and 55 % diclofenac removal) in a continuous flow fungal membrane bioreactor in non-sterile environment at 2 days hydraulic retention time (HRT) [129]. A novel strategy was employed for degradation of HMW-PAHs by Bhattacharya et al. [125] consisting of biphasic approach using white-rot fungus *P. chrysosporium.* Bioremediation of benzo[*a*]pyrene under nutrient sufficient (ligninolytic) culture conditions resulted in up-regulation of PAH oxidizing monooxygeneses with concomitant formation of P450-hydroxylated metabolite which was further removed during subsequent non-ligninolytic phase. Importance of another novel strategy based on biopurification systems in promoting bioremediation of pesticides containing wastewaters by means of highly active biological mixture, in particular white-rot fungi was highlighted in a review by Rodríguez-Rodríguez et al. [20]. The sustainability and environment friendly nature of bioremediation was displayed in the bioremediation of sewage sludge from sewage treatment plant with mixed filamentous inoculum in a large-scale bioreactor by employing a continuous process [130]. In addition to the fungi alone, their co-cultures with bacteria in a synergistic degradation system consisting of *Fusarium* sp. PY3, *Bacillu*s sp. PY1, and *Sphingomonas* sp. PY2 effectively removed pyrene up to 96.0 % and volatilized arsenic up to 84.1 %, while bioremediation ability was 87.2 % in contaminated soil with 100 mg/kg pyrene [131]. Another unique and innovative approach for removal of PAHs was adopted by Cobas et al. [132] who demonstrated 90 % removal of phenanthrene in 14 days by developing permeable novel reactive biobarriers of *Trichoderma longibrachiatum* on nylon sponge. Fungal biocatalysis is being used in the whole cell systems for the textile wastewater treatment [133].

Fungal Proteomics, Genomics and Bioremediation

Numerous fungi are capable of degrading recalcitrant organic pollutants in a broad range of habitats and conditions and they can be exploited in variety of biotechnological applications including bioremediation. For instance, a fungal strain, *Byssochlamys nivea* can grow on pentachlorophenol-contaminated soil samples, however, its

benefit to humankind is limited due to lack of reference genomic data providing information on biochemical processes. Environmental genomics techniques can help in advanced treatment of waste site by understanding the microbial physiology and ecology which are being applied to the field of bioremediation [134, 135]. With the current interest in fungal genomics, there has been an increase in the availability of complete sequences of fungal genomes for genome-wide comparison of their bioremediation abilities [136]. In order to bridge the gap of sequence data and to study genetic basis of diversity, 3′-cDNA libraries have been created by deep sequencing using a next generation sequencing approach. This could enable structural and functional investigations for assessing the role of catabolic processes involved in degradation of recalcitrant organic pollutants [137]. Whole genome sequence analysis can reveal the capability of fungi for multiple metabolic adaptations owing to diversified enzyme functions such as cytochrome P450 monooxygenase [123]. Phytochelatin synthase (PCS) is an enzyme catalyzing the biosynthesis of phytochelatin from glutathione which protects cells against the toxic effects of non-essential heavy metals. The genome analysis of fungi is helpful in tracing such genes like *pcs* and studying their evolutionary aspects [138]. Other genomic tools such as multiplex terminal restriction fragment length polymorphism (M-TRFLP) have enabled studies on different taxa in an ecosystem by simultaneously profiling multiple microbial taxonomic groups. This tool can be useful in identifying bio-indicators of pollution, environmental health and for studies on the microbial response to environmental stress [139]. Nuclease-mediated Genome Editing is a newer advance in sequencing techniques as is also TAL effector nuclease (TALEN) which is a new engineered nuclease tool for yeast and can be applied to other fungal species [140].

The application of fungal genomics in bioremediation can be enhanced by use of bioinformatics tools. Genomic and proteomic analysis generates a huge amount of data and for the interpretation, use of bioinformatics and statistical algorithms are essential. Since, bioremediation technology explores the microbial potential for biodegradation of xenobiotics compounds, bioinformatics can help in deeper understanding about the application of genomics and proteomics in bioremediation studies [141]. This approach consisting of homology-based 3D model in conjunction with ligand docking simulations was applied by Syed et al. [98] in order to elucidate the potential versatility of fungal P450 enzyme system (CYP63A2) for oxidizing HMW-PAHs of various ring sizes in comparison to the mammalian and bacterial systems. The authors also constructed recombinants of CYP63A2 enzyme and demonstrated formation of PAH metabolites from HMW-PAHs indicating difference in activity between fungal and mammalian P450 enzyme systems which was attributed to the extraordinarily large active-site in fungal enzyme. Sakaki et al. [10] used this concept to enlarge the space of the substrate-binding site of CYP1A1-P450 system thereby resulting in generation of ability to metabolize 2,3,7,8-tetrachloro-dibenzo-*p*-dioxin which otherwise was absent in the wild type CYP1A1. Comparative metabolic genomics lead to the finding that a particular *A. niger* sp. had more than 1100 unique enzyme-encoding genes many of which were additional copies of orthologs in the compared fungi and this genetic multiplicity enabled *A. niger* to adapt and survive in diverse conditions [142].

Engineering and manipulating fungal enzymes can help to increase their activities and achieve efficient bioremediation. With reference to genomics of fungal detoxification enzymes such as laccases, Wong et al. [99] developed a robust expression platform from *L. edodes* along with application of screening substrate, guaiacol, for more efficient "green" applications. On similar lines, Kalyani et al. [143] developed a highly efficient recombinant laccase from yeast *Yarrowia lipolytica* for hydrolysis of wood biomass. The authors performed a modified thermal asymmetric interlaced polymerase chain reaction for obtaining 1557-bp yeast laccase gene (YILac) from *Y. lipolytica* which encoded a 519 amino acid protein. This gene was cloned in *Pichia pastoris* followed by demonstration of removal of phenolic compounds from acid treated woody biomass. From the above studies it is clear that fungal genomics has scope for application in future in determination of pollution levels in various environmental matrices which could be achieved by monitoring of specific marker genes responsible for detoxification of pollutants.

Similar constructs of recombinant laccase from *Pleurotus eryngii* ERY4 laccase gene in *S. cerevisiae* host was biologically inactive. Chimerical enzymes iso-form obtained after gene modifications named 4NC3 (both N- and C-terminal region substitution) showed high activity, pH as well as temperature stability, and multiple substrate affinity [144]. In another study, *Phanerochaete flavidoalba* laccase gene was expressed in *A. niger* with good amount of active recombinant enzyme (rLac-LPFA) (30 mg/L). The recombinant enzyme exhibited stability at pH 2–9 and organic solvents along with higher decolouration and biotransformation of synthetic textile dyes, Remazol Brilliant Blue R (RBBR) and Acid Red 299 (NY1) [145]. Additionally, fungi can find application in phytoremediation if their potential genes of enzymes like peroxidases, laccases are expressed effectively in plants [146]. The role of AMF in phytoremediation of groundwater contaminated with ammonia, benzene and methyl *tert*-butyl ether was assessed by analysis of nuclear large ribosomal subunit fragment, amplified by nested PCR which showed good AMF colonization with presence of

Funneliformis mosseae and *Rhizophagus irregularis* [53]. Constitutive expression of *Ganoderma lucidum* laccase synthetic genes *GlLCC1* and *POXA 1B* from *P. ostreatus* was achieved in *P. pastoris* [147]. The broad substrate specificity of laccase for attacking multiple compounds makes application of recombinant enzyme expression techniques for production of high activity, environmental friendly enzyme desirable. Another such example can be that of the expression of cytochrome P450 monooxygenase from *F. oxysporum* in *Saccharomyces cerevisae* [13]. For exploiting the tremendous potential of fungi for azo dye degradation, there is a need for understanding cellular mechanisms for azo dye degradation. A potential strain *Penicillium oxalicum* SAR-3 with broad-spectrum catabolic ability for different azo dyes possessed many novel genes for azo dye degradation which coded for ABC transporters and peroxidases along with stress-responsive genes. The occurrence of 183 unique expressed sequence tags (ESTs) was detected by a forward suppression subtractive hybridization (SSH) cDNA library of *P. oxalicum* SAR-3 in presence and absence of azo dye Acid Red 183 [148].

The oxidative stress response pathways activated in the presence of the xenobiotics β-Hexachlorocycloalkane and toluene in *Penicillium griseofulvum* were studied by Phenotype MicroArray technique [149]. In *A. niger*, overexpression of *acrA* encoding a putative plasma membrane arsenite efflux pump occurs in presence of arsenic. This gene formed the basis for development of a putative biosensor strain which was basically a construct of the native promoter of *acrA* fused with *egfp* [150]. Such constructs can find application as effective biosensors in bioremediation monitoring. Though, evolution in molecular biology techniques is promising for developing more economic and promising bioremediation methods, there is a need for taking care of ethical issues before the genetically modified fungi could be used for effective bioremediation of hazardous pollutants [151].

Degradation Pathways in Fungi

Different degradative pathways have been investigated in fungal bioremediation and such studies are of extreme importance for understanding of downstream pathways for bioremediation of pollutants and the mechanisms involved in the reactions. Various databases like MetaCyc database (MetaCyc.org) are helpful in describing metabolic pathways and enzymes for aspects like bioremediation [152]. Absorption onto the fungal biomass has been suggested to be one mechanism of pollutant removal in addition to action of enzymes such as laccases as shown during transformation of endosulphan to endosuplhan sulphate and little amount of endosulpan ether in presence of white-rot fungi *T. versicolor* and *P. ostreatus* [153]. Electron spray ionization (ESI) analysis indicated that the key mechanism of fungal decolorization of synthetic dyes involved N-demethylation [154]. On the other hand, transformation of anthracene by *Armillaria* sp. F022 occurred through two alternative routes which were laccase mediated ring-cleavage reactions, first consisting of oxidation of anthracene to anthraquinone, benzoic acid, and second converting anthracene to other products, 2-hydroxy-3-naphthoic acid and coumarin [155]. Though, a lot of information is available about the application of fungal cultures and enzymes in bioremediation studies, very little is known about effect of bacterial-fungal ecological interactions on removal of PAHs from soils. Recently, degradation pathways of monochlorophenols in *Aspergillus nidulans* were studied using metabolomics. Degradation intermediates included 3-chloro-cis,cis-muconate as well as uncommon compounds from 4-chlorocatechol and 3-chlorocatechol degradation pathways yielding 3-chlorodienelactone and catechol respectively [156]. *F. solani* and *Arthrobacter oxydans* were shown to dissipate PAHs in vitro up to 46 % after 21 days [157]. White-rot fungi can degrade polychlorinated PCDDs and PCBs. White-rot fungus *Phlebia* was studied for dieldrin degradation and over 50 % of dieldrin was removed in 42 days which was attributed to hydroxylation reactions in the pathway leading to three hydroxylated metabolite products. These fungi were also found to degrade aldrin (over 90 %) in just 28 days by attacking methylene moiety leading to formation of new metabolites like 9-hydroxyaldrin and two carboxylic acid products [158]. Further, application of proteomics, gene expression studies, and the use of gene-replacement mutants have helped to assign most of the steps in well known but less understood 3-oxaloadipate pathway of aromatic compound degradation to particular genes. The study showed the formation of catechol from salicylate either directly or through 2,3-dihydroxybenzoate. Additionally, the study indicated successive muconate isomerisation reactions in the catechol branch [159].

Conclusion

Though there have been isolated reports on the bioremediation potential of fungi, in-depth assessment of the multifaceted role of fungi in bioremediation of xenobiotic compounds with reference to features employed by the fungi for performing this task is lacking. In this review, we have tried to bring together different aspects describing diverse and novel metabolic capacities of fungi, and their role in bioremediation potential on a common platform. The bioremediation potential of fungi from extreme

environments has been elaborated which has indicated that heavy metal removal by fungi and nanoparticle synthesis from them was a potential area of research. In addition to well-studied enzymes like peroxidases and laccases, some stress response proteins like ABC transporters play active roles in fungi to cope up with many toxic pollutants and there is a need for exploring these genes further. The recent research being carried out for complete understanding of bioremediation pathways and advances in genomic research indicate that whole genome studies can help to understand and explore the biodegradation pathways. The genes of interest thus obtained can not only be used in the respective organisms but can also be used in various expression systems to enhance bioremediation processes. In addition, efficient biomarkers for bioremediation can emerge out from gene expression studies in fungi which can further aid in bioremediation studies employing fungal systems.

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