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PHYTOMORPHOLOGY

Potential Role of Fungi in Bioremediation of Hazardous Chemicals from Soil: Current Perspectives

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Abstract

Bioremediation encompasses the implementation of cost-effective and environmentally friendly methods that transform toxic and hazardous chemical pollutants into non-hazardous products through the action of living organisms. The specific use of fungi in bioremediation is referred to as mycoremediation. Fungi exhibit diverse metabolic capabilities that enable the degradation of various chemical contaminants, either through chemical modifications or by influencing the bioavailability of these substances. Their efficacy in bioremediation is primarily attributed to their ability to form extensive mycelial networks and the broad versatility of their enzymes, which can utilize organic pollutants as a source of growth. Furthermore, other hazardous chemicals can be broken down through co-metabolic pathways. This review highlights various groups of fungi involved in the bioremediation of dangerous and persistent chemical compounds, including pesticides, petroleum, bleached kraft pulp, textile dyes, and effluents from industries such as textiles, pharmaceuticals, personal care products, and leather tanning. It also examines the mechanisms of detoxification and bioremediation facilitated by fungal enzymes and cytochromes, the application of mycoremediation across various types of environmental pollution, and the technological advancements in fungal bioremediation.

Keywords: Recalcitrant compounds, Hazardous chemicals, Bioremediation, Mycoremediation, Ligninolytic enzymes, White-rot fungi, Laccase

Introduction

Soils represent a complex amalgamation of organic matter, minerals, water, air, and countless organisms, including bacteria, fungi, insects, and earthworms. Often referred to as the "skin of the earth," soil resides at the immediate surface of the planet and serves as a crucial medium for the growth of terrestrial plants, making it essential for life on Earth. Furthermore, soil plays a significant role in modifying the atmosphere by absorbing gases, providing habitats for animals, conserving and purifying water, and recycling nutrients and minerals. All living organisms depend on soil, either directly or indirectly, for their growth and development. However,

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industrialization, urbanization, and rapid development have led to significant contamination of the soil environment due to the introduction of chemical pollutants in substantial quantities. In recent years, the use of organic and inorganic chemicals in agriculture has escalated to meet the food demands of a growing global population. This has resulted in soil, water, and air contamination through agricultural runoff and leaching. Landfilling, an age-old practice for waste disposal, has emerged as a significant environmental concern. Numerous studies indicate that toxic chemicals can leach from landfills and dumping sites, contaminating surrounding areas, including soil and water. This landfilling practice encompasses the disposal of biomedical waste, industrial byproducts, nuclear waste, e-waste, sludge, and various types of fuels. Additional contributors to soil contamination include intensive farming, excessive use of fertilisers, herbicides, and pesticides, as well as mining and smelting, accidental oil spills, leaks from underground storage tanks, and acid rain.

Remediating contaminated soil pollutants is a complex, time-consuming, and costly endeavour that requires expertise in chemistry, industrial chemistry, geology, geographic information systems, and hydrology (Adnan et al., 2024). Soil contamination has emerged as a global issue, resulting in significant environmental degradation and severe health consequences for all living organisms (Orloff & Falk, 2003; Gaur et al., 2014; Savita et al., 2019). While various physical and chemical techniques exist for removing soil contaminants, they often entail high costs and can generate byproducts that pose further environmental risks (Gaur et al., 2014). In contrast, bioremediation

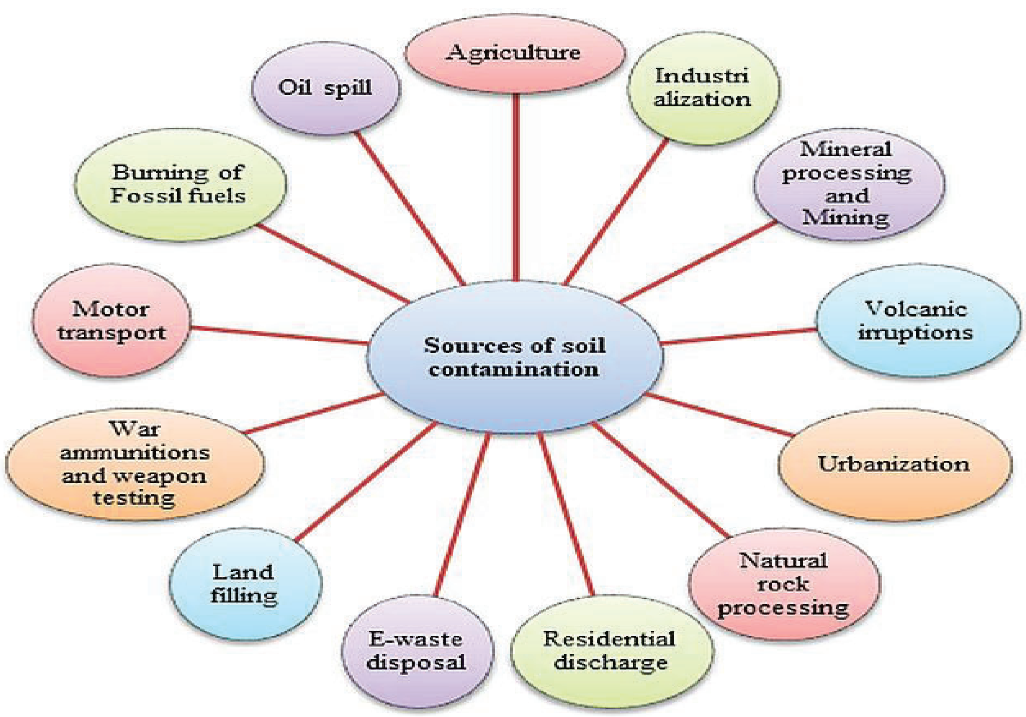

Figure 1. Different sources of chemical contaminants in the soil

has gained recognition as the most environmentally friendly, cost-effective, and efficient approach for transforming toxic and resistant compounds into simple, non-toxic chemicals through natural biological processes. This process utilizes microbes and certain plants to eliminate contaminants from the soil through their metabolic activities, including bio-stimulation, bio-augmentation, and natural attenuation, which can be employed individually or in combination. This review aims to explore the extensive bioremediation potential of fungi, the mechanisms involved in detoxification and remediation, the application of mycoremediation across various types of environmental pollution, and the recent technological advancements in fungal bioremediation.

Types of chemical contaminants and their sources

Contaminants refer to undesired substances present in the environment at concentrations exceeding permissible limits, which pose risks to both ecosystems and human health. These contaminants can arise from natural sources or be xenobiotic (man-made). Chemical contaminants have emerged as a significant challenge to ecosystem degradation due to accidental and intentional releases from industries, excessive use in agriculture, and widespread utilisation in daily life (Fig. 1). Depending on their disposal methods, chemical contaminants can be categorized as biodegradable or non-biodegradable (persistent). Non-biodegradable chemical contaminants are persistent compounds that remain in the ecosystem for extended periods, gradually breaking down into harmless substances over time. Persistent chemical contaminants are classified into organic, inorganic, and radionuclides (Fig. 2).

Organic contaminants

These carbon-based compounds enter the soil through the industrial release of waste, oil spills, war ammunition, and agricultural runoff. The typical organic chemical contaminants are polyaromatic hydrocarbons (PAHs), halogenated solvents, petroleum hydrocarbons, organic solvents, endocrine-disrupting drugs, Dichlorodiphenyltrichloroethane(DDT), polychlorinated dibenzo-p-dioxins (PCDDs), Phenylcyclohexylpiperidine (PCP), polychlorinated dibenzofurans (PCDFs), polychlorinated biphenyls (PCBs), Dieldrin, pesticides, herbicides, insecticides, fungicides, fertilizers, explosives such as Trinitrotoluene (TNT) and Royal Demolition Explosive (RDX) (Rodriguez-Campos et al., 2014; Hüffer et al., 2019; Milyukin & Gorban, 2021; Ciemniak et al., 2023).

Inorganic chemical contaminants

Mineral-based compounds enter the soil through various channels, including agricultural runoff, direct discharge from industrial processes, e-waste disposal, landfills, the decay of natural deposits, and leaching from mining sites. Inorganic contaminants include heavy metals such as mercury, lead, cadmium, nickel, and selenium, as well as metalloids (Wen et al., 2021; Dada et al., 2021).

Radionuclides

Alpha particles, beta particles, radium, and uranium are significant radionuclides that may arise from the erosion of natural mineral deposits, leaching from mining sites where radioactive materials such as radium and uranium are extracted, and through the alpha or beta decay of heavy radioactive atoms (Chauhan et al., 2013; Harrison et al., 2021).

Potential of fungi for bioremediation (Mycoremediation)

Persistent chemicals must be exposed to microbial catalysts to undergo biological degradation. However, these chemicals often escape the aquatic microhabitat of degrader microorganisms, tending to adsorb onto surfaces and precipitate or accumulate in the tiny pores of soil, rocks, and organic matter. This process decreases their bioavailability (Bosco & Mollea, 2019). In some cases, these accumulations occur in toxic environments that are unsuitable for the growth of decomposer organisms due to insufficient water, minerals, or suitable electron acceptors. Such environments necessitate the development of model decontamination systems that can function under these adverse conditions. These systems should be designed to explore and track chemicals within the contaminated organic matter and soil. Moreover, the model machinery must be able to interact with other trophic levels, such as plants, and should not rely on the availability of contaminants as a substrate. Instead, it should transport water, minerals, electron acceptors, and other catabolically active decomposing organisms to the contaminated sites. It must also possess the ability to thrive in extreme environments characterized by dryness, high temperatures, acidity, and toxicity. Fungi exhibit many of these desirable traits and are particularly well-suited for bioremediating persistent chemical contaminants. They produce extensive mycelial networks, and their enzymes exhibit low specificity for various contaminants as substrates (Boswell et al., 2007; Igiehon & Babalola, 2017). Additionally, the ecological characteristics and habitat versatility of fungi facilitate the bioremediation of chemicals in soil. Fungi can survive in terrestrial and aquatic environments, existing as saprobes, parasites, yeasts, or symbiotic partners in lichens and forming mycorrhizal associations with the roots of higher plants. Mycorrhizal associations are categorized into two main types: ectomycorrhizal and endomycorrhizal. These associations significantly enhance soil structure by binding soil particles, modifying soil chemistry, and promoting plant growth by mobilizing nutrients exchanged for photosynthetic assimilates. Fungi, known for their widespread distribution, can thrive in diverse environmental conditions and easily be dispersed via spores. They also utilize mycelium to remove toxic substances from contaminated sites (Zhang et al., 2013; Anastasi et al., 2013; Badia-Fabregat et al., 2015; Ahn et al., 2020; French et al., 2024). Mycoremediation is regarded as a safer and more effective technology compared to other microbial methods, as fungi prevent the bioaccumulation of chemical compounds within the ecological food chain (Harms et al., 2011; Dickson et al., 2019; Khatoon et al., 2021).

Mechanisms of mycoremediation

Various strategies can be employed for in-situ mycoremediation of toxic chemicals in contaminated soils, including biostimulation, bioaugmentation, bioattenuation, biosparging, and bioventing. In biostimulation, nutrients and supplements are introduced into the native microbial population to enhance the degradation of chemical compounds by promoting microbial growth. Conversely, the bioaugmentation strategy involves adding pre-cultured fungi to the existing microbial community in the contaminated soil to facilitate degradation (Stella,

Table 1. In-situ and ex-situ strategies for mycoremediation of contaminated soils

In-situ	
Biostimulation	Involves the injection of specific nutrients and optimal growth conditions
Bioaugmentation	Involves the addition of pre-grown cultures of fungi into the contaminated soil to increase the degradation process
Bioattenuation	Involves the passive remediation of contaminated soil without any human intervention
Biosparging	Involves air supply with pressure to degrade the petroleum products
Bioventing	Involves the supply of oxygen to contaminated soil for the growth of fungi, suitable for degradation of aerobically degradable contaminants
Ex-situ	
Bioreactors	Mycoremediation carried out in special containers/vessels in continuous or batch cultures, suitable for sewage sludge treatment
Biopiles	Involves the piling of contaminated soil, nutrients, compost, leachates etc.
Windrow	Involves periodic irrigation, aeration by turning the piled soil
Land farming	Involves placement and excavation of contaminated soil on impervious lined beds to check the mixing of leachates to groundwater

2020). Ex-situ mycoremediation of soil contaminants can be accomplished using bioreactors, biopiles, windrows, and landfarming (Table 1).

Biosorption/bioaccumulation: Biosorption refers to the rapid, biochemical, and reversible attachment of metal ions from aqueous solutions to the surface of biomass, which serves as an adsorbent. Fungi demonstrate greater efficiency in biosorption than bacterial cells, as their cell walls contain more tissue that acts as a biosorbent. This process encompasses various mechanisms, including precipitation, ion exchange, chelation, complexation with functional groups, intracellular bioaccumulation, electrostatic interactions, adsorption, and reduction (Sun et al., 2015; Pathak et al., 2017) (Fig. 3).

Mobilization: Mobilization activates toxic compounds through various biochemical reactions, transforming them from insoluble, stationary forms in sediments into mobile, liquid, or soluble phases. Fungi utilize several mechanisms, including methylation, alkylation, chelation via siderophores, and redox transformations, to mobilize these toxic contaminants from the soil. The biomethylation process enhances the bioavailability of heavy metals and other harmful chemicals,

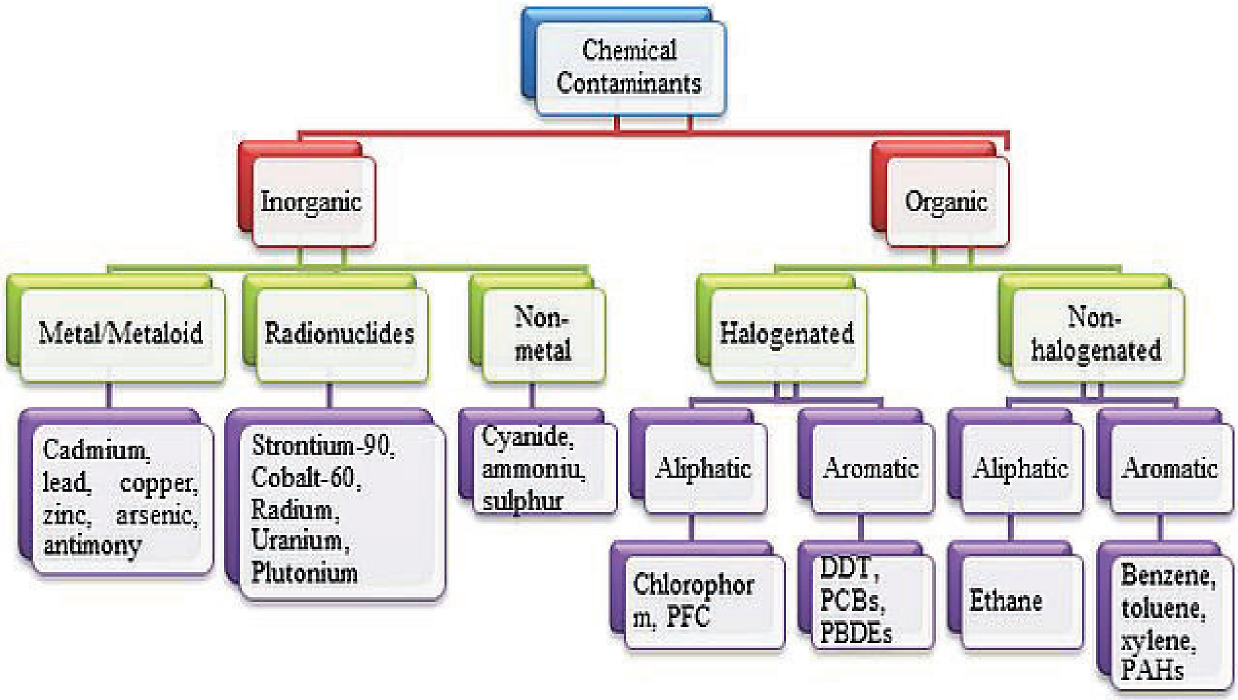

Figure 2. Different types of chemical contaminants are present in the soil

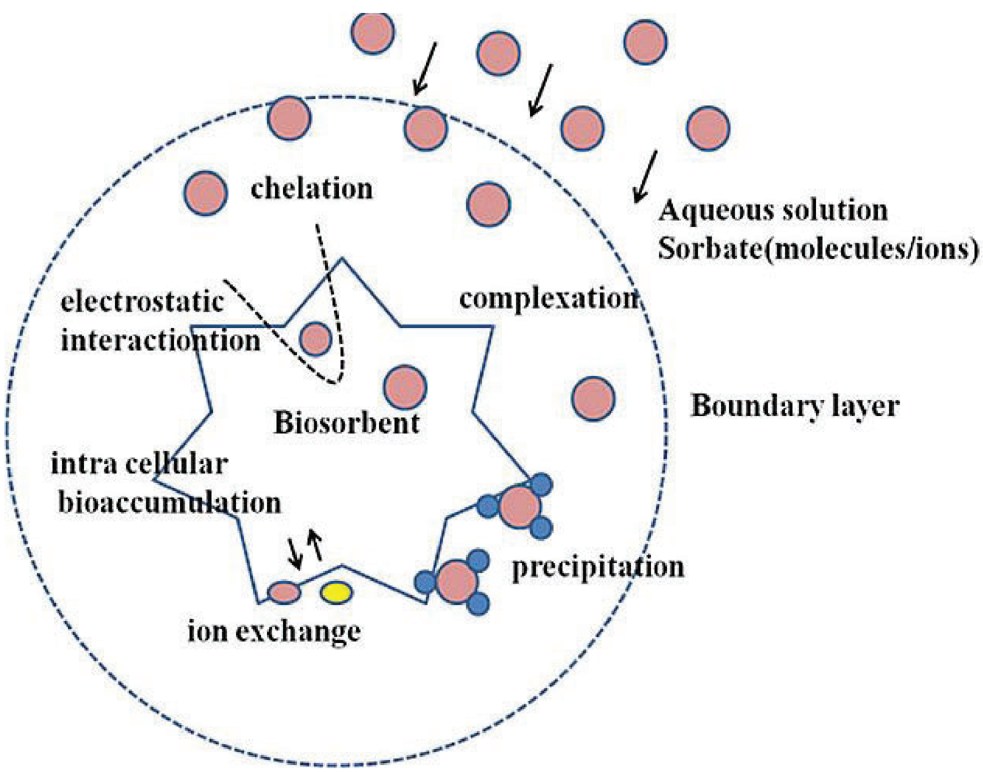

Figure 3. Processes involved in biosorption

facilitating their entry into microbial metabolic systems (Bolan et al., 2014; Raliya et al., 2016; Kunhikrishnan et al., 2017).

Immobilization (Bioprecipitation): Immobilization is a process employed by fungi and other microorganisms to reduce the mobility and leaching potential of heavy metals and other soil contaminants by modifying their physical and chemical properties, including slight alterations in pH and alkalinity levels. Fungi utilize this process to stabilize pollutants through ion exchange, adsorption, and precipitation (Liang et al., 2016; Kumari et al., 2016; Tamayo-Figueroa et al., 2019). In mycoremediation, fungi implement two primary strategies:

1. Stabilization: Fungi secrete specific enzymes and other compounds that facilitate the precipitation of heavy metals as metal hydroxides, thereby reducing their mobility and toxicity.

2. Solidification: The hyphal structures of fungi enhance the solidification of heavy metals and other pollutants through various mechanisms, including combining pollutants with water, chelation, biosorption, and precipitation. Fungal hyphae can bind directly with heavy metals to form complexes that mitigate their mobility and toxicity. Additionally, fungi produce enzymes and organic acids that aid in the chelation and precipitation of heavy metals in the soil (Carolin et al., 2017; Yin et al., 2019; Dhar et al., 2021; Sahu & Behuria, 2021).

Redox transformation (Biological oxidation and reduction): Fungi and other microbes harness reduction and oxidation reactions to mobilize metals, heavy metals, metalloids, and organometallic compounds, collectively referred to as redox transformations. Fungal enzymes play a crucial role in catalyzing the reduction of toxic metal compounds into non-toxic forms. In some instances, these redox transformations can facilitate the decreased solubility of soil contaminants. For example, enzymatic reduction can convert U(VI) into a highly insoluble U(IV) variant. This process generally involves c-type cytochromes (Lloyd et al., 2002). Microorganisms, through various enzymes, can catalyze the transformation of heavy metals from one chemical form to another (Khatoon et al., 2021).

Major classes of fungal enzymes involved in the mycoremediation

Laccases: Laccases are multi-copper oxidases derived from plants, bacteria, and fungi. These enzymes facilitate the one-electron oxidation of various phenolic compounds, leading to cross-linking, and they are also capable of cleaving aromatic compounds. Laccases are regarded as eco-friendly enzymes, as they produce water as a byproduct and require molecular oxygen as a co-substrate for their catalytic activity. Fungal laccases are predominantly extracellular enzymes characterized by four copper-blue oxidases that can reduce dioxygen to water. They can be sourced from edible mushrooms such as *Agaricus bisporus* and *Pleurotus ostreatus*. The Carbohydrate-Active Enzymes Database indicates that 74 fungal strains, primarily from the Basidiomycota group, are known to produce laccase (Yoshida, 1883; Thurston, 1994). Notable fungi that produce laccases include *Armillaria* sp., *Cotylidia versicolor, Exophiala xenobiotica, Pleurotus pulmonarius, P. chrysosporium, P. eryngii, Mortierella* sp., *Thermoascus crustaceus, Trametes villosa,* and various white-rot basidiomycetes (Prasad et al., 2018; Bosco & Mollea, 2019).

Lignin peroxidases (LiP): They, also known as diaryl propane oxygenases, are extracellular enzymes with an approximate molecular weight of 40 kDa. These heme-containing enzymes facilitate the breakdown of lignin through a hydrogen-peroxide-dependent oxidation process. Recognized for their extensive substrate specificity, LiPs are primarily secreted by white-rot fungi and play a vital role in the decomposition of lignin, as well as various environmental pollutants, including polycyclic aromatic hydrocarbons (PAHs), polychlorinated biphenyls (PCBs), pentachlorophenol (PCP), and certain herbicides (Christian et al., 2005; Diez, 2010; Ellouze & Sayadi, 2016). Common fungal species that produce LiPs include *Coriolus versicolor, Irpex lacteus, Panus tigrinus, Phanerochaete chrysosporium, Pleurotus pulmonarius, Trametes versicolor*, and *Trametes* sp. These enzymes are capable of oxidizing a diverse range of phenolic substances, such as guaiacol, syringic acid, and vanillyl alcohol, as well as certain non-phenolic aromatic compounds (Wong, 2009; Mäkelä et al., 2015; Singh NS et al., 2021).

Manganese peroxidases (MnP): Manganese peroxidase (MnP), with a molecular weight ranging from 40 to 50 kDa, is an extracellular, heme-containing enzyme commonly secreted by white rot fungi such as *Ganoderma* spp, *Coriolus versicolor, Pleurotus tigrinus, P. pulmonarius, Trametes* spp, and *Bjerkandera adusta*, among others (Wong, 2009; Singh NS et al., 2021). MnP requires hydrogen peroxide (H_2O_2) and manganese ions (Mn^{2+}) as cofactors for its oxidative activity and is adept at degrading various phenolic and other complex compounds. The enzyme was first identified in *Phanerochaete chrysosporium* by Kuwahara et al. (1984). Since the enzyme's activity is dependent on Mn^{2+} ions, elevated concentrations of Mn^{2+} lead to increased production of MnP, whereas lower concentrations result in a rise in lignin peroxidase (LiP) production (Wong, 2009; Mäkelä et al., 2015; Singh AK et al., 2021).

Tyrosinases: Tyrosinases are copper-containing enzymes primarily produced by fungi belonging to the Ascomycota, Basidiomycota, and Mucoromycotina groups. These enzymes function as catalysts in the breakdown of phenolic pollutants in soil, playing a crucial role in resolase and catecholase activities (Halaouli et al., 2006). In addition to tyrosinases, several other extracellular fungal enzymes play a vital role in the degradation of soil contaminants. These include angular dioxygenase, catalases, dehalogenases, haem-thiolate peroxygenases, and haem-thiolate chloroperoxidase derived from *Caldariomyces fumago*, as well as dye-decolorizing peroxidases, peroxidase from *Coprinopsis cinerea*, and versatile peroxidases (Hofrichter & Ullrich, 2006). Fungi also possess cell-bound enzymes, including aromatic nitroreductases, quinone reductases, various transferases, reductive dehalogenases, reductive nitrogenases, and phenol 2-monooxygenases (Harms et al., 2011; Ahmed et al., 2020; Danouche et al., 2021).

Fungal cytochromes in bioremediation

The Cytochrome P450 (CYP450) is predominantly produced by white rot fungi and plays a vital role in the degradation of various organic pollutants (Jiao et al., 2020; Pratiwi & Chi, 2022). These enzymes facilitate the intracellular detoxification of xenobiotic substances, either independently or in conjunction with extracellular enzymes, through a range of biochemical reactions, including the epoxidation of C=C bonds, heteroatom oxygenation, hydroxylation, dealkylation, dehalogenation, and reduction (Olicón-Hernández et al., 2017; Sarparast et al., 2020). Fungal species have two isoforms of P450: cytosolic and mitochondrial (Deshmukh et al., 2016). The CYP63A2 P450 monooxygenase, found in the white-rot fungus *Phanerochaete chrysosporium*, plays a crucial role in oxidizing and transforming mutagenic and carcinogenic high molecular weight polycyclic aromatic hydrocarbons (PAHs), n-alkanes derived from crude oil, and endocrine-disrupting long-chain alkylphenols (APs) (Deshmukh et al., 2016; Syed et al., 2013; Zeynalov & Nagiev, 2015; Mohapatra et al., 2018). While CYP enzymes are found across all kingdoms and domains of life, some species within Basidiomycota contain approximately 150 CYP genes organized into 12 enzyme groups. Fungi demonstrate a high abundance of CYPs, although only 12 clans are implicated in xenobiotic degradation, including CYP52, CYP53, CYP55, and CYP505 (Olicón-Hernández et al., 2017). The distribution of these CYP clans varies among fungal taxa: CYP52, CYP505, and CYP55 are predominantly associated with Ascomycota, whereas CYP53 is chiefly found in Basidiomycota (Deshmukh et al., 2016).

Degradation pathways in fungi

Fungi utilize various pathways to degrade environmental contaminants, employing different mechanisms and processes. Research into these pathways is crucial for understanding the subsequent steps involved in the mycoremediation of soil pollutants. The degradation of contaminants by fungi occurs primarily through two main pathways: extracellular enzymatic degradation and intracellular processes. The intracellular pathway begins when contaminants interact with the fungal cell, where degradation is facilitated by cell-associated enzymes, including cytochrome P450, nitroreductases, and various transferases, through oxidation and reduction reactions. Fungi also produce a range of extracellular enzymes that are secreted to catabolize various chemical compounds. These enzymes exhibit minimal specificity for their substrates, allowing them to metabolize a broad spectrum of soil contaminants. Common extracellular enzymes include laccases, lignin peroxidases, manganese peroxidases, and catalases (Viswanath et al., 2014). These enzymes are essential in breaking down recalcitrant compounds into simpler forms or solubilizing them to enhance their absorption by fungal cells. Additionally, they can immobilize pollutants through bio-precipitation, converting them into bound residues within the soil (Fig. 4). Fungi can absorb hazardous chemicals directly or after their extracellular degradation by enzymes, which prepares them for further catabolism. The Cyt-P450 system initiates the intracellular attack, while nitroreductases facilitate conjugate formation. Subsequently, transferase enzymes convert these conjugates into various metabolic intermediates, which may be stored within the fungal cell, excreted as metabolites, or processed through redox transformations into CO_2 and other metabolites. These excreted fungal metabolites are non-toxic to the environment and can persist in the soil as bound residues.

Mycoremediation of toxic organic compounds

White rot fungi have the remarkable ability to degrade complex organic compounds, including lignin and cellulose. Given that polycyclic aromatic hydrocarbons

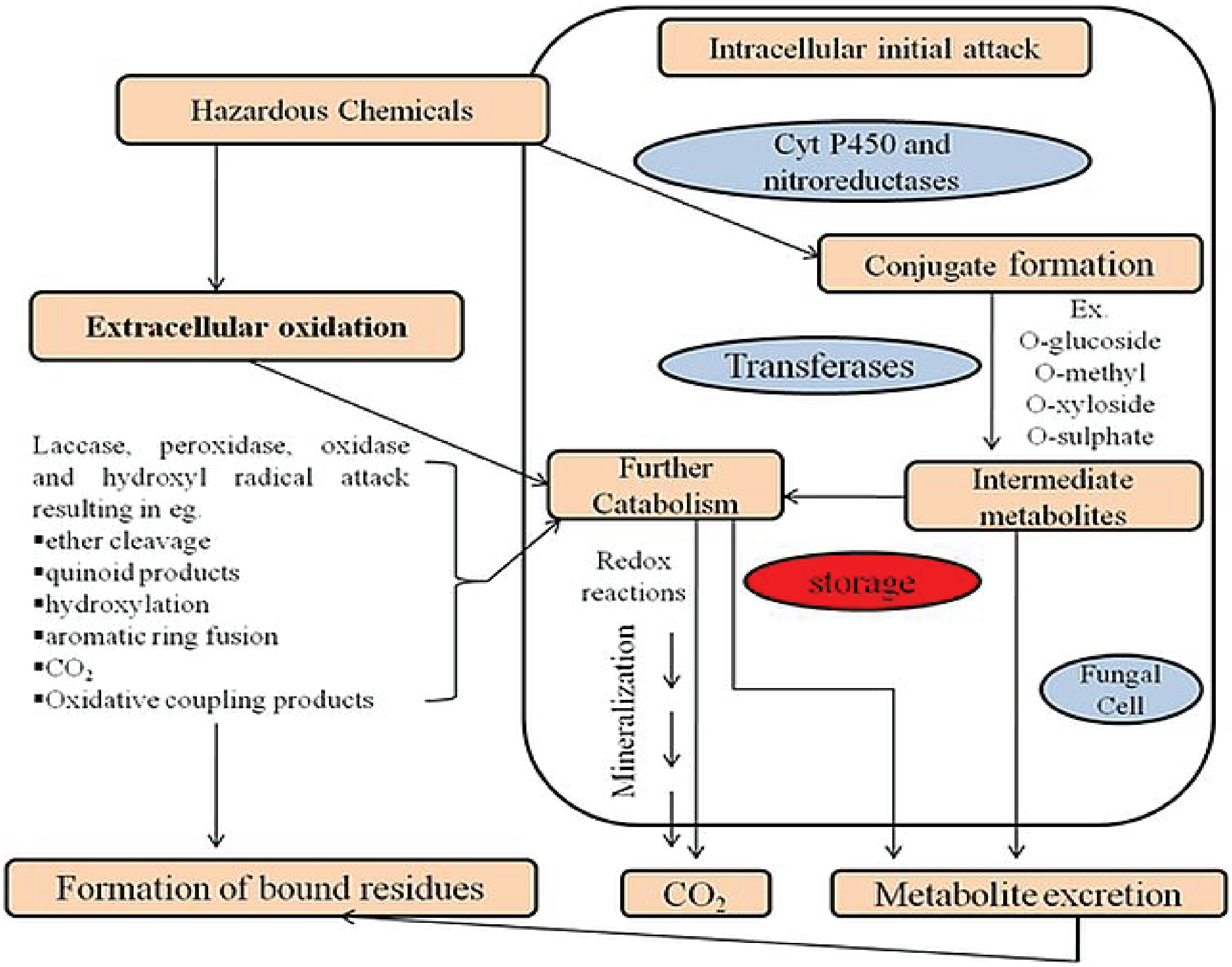

Figure 4. Degradation pathways in fungi (Adopted and modified from Harms et al., 2011).

(PAHs) share structural similarities with lignin, the ligninolytic enzymes responsible for lignin degradation can also effectively break down PAHs in contaminated environments (Ijoma & Tekere, 2017). Ligninolytic fungi can degrade both low- and high-molecular-weight PAHs by secreting extracellular enzymes such as laccases, lignin peroxidases, and manganese peroxidases (Khatami et al., 2019; De Beeck et al., 2021). Additionally, cytochrome P-450 monooxygenases are essential for the metabolism of PAHs (Syed et al., 2013; Zeynalov & Nagiev, 2015; Mohapatra et al., 2018). The extracellular ligninolytic enzymes initiate PAH degradation by catalyzing their oxidation into quinones, which subsequently undergo ring fission and are eventually converted into carbon dioxide (CO_2) (da Silva Vilar et al., 2022). Intracellular degradation of PAHs begins with cytochrome P-450 enzymes, which transform PAHs into arene oxides in the presence of oxygen. These arene oxides undergo further transformation, where non-enzymatic rearrangement leads to phenol formation, while epoxide hydrolase converts them into trans-dihydrodiols. The complete degradation pathway of PAHs in soil, supported by fungal enzymes and cytochrome P-450s, is illustrated in

Figure 5. Notably, white-rot fungi such as *Phanerochaete chrysosporium* and various species of *Polyporus are* renowned for their capacity to degrade a wide range of soil pollutants, including PAHs, polychlorinated biphenyls (PCBs), and petroleum-based compounds (Ijoma & Tekere, 2017; Lee et al., 2020; Khatoon et al., 2021). Other fungal genera, including *Aspergillus, Cladosporium, Fusarium, Penicillium, Rhizopus*, and *Trichoderma*, have also demonstrated considerable effectiveness in degrading toxic substances, such as polycyclic aromatic hydrocarbons (Aydin et al., 2017; Gupta & Pathak, 2020; Khatoon et al., 2021). Moreover, *Pleurotus ostreatus* has shown its potential to degrade PCBs from contaminated soils. Table 2 lists various fungal species involved in mycoremediation efforts, while Table 3 summarises the fungal enzymes implicated in the degradation and metabolism of harmful soil pollutants.

Mycoremediation of heavy metals, metalloids, radionuclides and pesticides

Heavy metals exhibit a high degree of toxicity, as their entry into the food chain can lead to carcinogenesis, multiple organ failure, and other severe health complications. Harmful elements like mercury, lead, arsenic, chromium, and cadmium must be removed from the soil when their concentrations exceed safe levels to protect human health and the ecosystem. Fungi contribute substantially to the removal of these heavy metals

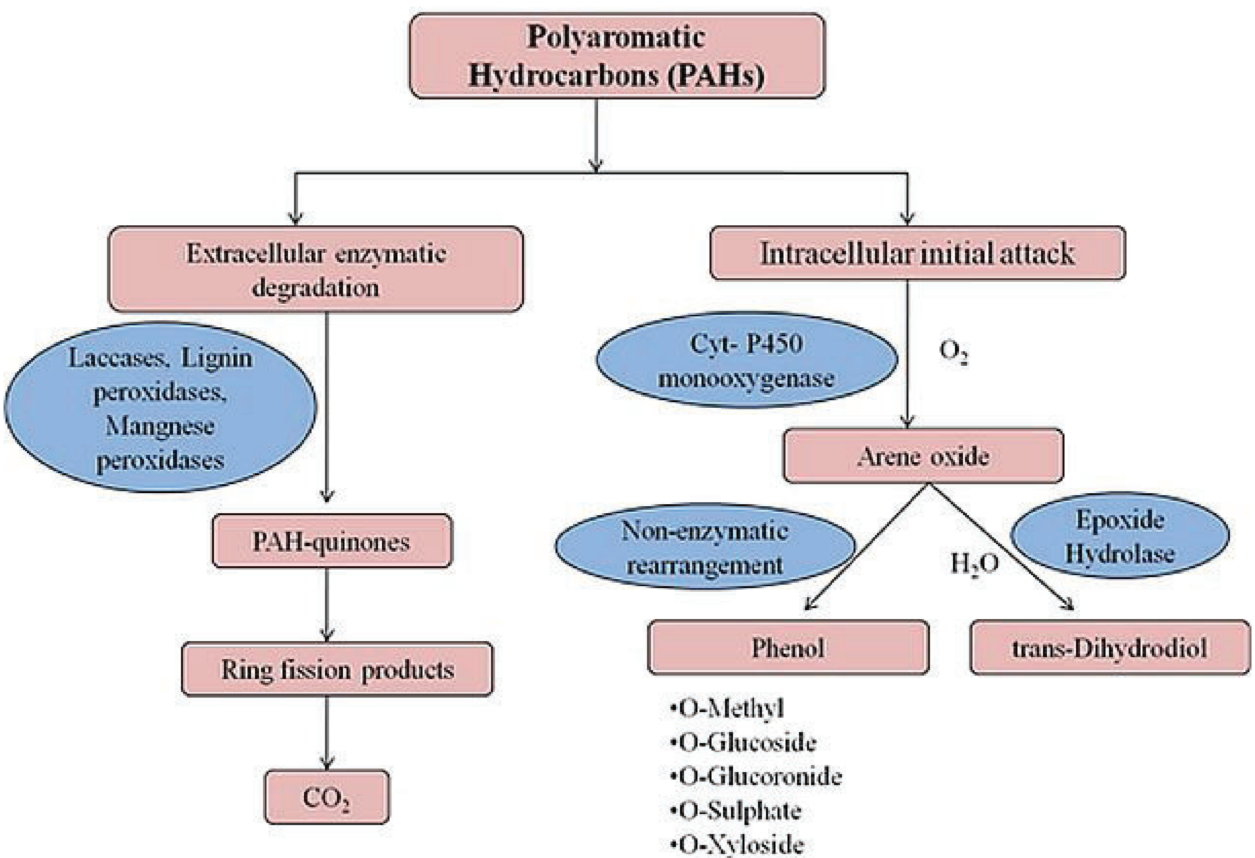

Figure 5. Extracellular and intracellular degradation pathways of PAHs

Table 2. Groups of fungi involved in the degradation of organic chemicals (Phylogenetic classification of fungi by Hibbet et al., 2007) Source: modified after Harms et al. (2011)

Phylum	Subphylum	Ecological features	Chemicals degraded
Fungi			
Microsporidia	Kickxellomycotina	Parasites of animals and fungi and can be as saprobes	PAHs
	Zoopagomycotina	Parasites of fungi, nematodes and protozoa	--
	Entomophthoromycotina	Parasites of insects	PAHs
Blastocladiomycota	Mucoromycotina	They are mostly parasites, saprobes, or ectomycorrhizal symbionts	PAHs, pesticides, synthetic dyes, Benzoquinoline, biphenyl and TNT
Neocallimastigomycota	--	They are gut symbionts of herbivorous ruminants	--
Chytridiomycota	--	Saprobes and parasites, found in freshwater and moist soil environments	PAHs
Glomeromycota	--	Arbuscular mycorrhizal symbionts	PAHs and pesticides
Dikarya			
Ascomycota	Pezizomycotina	Mostly saprobes	PAHs, crude oil, coal tar oil, TNT, endocrine-disrupting chemicals (EDCs)
	Saccharomycotina	Pathogens of plants and animals	PAHs and TNT
Basidiomycota (53)	Agaricomycotina	Saprobes, ectomycorrhizal symbionts	Hydrocarbons, petroleum based products, dyes explosives, agricultural and industrial chemicals

through different strategies. Fungi secrete various organic acids (oxalate and citrate) and siderophores that lower the pH in the mycosphere, increasing the mobilization of metals. Moreover, siderophores function as metal-binding agents to capture iron and can be associated with other metals, supporting processes such as bio-precipitation and biosorption of multiple metal ions (Harms et al., 2011; Oyetibo et

Table 3. Major fungal enzymes are involved in the degradation of organic contaminants

Enzyme	Site of action	Phylum/ subphylum	Chemicals degraded	References
Laccases	Extracellular	Ascomycota and Basidiomycota	Hydrocarbons, petroleum based products, dyes explosives, agricultural and industrial chemicals	Becker et al., 2017; Longe et al., 2018; Wang et al., 2019
Lignin peroxidases (LiP)	Extracellular	Basidiomycota (White rot fungi)	Hydrocarbons, petroleum based products, dyes explosives, agricultural and industrial chemicals	Datta et al., 2017; Singh AK et al., 2021
Manganese Peroxidases (MnP)	Extracellular	Basidiomycota	Hydrocarbons, petroleum based products, dyes explosives, agricultural and industrial chemicals	Fernández-Fueyo et al., 2014
Lipase	Extracellular	Ascomycota and Basidiomycota	PAHs	Al-Hawash et al., 2018; Kundys et al., 2018; Duan et al., 2019
Catalase	Extracellular	Ascomycota and Basidiomycota	Heavy metals	Syed et al., 2013; Deshmukh et al., 2016; Zeynalov & Nagiev, 2015

al., 2017). In addition, fungal cell walls also play a significant role in removing heavy metals, dyes, and phenolic substances from contaminated environments, as they are composed of chitin and chitosan, which function as natural biosorbents (Singh et al., 2020; Ramírez Calderón et al., 2020). Glomalin proteins produced by fungi contain multiple functional groups (amine, hydroxyl, carboxyl, sulfhydryl, and phosphate). They provide a negative charge to the fungal cell wall, enabling them to bind heavy metals and dyes effectively (Ayele et al., 2021). Fungal cells possess specialized metal transport proteins (MTPs) that enable the absorption of essential metals while interacting with harmful or non-essential metals. These metals are sequestered and immobilized in the cytoplasm by forming complexes with metallothioneins (MTs) and phytochelatins (PCs), which are subsequently transported to vacuoles for storage. Redox and metal transformation reactions, including methylation and alkylation, also contribute to metal volatilization. Cytoplasmic streaming within fungal mycelium facilitates the transport of metals throughout the fungal network and to symbiotic plant partners. Certain fungi demonstrate resilience in heavily contaminated soils due to their enzymatic activity. Enzymes such as laccase, lignin peroxidase, and manganese peroxidase play a significant role in the bioremediation of various soil pollutants (Karigar & Rao, 2011; Kadri et al., 2017; Sharma et al., 2018; Chandra, 2019). Various fungal species, including *Agaricus* spp, *Amanita* spp, *Aspergillus niger, A. fumigatus, Boletus* spp, *Cortinarius* spp, *Leccinum* spp, *Mucor* spp, *Penicillium simplicissimum, P. brevicompactum, Phellinus* spp, *Saccharomyces cerevisiae, Suillus* spp, *Termitomyces clypeatus*, and *Trichoderma* spp, have demonstrated high efficiency in removing heavy metals and dyes from polluted soils (Verma & Sharma, 2017; Kumar et al., 2019; Kumar & Dwivedi, 2021; Singh et al., 2021; Sharma et al., 2021).

Metalloids exhibit properties that fall between those of metals and non-metals, with examples including antimony, arsenic, boron, germanium, silicon, and tellurium. Fungi play a vital role in the remediation of metalloids and heavy metals. Certain species, such as *Alternaria, Aspergillus*, and *Cladosporium*, facilitate the microbial leaching of metals and metalloids, including aluminium, calcium, iron, and silicon, precipitating them at contaminated sites (Liang & Gadd, 2017). The concentration of heavy metals has a significant impact on fungal enzyme activity. For example, at low levels of mercury (Hg), copper (Cu), and cadmium (Cd), manganese peroxidase (MnP) activity diminishes, while at higher concentrations of these metals, MnP activity increases (Zeng et al., 2012; Enespa & Chandra, 2017).

Radioactive forms of elements are referred to as radionuclides (US-EPA). Among the most prevalent radionuclides are radium, uranium, thorium, cobalt-60, plutonium, and strontium-90. These radionuclides cannot be destroyed through physical or biological processes, but their activity can diminish over time due to natural decay. Interestingly, microbes such as fungi can influence the bioavailability of nutrients through sequestration within their bodies and by binding them to soil particles. Fungi play a vital role in regulating radionuclides in the ecosystem by (1) limiting their mobility, (2) facilitating phytoremediation via increased accumulation as mycorrhizae, (3) absorbing radionuclides into fungal biomass (mycoremediation), and (4) binding radionuclides to surface materials (Gadd, 2007; Rashid et al., 2016). Fungi demonstrate a greater affinity for radionuclides compared to plants. For instance, Ding et al. (2015) found that incorporating Fe_3O_4 nanoparticles in aqueous solutions at pH 7.0 enhanced the sorption of Sr, U, and Th by *Penicillium* mycelia. The saprophytic basidiomycete *Pleurotus eryngii*, along with ectomycorrhizal fungi such as *Hebeloma cylindrocarpon* and six other species, has shown the ability to uptake Sr-90, Am-241, and plutonium-239+240 (Baeza & Guillén, 2007). Mycorrhizal fungal fruit bodies tend to accumulate higher levels of radioactive elements than other organisms in terrestrial ecosystems (Zhdanova et al., 2004; Dighton et al., 2008). Common ectomycorrhizal fungi involved in the remediation of radionuclides include *Amanita, Boletus, Lactarius, Leccinum, Paxillus, Suillus*, and *Tylopilus* (Baeza & Guillén, 2007; Dighton et al., 2008).

Pesticides, including fungicides, insecticides, herbicides, and nematicides, are widely used in agriculture to manage pest populations. These substances contain harmful chemicals, including Endosulfan, Glyphosate, Fipronil, Paraquat, and Aldrin, all of which possess carcinogenic properties. The persistent nature and intricate chemical structures of these pesticides are significant drawbacks, resulting in slow environmental degradation (Andreu & Picó, 2004; Verma et al., 2014).

Fungi such as *Aspergillus tamarii* and *Botryosphaeria laricina* show great potential in effectively degrading Endosulfan and its derivatives (Akhtar & Mannan, 2020). Additionally, studies indicate that *Aspergillus glaucus* can break down Fipronil and its derivative, fipronil sulfone, using ligninolytic enzymes (Zhou et al., 2021; Singh et al., 2021). The enzymatic activity of *Trametes maxima,* as well as a co-culture of *T. maxima* and *Paecilomyces carneus*, has been shown to facilitate the degradation of Atrazine and Paraquat (Akhtar & Mannan, 2020). Fungi produce a variety of enzymes, including laccases, lignin-degrading enzymes, oxidoreductases, and peroxidases, that can effectively break down pesticide residues in the soil. *Aspergillus flavus, Penicillium spiculisporus*, and *P. verruculosum* have been recognised for their ability to degrade xenobiotic compounds, such as Glyphosate, through the action of fungal enzymes (Vijaya Kumar, 2017; Akhtar & Mannan, 2020; Zhou et al., 2021; Singh et al., 2021). Species like *Auricularia auricula, Agrocybe semiorbicularis, Dichomitus squalens, Coriolus versicolor, Phanerochaete chrysosporium, Flammulina velutipes*, and *Pleurotus ostreatus* are capable of degrading a wide range of pesticides, including dichlorodiphenyltrichloroethane (DDT), Chlordane, Aldrin, Dieldrin, Atrazine, Terbuthylazine, and Heptachlor (Odukkathil & Vasudevan, 2013; Akhtar & Mannan, 2020).

Conclusions

This review highlights that mycoremediation is an efficient, cost-effective, and eco-friendly approach for transforming, degrading, or removing toxic pollutants in soil. Fungi possess a diverse array of extracellular and intracellular enzymes that are essential for breaking down harmful pollutants in the soil. Additionally, fungi have intracellular processes that convert toxic substances into non-toxic forms through biotransformation, immobilization, and biosorption. They can be applied both on-site and off-site for bioremediation, offering distinct advantages over bacteria due to their unique morphology and metabolic capabilities. However, the underlying mechanisms of mycoremediation remain not fully understood and warrant further investigation. Additional research is needed to identify novel fungal strains and optimize bioremediation conditions for effective treatment. Genomic and proteomic studies could provide valuable insights into the genes and proteins involved in these processes, thereby enhancing our understanding of fungal bioremediation. Future research should focus on identifying and selecting highly effective fungal species for soil remediation applications.

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