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REVIEW ARTICLE

Mycoremediation of heavy metals: processes, mechanisms, and affecting factors

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Abstract

Industrial processes and mining of coal and metal ores are generating a number of threats by polluting natural water bodies. Contamination of heavy metals (HMs) in water and soil is the most serious problem caused by industrial and mining processes and other anthropogenic activities. The available literature suggests that existing conventional technologies are costly and generated hazardous waste that necessitates disposal. So, there is a need for cheap and green approaches for the treatment of such contaminated wastewater. Bioremediation is considered a sustainable way where fungi seem to be good bioremediation agents to treat HM-polluted wastewater. Fungi have high adsorption and accumulation capacity of HMs and can be potentially utilized. The most important biomechanisms which are involved in HM tolerance and removal by fungi are bioaccumulation, bioadsorption, biosynthesis, biomineralisation, bioreduction, bio-oxidation, extracellular precipitation, intracellular precipitation, surface sorption, etc. which vary from species to species. However, the time, pH, temperature, concentration of HMs, the dose of fungal biomass, and shaking rate are the most influencing factors that affect the bioremediation of HMs and vary with characteristics of the fungi and nature of the HMs. In this review, we have discussed the application of fungi, involved tolerance and removal strategies in fungi, and factors affecting the removal of HMs.

Keywords Metal tolerance · Molecular mechanism · Heavy metal · Reactive oxygen species · Bioprecipitation · Bioremediation

Introduction

The present scenario of industrial and developmental activities is altering the natural flow of the materials and introducing foreign compounds into the environment (Faisal and Hasnain 2004). Environmental pollutants including halogenated solvents, petroleum hydrocarbons, explosives, agrochemicals, heavy metal/loids, and radionuclides are a serious problem to the environment. Out of these pollutants, heavy metals (HMs) (cadmium; Cd, copper; Cu, mercury; Hg, lead; Pb, manganese; Mn, arsenic; As, nickel; Ni, zinc; Zn, iron; Fe, etc.) are extensively used in different types of industries and released in high amount with their disposing effluents. These contaminants directly or indirectly come into the environment. A few numbers of metals including Fe, Mg, Cu, Mn, Co, and Zn are the micronutrients for most of the organisms, while not for all living organisms, and increasing concentration from their limit causes toxicity (Manorama et al. 2016; Singh et al. 2016). HMs as micronutrients may play an essential role in metabolic activity, e.g., metalloenzyme (Tahir et al. 2017). Because of the high solubility of HMs in the aquatic medium, they can be easily absorbed or taken by the organisms. On the other hand, being metal, they are non-biodegradable and have multiple threats to living organisms due to their persistence in nature, high-toxicity characteristics, and long half-lives after coming into the food chain (Ali et al. 2015; Jamali et al. 2007; Mondal et al. 2017). They have multiple ways to come into the food chain such as by seeping in groundwater from wastewater, by drinking of water from the polluted water bodies, crop irrigation by wastewater, etc. (Jamali et al. 2007). After accumulation into the living organism, they cause multiple threats to humans (Table 1) as well as other living organisms. So, due to extensive use and toxicity, heavy metal has a rising number of environmental and health issues and has become a serious concern to resolve at present (Dhankhar and Hooda 2011; Mishra and Malik 2012).

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Table 1 Heavy metals permissible limit in drinking water (WHO Standard), their sources and human health impact

Metal species	Maximum permissible limit in drinking water* (mg L^{-1})	**Major sources	**Human health impact
Hg	0.006	Pesticides, batteries and paper industries	Damage to nervous system, Protoplasm poisoning
Cd	0.003	Electroplating, welding, pesticide fertilizer, Cd and Ni battery industries	Kidney damage, bronchitis, gastrointestinal disorder, bone marrow, cancer
Pb	0.01	Paints, pesticides, smoking, automobile emission, mining, burning of coal	Liver, kidney, and gastrointestinal damage, mental retardation in children
Cr	0.05	Chrome plating, ceramics, metallurgical processes, paints, dyes, magnetic tapes	Persisting diarrhea, skin ulceration, “chrome holes,” bronchial asthma
Cu	2.0	Agricultural fungicides, algicides, Fertilezers, plumbing corrosion, electroplating, photography	Gastrointestinal disorder, liver and kidney malfunctioning, nausea, vomiting, diarrhea, nd intestinal cramps, anemia
As	0.01	Pesticides, fungicides, metal smelters, mining of coal and ores	Loss of appetite, and nausea, vomiting, esophageal and abdominal pain, and bloody “rice water” diarrhea Bronchitis, dermatitis, skin thickening (hyperkeratosis) neurological disorders, muscular weakness
Mn	0.5	Welding, fuel addition, ferromanganese Production	Inhalation or contact causes damage to central nervous system
Ni	0.02	Nickel- or chromium-plated taps, bore-hole equipment	Skin sensitizer, dermatitis, prenatal mortality
Co	–	Aircraft engines, magnets, grinding and cutting tools, artificial hip and knee joints, glass, ceramics, and paints	Congestive heart failure, dermatitis, liver and kidney effects, nausea, vomiting, diarrhea, bleeding, coma
Zn	3.0	Refineries, brass manufacture, metal Plating, plumbing	Zinc fumes have corrosive effect on skin, cause damage to nervous membrane
Fe	–	Blister packaging, iron pipes, and cookware	Liver, cardiovascular system, and kidney malfunctioning

*WHO’s drinking water standards, 2017, **sources of pollutants and their impact on human health is adopted from Ayangbenro and Babalola (2017) and Dhankar and Hooda (2011)

From the last 4 to 5 decades, it has been greatly focused to control hazardous chemicals, especially toxic HMs. At present, there is a great requirement for economical and efficient techniques for treating HM-contaminated industrial wastewater (Dhankhar and Hooda 2011). There are some conventional technologies including chemical coagulation, adsorption, precipitation, membrane filtration, reduction, and ion exchange that are being used to treat HM-polluted wastewater (Barakat 2011; Fu and Wang 2011). However, most of these methods are ineffective to remove HMs below 100 mg/L (Dixit et al. 2015) and generates secondary pollution (Kumar et al. 2019). Their high cost and eco-unfriendly nature limits its application and required an alternative cheap and eco-friendly technique to treat HMs contaminated wastewater. Bioremediation has been considered an eco-friendly and sustainable alternative which implies the application of bacteria, fungi, and plants to treat wastewater and has taken great attention from the last 3 to 4 decades.

Microorganisms can survive in almost every adverse environment because of their innate ability to take up the pollutants as nutrients like HMs due to accumulative and absorptive capability. Microorganisms have the ability to not only accumulate or adsorb HMs but also reduce HMs from a toxic to non/less-toxic form (Chen et al. 2019; Sakthivel et al. 2016; Kumar and Dwivedi 2019b). A number of microorganisms have been explored for the mobilization and immobilization potential of metal ions, thereby varying their accessibility to plants (Birch and Bachofen 1990; Bachofen 1990; Deng et al. 2013; Rhee et al. 2014). Fungi have been reported to exhibit significant tolerance/resistance towards HMs and turn out to be dominant organisms in some contaminated aquatic water bodies and other habitats (Gola et al. 2016; Kumar and Dwivedi 2019a; Mishra and Malik 2012). The tolerance and accumulation characteristics of fungi are the major criteria for selection to introduce their application in the field of bioremediation. In the case of growing fungi, their application in remediation is called mycoremediation. *Aspergillus niger* (Fomina et al. 2017; Holda and Mlynarczykowska 2016; Mondal et al. 2017; Sriharsha et al. 2017; Tahir et al. 2017) and *Trichderma harzianum* (Adebiyi 2017; Cecchi et al. 2017; Mohammadian et al. 2017) are reported as multi-metal-tolerant fungi. Numbers of species from a diverse group of fungi (*Penicillium*, *Aspergillus*, *Trichoderma*, *Fusarium*, *Rhizopus*, etc.) have been reported which have different types of HM removal capacity. Several mechanistic strategies are involved in microorganisms (bacteria, fungi, and algae) for resistance towards metals including enzymatic detoxification, accumulation inside the cell via active/passive uptake, adsorption on their outer cell structures, precipitation on the cell surface, exclusion by permeability barrier and efflux pumps, and alteration of the cellular objects (Bruins et al. 2000; Kumar and Dwivedi 2019a, 2020; Kumar et al. 2019; Merroun et al. 2001; Zhang et al. 2005; Cao et al. 2018; Yin et al. 2011; Dang et al. 2018). In the HM removal, resistance/tolerance, and homeostasis, fungi go through one or a combination of more than one of the basic mechanisms.

In this review, we have elaborated the process of the application of fungi in the removal of HMs and mechanism which are involved in HM tolerance and their removal. The most influencing parameters including solution pH, initial concentration of HMs, temperature, contact time, doses of adsorbent, and agitation rate have been also discussed in this paper.

Metal tolerance in fungi

Tolerance is the ability of an organism to survive in an adverse environment. HMs are toxic for most of the organisms. The ability of fungi to grow in HM-polluted environment is the metal tolerance of the fungi (Mondal et al. 2017; Mohammadian et al. 2017). There are some mechanisms in fungi to tolerate and detoxify the HMs such as enzymatic detoxification, accumulation inside the cell via active (transport systems) and/or passive (diffusion) uptake mechanism, exclusion by permeability barrier, adsorption on extracellular structures (cell wall, capsule, slime), extra- and intracellular precipitation, efflux pumps, the adjustment in the cellular targets, methylation, volatilization and chelation of metal/loids, etc. (Baldrian 2003; Gadd 2007; Merroun et al. 2001; Zhang et al. 2005) in which some mechanisms are based on the production of an extracellular and intracellular chelating agent (for the molecular mechanism of HMs tolerance and removal, see "Heavy metal tolerance and removal mechanism in fungi") (Gadd 2007; Cao et al. 2018; Yin et al. 2011; Dang et al. 2018). Many morphological responses also have been observed in fungi under the presence of HMs. Growth inhibition, change in color morphology, cell elongation, constriction, protrusion less, ruptured, snubbed/flatted, and outward growth of mycelia are reported in the presence of HMs in several studies (Chen et al. 2017; Kumar and Dwivedi 2019a, b; Long et al. 2015). Contaminated sites (soil and water) are the major source to isolate the metal-tolerant fungi (Mohammadian et al. 2017). Fungal response to metal and their resistance depends on the concentration, toxicity, and bioavailability of HMs and characteristics of the fungi (Baldrian 2003). The resistance nature of the fungi varies with the genetic background of the fungi, HMs concentration, existing environmental condition, nutrient availability, and types of HMs. *Aspergillus niger* (Cu, Pb, Cr, Zn, Cr, Ni, and V) (Coreño-Alonso et al. 2014; Sepehr et al. 2014; Iram and Sumera 2015; Saravanan et al. 2015; Holda and Mlynarczykowska 2016; Sakthivel et al. 2016; Fomina et al. 2017), *Trichoderma harzianum* (Cd, Pb, Cu, Zn Ni, Fe) (Adebiyi 2017; Cecchi et al. 2017; Mohsenzadeh 2014) and *Aspergillus flavus* CR500 (Kumar and Dwivedi 2020) are the some of the multimetal-resistant fungal species. Table 2 lists many fungal species that have the potential to tolerate HMs.

Table 2 depicts that most of the fungal species that are reported for their tolerance towards HMs belong to the class ascomycetes. This class of fungi is also very widely distributed in different type of habitats and play an important role in an ecosystem like nutrient cycling and soil stabilization (Challacombe et al. 2019). However, there is no clear evidence that relates them to each other that is why they are highly metal tolerant and belongs to the same class of fungi. To get insight on the ascomycetes, here it is to be mentioned that Challacombe et al. (2019) investigated the genomic and secrotomic similarities to assess their role in biomass decomposition and pathogenesis in the arid environment by five different fungal species (*Aspergillus* CK392, *Coniochaeta* CK134, *Embellisia* CK46, *Chaetomium* CK152, and *Phoma* CK108) of ascomycetes class. In genome and secretome analysis, they found that all the tested fungi have a melanized structure and genetically capable to synthesize melanin which makes these tested ascomycete fungi survive in an arid environment. There are also some categories of proteins that are expressed in all tested conditions and common to some of the fungi which provide the common nature of the ascomycete fungus. In the case of metal tolerance in fungi, the listed studies in Table 2 are not much focused on the HM tolerance mechanism, so a clear insight on fungal (from the ascomycete class) tolerance towards HMs is not clear. But, the metal tolerance and removal mechanism that has been discussed in "Heavy metal tolerance and removal mechanism in fungi" is common for all the types of fungi, not only specific to the ascomycetes. Besides, it is a question remains to resolve that why the majority of HMs tolerant fungus belongs to the ascomycete class and need detailed experimentation as investigated by Challacombe et al. (2019) to resolve this question.

Heavy metal removal by fungi

The interaction between fungi and HMs may be positive (no or less affected with the presence of HMs) or negative (inhibition of growth and metabolic rate or death of the fungus in presence of HMs). The positive interaction of fungi with HMs (higher fungal resistance towards HMs) seems to be a new approach of fungi in HM removal from wastewater. The researchers have reported a number of fungi having multi-metal removal capacity in growing/viable form and in the dead biomass form of the fungi (Chakraborty et al. 2014; Kan et al.

Table 2 The Heavy metal tolerant fungi applied in removal HMs in growing form

Class of fungi	Name of the fungi	Name of the pollutants	References
Ascomycetes	*Aspergillus aculeatus*	Cd	Xie et al. (2014)
	Aspergillus flavus	Cu, Pb, Cr, and Cd	Iram and Sumera, (2015), Qayyum et al. (2016)
	Aspergillus flavus strain KRP1	Hg	Kurniati et al. (2014)
	Aspergillus foetidus	Cd	(Chakraborty et al. 2014)
	Aspergillus fumigates	Cr	Panda et al. (2014) Sakthivel et al. (2016)
	Aspergillus fumigatus PD-18	Cd, Cr,Ni, Pb, and Zn	Dey et al. (2016)
	Aspergillus niger	Cu , Pb , Cr, Zn, Cr, Ni, and V	Coreño-Alonso et al. (2014), Sepehr et al. (2014), Mirazimi et al. (2015), Iram and Sumera (2015), Saravanan et al. (2015) Holda and Mlynarczykowska (2016), Olubunmi and Bernard (2016), Sakthivel et al. (2016), Fomina et al. (2017), Mondal et al. (2017), Sriharsha et al. (2017), Tahir et al. (2017)
	Aspergillus niger (CMCC98003)	Pb, Hg, and Cd	Cui et al. (2018)
	Aspergillus niger A40	Pb	Sharma and Pathak 2017
	Aspergillus niger MSR4	Cr	Melvin et al. (2015)
	Aspergillus niger strain SF-6095	Cr	Manorama et al. (2016a, b)
	Aspergillus oryzae	Cr	Sepehr et al. (2014)
	Aspergillus sp.	Cu, Zn, and Cr	Pundir and Dastidar (2015), Sathvika et al. (2015), Pundir et al. (2018)
	Aspergillus sp. UF3	Lead and Strontium	Dhami et al. (2017)
	Aspergillus terreus	Pb, Cr, and Cu	Khadiga et al. (2017), Sriharsha et al. (2017)
	Aspergillus terreus AML02	Cd, Pb, and Zn	Dey et al. (2016)
	Aspergillus terreus PD-17	Cd, Cr, Ni, Pb, and Zn	Dey et al. (2016)
	Acremonium persicinum	Cd, Pb, Cu, and Zn	Mohammadian et al. (2017)
	Acremonium sp.	Cr	Herath et al. (2014)
	Beauveria bassiana	Zn, Cu, Cd, Cr, and Ni	Gola et al. (2016)
	Beauveria bassiana 4580	Cd, Cr, Ni, Pb, and Zn	Dey et al., (2016)
	Botrytis cinerea	CuO	Kovacec et al. (2017)
	Candida albicans	Cd	Nadeem et al. (2015)
	Chaetomium globosum	Cu	Karunasekera et al. (2017)
	Cheatomium .sp	Co, Zn, Cd	Sani et al. (2017)
	Cyberlindnera jadinii M9	Cr	Irazusta et al. (2018)
	Exophiala sideris	As	Seyedmousavi et al. (2011)
	Flammulina velutipes	Cu, Zn, and Hg	Li et al. (2018a, b, c)
	Fusarium oxysporium	Cr and Pb	Migahed et al. 2017
	Fusarium oxysporum UF8	Pb and Sr	Dhami et al. (2017)
	Fusarimum solani	Cd	Kumar et al. (2019)
	Humicola sp.	Cd	Netpae et al. (2015)
	Neurospora sp.	Pb, Ni, Co, Cr, Cu, and Zn	Joshi (2014), Desai et al. (2016)
	Paecilomyces chysogenum	Cr	Olubunmi and Bernard (2016)
	Paecilomyces fumosoroseus 4099	Cd, Cr, Pb, and Zn	Dey et al. (2016)
	Paecilomyces javanicus	Pb	Rhee et al. (2016)
	Penicillium chrysogenum	Zn and Cu	Tahir et al. (2017)
	Penicillium chrysogenum CS1	Cr and Pb	Qian et al. (2017)
	Penicillium griseofulvum MSR1	Cr	Abigail et al. (2014)
	Penicillium janthinillum (GXCR)	Cu, Pb, and Cd	Cai et al. (2016)
	Penicillium simplicissimum	Cd, Pb, Cu, Zn, and Cr	Xu et al. (2015), Mohammadian et al. (2017)
	Penicillium simplicissimum (iso 10, KP713758)	Al, Cr, Pb	Chen et al. (2017)
	Penicillium sp.	Ni, Cd, and Cr	Netpae et al. (2015), Butt et al. (2017), Costa and Tavares (2017)
	Phialophora malorum	Cu	Karunasekera et al. (2017)
	Phialophora mutabilis	Cu	Karunasekera et al. (2017)
	Saccharomyces cerevisiae	Cu	Sivakumar et al. (2017)
	Saccharomyces cerevisiae (transgenic strains)	Co, Mn, and Ni	Ruta et al. (2017)
	Simplicillium chinense	Al, Cr, and Pb	Chen et al. (2017)
	Trichoderma asperellum	Cd	Mohsenzadeh 2014
		Al, Cr, and Pb	Chen et al. (2017)

Table 2 (continued)

Class of fungi	Name of the fungi	Name of the pollutants	References
	Trichoderma asperellum (iso 11, KP792512)		
	Trichoderma asperellum PTN7	Cr	Chang et al. (2016)
	Trichoderma ghanense	Cd, Cu, Pb, As, and Fe	Oladipo et al. (2017)
	Trichoderma harzianum	Cd, Pb, Cu, Zn Ni, Fe	Mohsenzadeh (2014), Adebiyi (2017), Cecchi et al. (2017), Mohammadian et al. (2017)
	Trichoderma koningiopsis	Cu	Salvadori et al. (2014)
	Trichoderma logibrachiatum	Pb	Devi et al. (2017)
	Trichoderma sp.	Cd	Bazrafshan et al. (2015)
	Trichoderma tomentosum	Cd	Mohsenzadeh 2014
	Trichoderma viride	Cr and Pb	Sugasini and Rajagopal (2015), Migahed et al. (2017)
	Wickerhamomyces anomalus M10	Cr	Irazusta et al. (2018)
Basidimycetes	*Antrodia xantha Shiga-1F*	Cu	Hattori et al. (2015)
	Auricularia polytricha	Cu, Zn, and Hg	Yang et al. (2014), Li et al. (2018a, b, c)
	Cantharellus cibarius Fr.	Cd	Drewnowska et al. (2017)
	Coriolopsis sp. (1c3 KM403574)	Al, Cr, Pb	Chen et al. (2017)
	Fomitopsis cf. meliae	Zn, Cu, and Pb	Kaewdoung et al. (2016)
	Fomitopsis meliae	Cd, Cu, Pb, and Fe	Oladipo et al. (2017)
	Fomitopsis palustris TYP-0507	Cu	Hattori et al. (2015)
	Ganoderma aff. Steyaertanum	Zn, Cu, Cd, and Pb	Kaewdoung et al. (2016)
	Phanerochaete chrysosporium	Cd, Cr, Zn, Pb, Cu, and Ni	Sepehr et al. (2014), Chen et al. (2015), Zuo et al. (2015), Huang et al. (2017a, b), Zhang et al. (2018a)
	Pleurotus eryngii	Cu, Zn, and Hg	Li et al. (2018a, b, c)
	Pleurotus florida	Cu	Packiyam and Ragunathan et al. (2014)
	Pleurotus ostreatus	Cu, Zn, Hg, and CdS	Borovaya et al. (2015), Li et al. (2018a, b, c)
	Pleurotus ostreatus HAU-2	Cd and Cr	Li et al. (2017)
Deuteromycetes	*Alternaria sp.*	Ni and Cd	Netpae et al. (2015), Costa and Tavares (2017)
Zygomycetes	*Mucor*	Cr	Sakthivel et al. (2016)
	Mucor indicus	Pb	Samadi et al. (2017)
	Rhizomucor pusillus	Pb, Cr, and Cd	Qayyum et al. (2016)
	Rhizophagus irregularis	Cd	Yao et al. (2013), Huang et al. (2018)
	Rhizopus arrhizus UCP 402	Cd	Freitas et al. (2015)
	Rhizopus microspores	Cd, Cu, As, and Fe	Oladipo et al. (2017)
	Rhizopus oryzae	Zn and Cu	Tahir et al. (2017)

2015; Kariuki et al. 2017; Li et al. 2018a, b, c; Xu et al. 2015; Zang et al. 2017). In the field of bioremediation, fungi have great potential for their application in HM remediation. In the ecosystem, fungi are already working as decomposers with a huge number of enzymatic activity which specify them for remediation of HMs and other pollutants.

Fungi and their process of application

HM pollution is a serious problem of the environment to be a concern. The issues of HM pollution in water are an important concern due to their harmful impact on human health as well as the environment. The researcher reported a diverse group of fungi for the reduction of HMs from wastewater in which *Aspergillus*, *Trichoderma*, *Fusarium*, *Penicllium* species have the potential to remediate many HM-contaminated wastewater (Chen et al. 2017; Dey et al. 2016; Dhami et al. 2017; Mohsenzadeh 2014; Pundir et al. 2018; Sharma and Pathak 2017; Xie et al. 2014; Kumar and Dwivedi 2021). In remediation of HMs, fungi have been used in two ways: (a) in growing form and (b) in dead biomass form. In growing/viable form, the fungus should have a tolerance ability towards pollutants (HMs) because HMs may be toxic in nature and can inhibit the growth of the fungi, while in the case of dead or dried biomass form, the heavy metal removal is basically driven by surface functional groups of biomass, so there is no need for tolerance characteristics of fungus. In fact, there is the importance of adsorption characteristics of fungus biomass for a particular pollutant that has been selected to be removed from contaminated water. An overview of the remediation of HMs by fungi from wastewater is shown in Fig. 1.

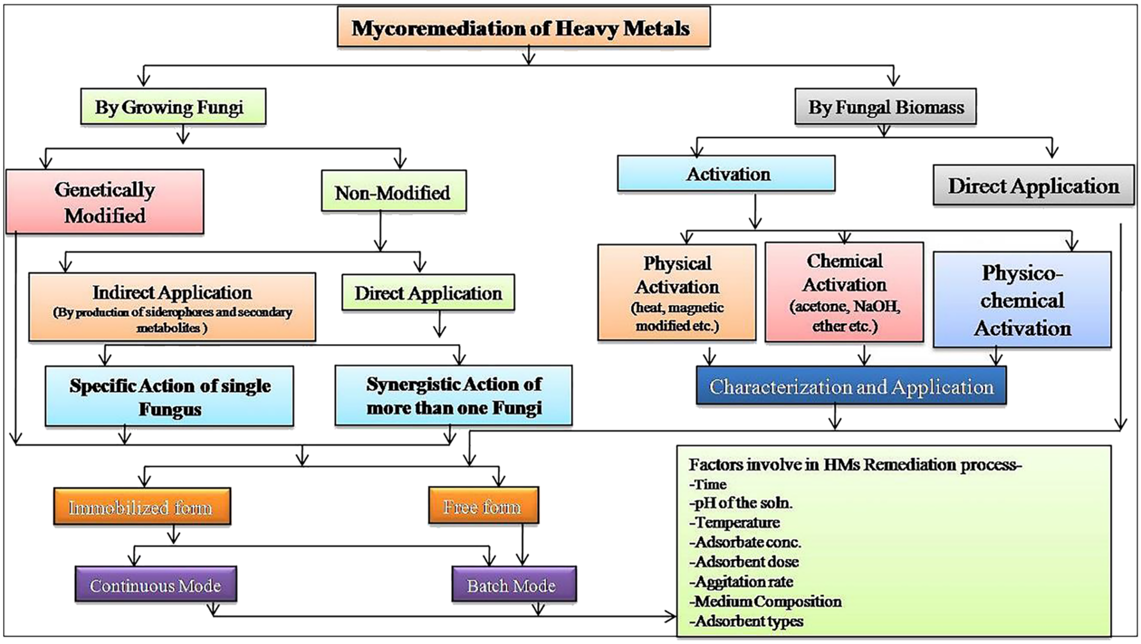

Fig. 1 Techniques in removal of heavy metal by growing fungi and fungal biomass from wastewater

Growing form of fungi

Fungi application in growing form is an important method which is based on the tolerance and metabolic rate of selected fungi against a particular pollutant. The benefit of growing fungus utilization in wastewater is that it has the self-replenishment ability which specified its use in continuous condition. Fungal tolerance towards HMs may be because of bioaccumulation or biotransformation (biosynthesis or bioreduction) or surface adsorption, etc. In the growing form, fungi are applied by their immobilization on any supporting medium (later discussed in "Effluent treatment process development") for application in continuous mode (Sathvika et al. 2015; Sriharsha et al. 2017) or their direct implementation with contaminant solution in batch mode (Chang et al. 2016; Li et al. 2018a, b, c; Oladipo et al. 2017). Some fungal species such as *Aspergillus niger* have the capacity to remove different types of HMs such as lead, Pb; cadmium, Cd; nickel, Ni; chromium, Cr; copper, Cu; cobalt, Co; zinc, Zn; and manganese; Mn (Fomina et al. 2017; Iram and Sumera 2015; Holda and Mlynarczykowska 2016; Mirazimi et al. 2015; Mondal et al. 2017; Olubunmi and Bernard 2016; Sakthivel et al. 2016; Sriharsha et al. 2017; Tahir et al. 2017). *Trichoderma harzianum* and *Trichoderma viride* showed tolerance against Cd, Pb, Cu, Zn Ni, and Fe and reported as multi-metal-adsorptive fungi (Joshi et al. 2011; Mohsenzadeh 2014; Migahed et al. 2017; Sugasini and Rajagopal 2015; Wang et al. 2013). A number of fungal species have been reported to remove HMs from the aqueous system and some of them are listed in Table 3 which has been used in the growing form in batch mode and some of them in continuous mode too.

Fungal biomass form

Fungal biomass basically represents the dead and dried biomass of the fungi. In this case, HM removal is mainly driven by the adsorption mechanism which depends on the functional groups available on the cell surface of the applied fungal biomass. Surface functional group availability varies with the molecular composition of adsorbent (fungal biomass) and its surface area. However, the physicochemical modification of biomass enhanced the adsorption potential of pollutants. There are two types of techniques used to enhance the adsorption properties of biomass: physical and chemical treatment.

Physical treatment Physical modification is basically done to create uniqueness (such as increase the surface area) in fungal biomass such as heat treatment which generally applies to remove the moisture from the adsorbent. But, sometimes, it is helpful in the reduction of the anti-adsorptive functional group and also helpful to expose some adsorptive functional groups (active sites). Heat or thermal activation of biomass since ancient times such as biochar preparation. Conversion of fungal biomass into a micro/nanoscale adsorbent is the emerging research field which is attributed to fast-growing fungi, because the fast-growing fungi can be easily cultivated for the large-scale production of biomass. The micro/nanoconversion of fungal biomass increases the surface area which is directly associated with an increase in the availability of active sites. Inthorn et al. (2014) reported magnetically modified biogenic manganese oxides (MMBMOs) by *Acremonium strictum* strain

Table 3 Fungal species and their heavy metal removal capacity from different type of medium and their affecting factors

S.N.	Name of the fungi	Name of the pollutant	Removed amount	Applied medium	Initial concentration of pollutant	pH of the medium	Incubation temperature	Duration of experiment	Agitation rate	Reference
1	*Aspergillus flavus*	Cu (II)	97%	Aqueous solutions	–	9	–	20 h	150 rpm	Iram and Sumera (2015)
		Pb(II)	99%	Yeast peptone glucose medium	–	–	25 °C	7 days	Two-step process, 150 rpm	Qayyum et al. (2016)
		Fe	94%	Fe-treated PDB medium	1000 mg/L	–	room temperature	14 days	–	Bano et al. (2018)
		Mn	91%	Mn-treated PDB medium	1000 mg/L	–	room temperature	14 days	–	Bano et al. (2018)
2	*Aspergillus flavus strain KRP1*	Hg	97.50%	–	10 mg/L	5.7	30 °C	7 days	130 rpm	Kurniati et al. (2014)
3	*Aspergillus foetidus*	Cd	79%	Liquid medium	100 mM	5	32 ± 1 °C	24 h	175 rpm	Chakraborty et al. (2014)
4	*Aspergillus niger*	Pb(II)	23%	Liquid medium	250 Mm	–	28 °C	24 h	120 rpm	(Chakraborty et al. 2014)
5	*Beauveria bassiana*	Cr(VI)	61.10%	Cr-treated composite media	30 mg/L	6.5–7.0	30 °C	5 days	150 rpm	Gola et al. (2016)
		Cd(II)	63.40%	Cd-treated composite media	30 mg/L	6.5–7.0	30 °C	5 days	150 rpm	Gola et al. (2016)
		Zn(II)	67.80%	Zn-treated composite media	30 mg/L	6.5–7.0	30 °C	5 days	150 rpm	Gola et al. (2016)
6	Indigenous fungal isolates (Mangalore, India)	Pb(II)	92.73%	Pb-treated dextrose peptone medium	–	6	28–30 °C	96 h	150 rpm	Gururajan et al. (2018)
7	*Mucor indicus*	Pb(II)	97–99%	Lead-treated sugar soln.	300 mg/L	–	–	24 h	–	Samadi et al. (2017)
8	*Penicillium simplicissimum*	Cu	230 mmol/kg	Cu-treated PDB medium	–	–	28 ± 1 °C	4 days	–	Mohammadian et al. (2017)
9	*Penicillium sp.*	Cd	140 mg/g	Aqueous solutions	100 mg/L	–	37 °C	–	150 rpm	Costa and Tavares (2017)
10	*Phanerochaete chrysosporium*	Pb(II)	91.30%	Aqueous medium	50 mg/L	–		168 h	–	Huang et al. 2017a, b
11	*Rhizomucur pusillus*	Cd	77%	Yeast peptone glucose medium	–	–	25 °C	7 days	two-step process, 150 rpm	Qayyum et al. (2016)
12	*Simplicillium chinense (KX425621)*	Pb(II)	80.60%	Aqueous solutions	100 mg/L	5 ± 0.2	25 ± 2 °C	7 days	150 rpm	Chen et al. (2017)
13	*Sterigmatomyces halophilus*	Cd	91%	Cd-treated PDB medium	1000 mg/L	–	Room temperature	14 days	–	Bano et al. (2018)
14	*Trichoderma asperellum*	Cd	91.06%	Aqueous solutions	100 mg/L	9	Room temperature	2 months	–	Mohsenzadeh 2014
15	*Trichoderma asperellum (KP792512)*	Pb(II)	57.10%	Aqueous solutions	100 mg/L	5 ± 0.2	25 ± 2 °C	7 days	150 rpm	Chen et al. (2017)

KR21-2 as an adsorbent in the removal of Cd^{2+}, Cu^{2+}, Ni^{2+}, and Co^{2+} which revealed a new field in biomass treatment.

Chemical treatment Chemical techniques are generally used to enhance the active sites and their uniform distribution on the surface of the adsorbent which is responsible for the adsorption of HMs. In the case of plant biomass, the researchers have used many types of chemicals (such as zero-valent iron) to enhance the adsorptive properties, while for fungal biomass activation workers have reported the use of some chemicals such as NaOH, HCl, acetone, ether, etc. to enhance the adsorptive properties of fungal biomass (Zang et al. 2017).

Generally, fast-growing fungi are used for adsorption of HMs because biomass cultivation is easy in the case of fast-growing fungi. *Pleurotus ostreatus* (Vaseem et al. 2017), *Pleurotus eryngii* (Kan et al. 2015; Amin et al. 2016a, b), *Aspergillus niger* (Hajahmadi et al. 2015; Holda et al. 2015), and *Agaricus* sp. (Ertugay and Bayhan 2010) are well known as fast-growing fungal species which have been applied in the dead form as an efficient adsorbent. Many fungal species have been used in the dead form which are listed in Table 4. Sometimes, fungal biomass is also applied after treatment with some chemicals to increase active sites on its surface. Zang et al. (2017) boiled *Auricularia auricular* biomass in 0.5 N NaOH solution, then applied in adsorption of Cr(VI) and reported incremental change in adsorption of Cr(VI).

Fungal biomass has a high potential to remove HMs from wastewater, however, their adsorption varies with types of pollutants, medium pH, pollutant's concentration, and agitation rate that are discussed in "Factors affecting removal of heavy metal." Another most important thing is the characteristics of biomass, basically surface functional groups that primarily affect the adsorption of HMs, which have been discussed in "Fungal cell wall and its role in metal sorption." In the HM adsorption investigation, many types of kinetic and isotherm models have been used to describe the effect of time on adsorption and HM interaction with the applied adsorbent. The most fitted kinetic model in adsorption of HMs by fungal biomass is the pseudo-second-order kinetic model (Hassan et al. 2018; Rashid et al. 2016); however, some studies also found that the pseudo-first-order kinetic model is best fitted in

Table 4 Fungal species used in dead and powdered form as HMs adsorbent from aqueous system

S. N.	Name of the fungi	HM pollutants	References
1	*Acremonium strictum* strain KR21-2 (magnetically modified biogenic manganese oxides)	Cd(II), Cd(II), Ni(II), and Co(II)	Inthorn et al. (2014)
2	*Agaricus bisporus*	Cu (II)	Ertugay and Bayhan 2010
3	*Artist's Bracket*	Cr	Pourkarim et al. (2017)
4	*Aspergillus nidulans*	Cd	Nascimento et al. (2015)
5	*Aspergillus niger*	Cr (VI), Zn(II), Co(II) and Cd(II)	Hajahmadi et al. (2015), Holda et al. (2015)
6	*Auricularia auricular*	Cr (VI)	Zang et al. (2017)
7	*Cladosporium resinae*	Cr(VI)	Ahluwalia and Goyal (2010)
8	*Fusarium equiseti* KR706303	Pb (II) and Cu (II)	Akinkunmi et al. (2016)
9	*Fusarium* spp.	Zn (II)	Velmurugan et al. (2010)
10	*Hypocrea lixii*	Ni (II)	Salvadori et al. (2015)
11	*Lepiota hystrix*	Pb (II) and Cu (II)	Kariuki et al. (2017)
12	*Paecilomyces variotii*	Cr(VI)	Ahluwalia and Goyal (2010)
13	*Pencillium fellutinum*	Ni and Zn	Rashid et al. (2016)
14	*Penicillium citrinum* KR706304	Pb (II) and Cu (II)	Akinkunmi et al. (2016)
15	*Phanerochaete chrysosporium*	Cr(VI)	Ahluwalia and Goyal (2010)
16	*Pleurotus eryngii*	Cu(II), Hg (II)	Kan et al. (2015), Amin et al. 2016a, b
17	*Pleurotus ostreatus*	Mn (II), Zn(II), Ni(II), Cu(II), Co(II), Cr(II), Fe(II)	Javaid et al. (2010), Vaseem et al. (2017)
18	*Schizophyllum commune*	Cu(II), Ni(II), Zn(II) and Cr(VI)	Javaid et al. (2010)
19	*Termitomyces clypeatus*	Cr (VI)	Ramrakhiani et al. (2011)
20	*Trametes versicolor*	Pb(II) and Cd(II)	Subbaiah et al. (2011)
21	*Trichoderma reesei*	Co (II), Cu(II), Ni(II), Pb (II) and Zn (II)	Ghaedi et al. (2013)

Table 5 HM adsorption efficiency of some fungal bioadsorbent and plant-originated biochar

Name of the adsorbent	Name of the pollutant	Metal concentration	pH	Temperature	Dose of adsorbent	Contact time	Removal	Fitted kinetic model	Isotherm model	Reference
Fungi used as bioadsorbent										
Pleurotus eryngii	Hg(II)	1 mg/L	7	30 °C	0.35 g	30 min	77.40%	Pseudo-second order	Freundlich model	Amin et al. 2016a, b
Neopestalotiopsis sp ASU1	Cd(II)	200 mg/L	7	30 °C	50 mg	30 min	185.3 mg/g	Pseudo-second-order	Langmuir model	Hassan et al. (2018)
Neopestalotiopsis sp ASU1	Zn (II)	200 mg/L	6	30 °C	50 mg	30 min	153.8 mg/g	Pseudo-second-order	Langmuir model	Hassan et al. (2018)
Pencillium fellutinum biomass immobilzed with Na-bentonite	Ni(II)	100 mg/L	6	30 °C	0.05 g	60 min	76 mg/g	Pseudo-second-order	Langmuir model	Rashid et al. (2016)
Pencillium fellutinum biomass immobilzed with Na-bentonite	Zn (II)	100 mg/L	5	30 °C	0.05 g	60 min	56 mg/g	Pseudo-second-order	Langmuir model	Rashid et al. (2016)
Aspergillus niger strain SF-6095	Cr(VI)	200 mg/L	2	Room temperature	1 g/L	300 min	98.25%	–	Langmuir Model	Manorama et al. (2016a, b)
Aspergillus awamori	Ni (II)	55 mg/L	6	25 °C	0.25 g/ 100 mL	3 h	7.5 mg/L	–	Redlich–Peterson	Shahverdi et al. (2016)
Aspergillus terreus	Cd(II)	20 mg/L	7	25 °C	1 g	90 min	94%	Pseudo-first-order	Freundlich isotherm	Shokoohi et al. 2020
Aspergillus terreus	Cr(VI)	20 mg/L	7	25 °C	1 g	90 min	89%	Pseudo-first-order	Freundlich isotherm	Shokoohi et al. 2020
Penicillium sp. M RF1	Ni(II)	639 mg/L	5.5	30 °C	7.5 g/L	140 min	74.60%	–	Freundlich isotherm model	Sundararaju et al. (2020)
Plant biomass originated biochar										
Artemisia argyi (AS600)	Cu(II)	50 mg/L	–	–	0.1 g/50 mL	45	18 mg/g	Pseudo-second-order	Langmuir model	Song et al. (2019)
Artemisia argyi (AS600)	Cr(VI)	50 mg/L	–	–	0.1 g/50 mL	45	15 mg/g	Pseudo-second-order	Freundlich isotherm	Song et al. (2019)
Tobacco petiole pyrolytic biochar (TPBC300)	Cr(VI)	250 mg/L	1	Ambient temperature	2.5 g/L	540 min	99.02%	Pseudo-second-order	Temkin model	Zhang et al. (2018a, b)
Rice husk biochar (RH700)	Pb	1 mM	6	–	0.1 g/20 mL	48 h	26.7 mg/g	Pseudo-second-order	Freundlich isotherm	Shi et al. (2018)
Date seed-derived biochar	Pb	0.50 mM	6	23 ± 2 °C	0.10 g/10 mL	24 h	0.045 mM/g	Pseudo-second-order	Langmuir and Freundlich	Mahdi et al. (2018)

HM adsorption to explain adsorption rate (Shokoohi et al. 2020) (Table 5).

To examine the relationship between the adsorption and equilibrium concentration, various sorption isotherm models are widely employed for fitting the data. These models basically determine the adsorption behavior of adsorbate (pollutant) on adsorbent (fungal biomass). The most fitted isotherm model in adsorption is the Langmuir and Freundlich isotherm model that describes the adsorption of HMs on fungal biomass (Amin et al. 2016; Hassan et al. 2018; Manorama et al. 2016). The Langmuir isotherm theory assumes monolayer adsorption of HMs over a homogeneous biosorbent surface. It supports the single-layer biosorption theory based on the assumption that all the biosorption sites have equal affinity for adsorbate molecules and there is no transmigration of adsorbate on the surface, while the Freundlich isotherm is an empirical isotherm employed to describe the heterogeneity of the system and support the multilayer adsorption of adsorbate on the surface of the adsorbent. Hassan et al. (2018) used *Neopestalotiopsis* sp ASU1 biomass for the biosorption of Cd(II) and Zn(II) and they found that the Langmuir isotherm model is best fitted in the Cd(II) and Zn(II) biosorption. While, the Freundlich isotherm model is well fitted in the biosorption of Hg(II) on the surface of *Pleurotus eryngii* (Amin et al. 2016). Some studies are listed in Table 5 which show that the Langmuir and Freundlich isotherm model is the most fitted and can be used to describe the HM biosorption onto the fungal biomass.

In recent days, plant biomass–originated biochar has also attracted the researcher and has been broadly investigated its application in HMs biosorption. Studies showed it as an efficient biosorbent for HMs removal. Biosorption is basically varied with the characteristic of the biosorbent and the nature of the pollutants, but the preparation cost of biochar may affect its use in the treatment of contaminated water. Because, studies have suggested that biochar prepared at high temperature (above 400 °C) are efficient in the biosorption of HMs (Shi et al. 2018). However, fungi can be cultivated on low graded waste materials (agro-waste) that enhance its applicability in the treatment of wastewater, and thus, water treatment costs can be reduced.

Another basic problem that is associated with the use of biochar, as well as fungal biomass, is its treatment and disposal after its final application in wastewater treatment which needs high cost. To remove this disadvantage, the researchers applied the reuse approach for these adsorbents where it can be washed with low-pH (< 4) or high-pH (> 8) washing solution to desorb the adsorbed HMs from the surface of the adsorbent and can be reused (Rashid et al. 2016). But, after a few cycles, the adsorption efficiency of the adsorbent gets reduced. On the other hand, used washing solution is corrosive and its direct disposal can cause a harmful impact on the environment. As an alternative to these disadvantages, different techniques have been developed and can be applied including the production of composite material and production of construction bricks, etc. (Isaza-Pérez et al. 2020).

Application of growing form of fungi

HM removal by single fungal species

Most of the studies in the field of bioremediation have been applied as a single bioremediation agent for the study. This approach is more basic and easy to optimize than the other influencing parameters. Similarly, in mycoremediation, one fungus has been used for the removal of one HM (Table 3) or more than one HM in most of the studies (Xu et al. 2015; Desai et al. 2016; Chen et al. 2017; Qian et al. 2017). It is found in the literature that most studies focus on only a single heavy metal for removal because all the fungal species are unable to tolerate all types of HMs, and due to metal toxicity, the growth of the fungus is severely inhibited at very less concentration of some HMs. Several studies targeted the binary metal solution for removal by tolerant fungus and some recent studies also targeted multiple metal–contaminated aqueous solution or wastewater for removal of multiple HMs with a single fungal isolate (Bano et al. 2018; Gola et al. 2016). But, it is to be remembered that very few isolates have been reported that have the potential to remove more than two HMs. So, this field needs to explore industrial effluent treatment due to the fact that industrial effluent contains multiple HMs. *Aspergillus flavus*, *A. gracilis* (Bano et al. 2018), *Beauveria bassiana* (Gola et al. 2016), *Aspergillus lentulus* (Mishra and Malik 2012) are the species that have the potential to remove multiple HMs from wastewater.

It is right that all types of fungal species are unable to tolerate more than one metal but possess many types of metabolic activities and are the major sources of the enzyme that is able to degrade many types of organic pollutants. The industrial, developmental, and agricultural activities produce not only heavy metal but also a number of organic pollutants that have a serious environmental concern. These pollutants may be dyes, phenolic products, pesticides, polyaromatic hydrocarbon, etc. In recent years, it attracted the researcher for simultaneous removal/biotransformation of HM and degradation of organic contaminants. This field of study is very emerging that offers a big gap for the study. Gola et al. (2018) investigated the applicability of *Beauveria bassiana* for the removal of dyes (reactive remazol red, Yellow 3RS, indanthrene blue, and Vatnovatic gray) and HMs (Cr(VI), Zn(II), Cu(II), Cd(II), Pb(II), and Ni(II)) from mix solution and a significant amount of removal was reported. *Acremonium* sp. P0997 showed efficient removal potential for polyaromatic hydrocarbon (naphthalene, fluorene, phenanthrene, anthracene, and fluoranthene present alone) and also has a high resistance to HMs (Mn^{2+}, Fe^{2+}, Zn^{2+}, Cu^{2+}, Al^{3+}, and Pb^{2+}) (Ma et al. 2014).

Synergistic application of two or more microbes

Synergistic microbial utilization is a novel approach in HMs remediation where two microbes are used with their synergistic action in HM removal. But here compatibility test is needed for both microbes with each other because microbe generally produces many types of metabolites in normal as well as in stressed conditions. So, these metabolites may have negative consequences on the synergist microbes, can inhibit the growth of synergists, and affect the HMs removal potential of the implemented system. Therefore, the compatibility test is an important step in this method and by this test, we can verify the survivability of both microbes with each other in normal or stress conditions. There can be made a pair of fungus-fungus or fungus-bacteria. The synergistic mechanism is also played by large plants with their rhizospheric fungi and other microbes which increases the HM tolerance capacity of plants (Xie et al. 2014; Yao et al. 2013). Some researchers worked on the synergistic action of a fungus with other fungi and bacterial species in HM remediation (Herath et al. 2014; Huang et al. 2018; Migahed et al. 2017; Olubunmi and Bernard 2016). The fungal consortium is the best example of the synergistic action of fungi that has more efficiency to remove HM from wastewater.

Heavy metal tolerance and removal mechanism in fungi

Fungal cell wall and its role in metal sorption

Heavy metal is frequently found in the polluted environment. HMs present in a polluted environment first interact with the cell surface of the organism. The fungal cell surface is different from the other organisms. So, to understand the interaction of the cell surface of the fungi with HMs and its possible role in adsorption and accumulation of metal, the structure of the cell wall of the fungi and its composition should be known. It is found with the electron microscopic investigation of the negatively stained cell wall of the fungi that the thickness of the electron-transparent internal layer is about 70–100 nm. However, the thickness of the cell wall may vary with fungal growth conditions and their genetic status, and an electron-dense outer layer (Osumi 1998). The brewing yeast may be composed of 200 nm of the electron-transparent inner layer. The inner layer maintained the mechanical strength of the wall, which is made up of chitin and β1, 3-glucan. It carries about 50–60% weight of the total dry weight of the cell wall (Moukadiri et al. 1999; Kang et al. 2018). The carbohydrate of the cell surface contains multiple phosphodiester bridges by their side chains resulting in abundant negative charges on the surface of the cell at physiological pH values (Jigami and Odani 1999). The negatively charged cell wall surface plays a crucial role in the adsorption of positively charged metal ion via electrostatic attraction (Kumar and Dwivedi 2019a). The heavily glycosylated mannoproteins of the outer layer of the cell wall (Cappellaro et al. 1994; Kang et al. 2018) is implicated in other cell-cell recognition mechanisms (Reynolds and Fink 2001) and also restricts the accessibility of plasma membrane and internal part of the cell to foreign compounds (enzymes, protein, and pollutants) (Cappellaro et al. 1994). Polysaccharides and β 1, 3-glucon generate an alkaline-sensitive linkage in the cell wall which supports fungal growth in an acidic medium (Moukadiri et al. 1999). These side chains also provide hydrophilic properties to the cell wall which may be useful to retain water on the fungal cell surface and provide resistance to drought conditions. About a one-third part of the wall (dry weight) is accounted for by the outer protein layer. The carbohydrate fraction of well-glycosylated mannoproteins of the outer cell wall layer frequently accounts for over 90% (w/w). The proteins of the cell wall are covalently linked to β 1, 3-glucan-chitin network either directly or indirectly via a β 1, 6-glucan moiety. Furthermore, some of the proteins are also disulfide-bonded to other proteins of the cell wall (Moukadiri et al. 1999; Kang et al. 2018) that may also provide active sites for metal sorption via metal-thiol group complexation (Kumar and Dwivedi 2019a). The numerous negative charges are on the cell surface of yeast due to phosphodiester bridges in both N- and O-linked mannosyl side chains (Jigami and Odani 1999) which are also helpful in metal binding via electrostatic attraction. It can be concluded that the fungal cell wall is mostly made up of protein, polysaccharides, polyphosphates, polypeptide, lipid, chitin, inorganic ions, etc. (Ayangbenro and Babalola 2017; Kang et al. 2018) which contain a number of functional groups such as –COOH, –OH, $–NH_2$, =NH, –SH, $–O–CH_3$, etc. These functional groups are also detected at different spectra with FTIR analysis and with some other techniques on dead fungal biomass (Sathvika et al. 2015; Kumar and Dwivedi 2019a, b; Kumar et al. 2019) which is mainly responsible for the adsorption of HMs on the surface of fungal cell.

Bioadsorption is basically a surface phenomenon that occurred on the surface of biomass. In the case of fungi, it can also be pronounced as mycoadsorption. Mondal et al. (2017) reported that IR (infrared) bands 3265 cm^{-1} (alcoholic –OH stretching), 1618 cm^{-1} (carboxylic acid(–COOH), and 1417 cm^{-1} (–C–H and –N–H stretching) of unloaded *Aspergillus niger* are shifted to 3280 cm^{-1} (–

OH and –NH stretching), 1614 cm^{-1} and 1361 cm^{-1} after adsorption of Cr(VI). They concluded that the –OH and –N–H groups are mostly accountable for the decontamination of Cr(VI). Lopez-Fernandez et al. (2018) reported a new band of 938 cm^{-1} in adsorption of U(VI) which shifted from 917 cm^{-1} (Romero-Gonzalez et al. 2016) represents the stretching of U=O associated with the accumulation of UO_2^{2+} on the surface fungal cell wall. The role of oxalic acid is signified by the IR spectrum at 2495 ± 5, 1700 ± 5, 1201 ± 5, 1261 ± 5, and 1126 ± 5 cm^{-1} and thiol groups (–SH) at 2561 ± 5 cm^{-1} respectively in the biosynthesis of PbS by *Aspergillus terreus* (Jacob et al. 2016) (Table 6). The decrease in the intensities of the IR spectrum ranges from 1650 to 1450 cm^{-1} and 1230 to 1030 cm^{-1} are recognized after adsorption of Cd(II) in *Thamnidium elegans* cells embedded in an acrylic network of p(3-methoxyprophyl) acrylamide p(MPA) enriched with 2-Akrylamido-2-methyl-1-propane sulfonic acid (AMPS). Copper ion adsorption with the amine, carboxyl, and phosphate groups was reported by Majumdar et al. (2008) (Table 6). Majumder et al. (2017) reported that C–O groups oxidized into C=O under Cr(VI) and also found the involvement of phosphate and sulfonyl groups in the coordination of chromate ions. They also found the shift in the peak from 1029 to 1033 cm^{-1} and 531 to 576 cm^{-1} which represented the formation of Cr(III)-phosphate compound and formation of $Cr(OH)_3$. Mohanty et al. (2016) reported that the IR band of 476.33 cm^{-1} and 417.51 cm^{-1} attributed to MnO_x stretching, bending, and wagging vibrations for Mn_2O_3 and MnO_2 respectively in the Mn-treated *Aspergillus oryzae* biomass.

Reactive oxygen species production and heavy metal

All living organisms showed many types of responses (morphological, physiological, and molecular) in stress conditions and also under HM stress condition due to its toxic characteristic. ROS production under HM stress is a more frequently reported phenomenon in plants and other living organisms (Singh et al. 2016). This phenomenon is also reported in fungi such as *A. flavus* CR500, *Fusarium solani*, *Trichderma lixii* CR700, *Penicillium janthinellum*, and *Pleurotus ostreatus* HAU-2 in the presence of Cr(VI), Cd, and Pb (Li et al. 2017; Kumar and Dwivedi 2019a, b; Kumar et al. 2019; Rafi et al. 2017; Teng et al. 2017). In the higher plants, many pathways have been reported for ROS production such as chloroplast, mitochondria, peroxisome, etc. (Singh et al 2016). However, in fungi, the overreduction of the electron transport chain in mitochondria might be a possible site for ROS production (Keunen et al. 2011). The well-known mechanism Haber-Weiss and Fenton reactions may also be involved in the production of ROS via reacting with redox-active heavy metals (Halliwell 2006; Keunen et al. 2011), although ROS production is a common phenomenon and its alleviation depends upon its production and consumption. Toxic HMs possibly accelerate the production of ROS in comparison with its consumption in fungi and also in other organisms such Cr(VI) increases the production of ROS in *T. lixii* CR700 and *A. flavus* CR500 (Kumar and Dwivedi 2019a, b). The hydroxyl ($OH^{\bullet}$), superoxide radical ($O_2^{\bullet-}$), singlet oxygen (O), and hydrogen peroxide (H_2O_2) are collectively called reactive oxygen species due to their high reactivity. Out of the four, the hydroxyl radical is the most reactive and highly damaging one (Singh et al. 2016). The ROS have positive and negative consequences for all types of organisms. ROS are unstable and very reactive and can react with proteins, membrane lipids, peptides, and macromolecules and oxidize them, causing many types of negative consequences or oxidative injuries and sometimes causing cell death (Sharma and Dietz 2009; Hossain et al. 2012). Collectively, negative consequences are called oxidative stress (Kumar and Dwivedi 2019a,b, Singh et al. 2016). Conversely, ROS has been also seen as a signaling molecule and reported as a regulator of several biomolecules. In HM stress conditions, ROS may work as signaling molecules for the production of glutathione, metallothionein, phytochelatins, and other thiolic compounds that work as metal-chelating agents and transport them into vacuoles or outside of the cell through an efflux pump (Kumar et al. 2019; Chen et al. 2019; Singh et al. 2016; Kumar and Dwivedi 2019a, b; Banerjee et al. 2019). A complex mechanism of metal tolerance, response, transportation, and accumulation in fungi are shown in Fig. 3.

Fungal response to oxidative stress and heavy metal

Enzymatic response to oxidative stress

The redox-active HMs highly induce the production of ROS in fungi, one of the major factors for damaging the cell constituents due to oxidative injuries. Fungi generally counter the oxidative stress by multiple antioxidant mechanisms. The antioxidant mechanisms are driven by many types of antioxidants (enzymatic and non-enzymatic) as the cellular immune system. The catalase (CAT), peroxidase (POD), and superoxide dismutase (SOD) are the major enzymatic antioxidants produced under HMs stress. *T. lixii* CR700 and *A. flavus* CR500 produce significantly CAT, POD, and SOD under Cr(VI) exposure to counter the ROS (Kumar and Dwivedi 2019a, b). *Pleurotus ostreatus* HAU-2 produces CAT, POD, and SOD under the presence of Pb stress (Li et al. 2017). They reduce/neutralize the ROS. SOD act with superoxide radical, while CAT reacts with H_2O_2 and catalyzes it into H_2O (Xu

Table 6 IR bands and observed functional group in HM-treated fungal biomass

Fungal biomass	IR band	Functional group stretching	Reference
Aspergillus niger	3265 cm^{-1}	Alcoholic –OH stretching	Mondal et al. (2017)
	1618 cm^{-1}	Carboxylic acid –COOH,	
	1417 cm^{-1}	–C–H, –N–H stretching	
	1031 cm^{-1}	amine –C–N stretching	
Rhodotorula mucilaginosa	1543 cm^{-1}	double bond of the carbonyl, C=O, group from amides	Lopez-Fernandez et al. (2018)
	1050 and 1150 and 1070-1150 cm^{-1}	C–O stretching	
	1390 cm^{-1}	Stretching of carboxylate anions (COO–)	
Mucorales fungi	3447 cm^{-1}	O–H stretching vibrations	Berger et al. (2018)
	2888 cm^{-1}	stretching vibrations of aliphatic C–H;	
	1657 cm^{-1}	carbonyl groups stretching of C=O	
	1555 cm^{-1}	N–H deformation in CONH plane, including amide	
	1381 cm^{-1}	CN bond stretching plus CH3 wagging	
	1086 cm^{-1}	C–O–C bonds	
Aspergillus terreus	2561 ± 5 cm^{-1}	Thiol group	Jacob et al. (2016)
	2495 ± 5, 1700 ± 5, 1261 ± 5, 1201 ± 5 and 1126 ± 5 cm^{-1}	involvement in biosynthesis of PbSe	
Aspergillus fumagatus	3383 cm^{-1}	Amide C=O	Kalyani et al. (2018)
	2361 cm^{-1}	O–H stretching acid	
	1723 cm^{-1}	C=O stretching of Aldehyde, Ketone, Ester	
	1581 cm^{-1}	C=C stretching Aromats	
	1389 cm^{-1}	C–O stretching	
	1112 cm^{-1}	C–C stretching of Ketones	
	616 cm^{-1}	C–Cl stretching Chloroalkanes	
Polyethylenimine-Modified *Penicillium chrysogenum* biomass	3200 to 3600 cm-1	overlapping of OH and NH stretching	Deng and Ting (2005)
	1115 cm^{-1}	alcoholic C–O stretching	
	1161 cm^{-1}	C–N stretching vibration	
	1663 cm^{-1}	CdO stretching in carboxyl or amide groups	
	1551 cm^{-1}	N-H bending	
	1740 cm^{-1}	–COO– stretching of ester	
Thamnidium elegans cells in acrylic network of p(3-Methoxyprophyl) acrylamide p(MPA) enriched with 2-Akrylamido-2-methyl 1-propane sulfonic acid (AMPS)	3442 and 3078 cm^{-1}	O–H and N–H stretching	Çelik et al. (2017)
	2932 cm^{-1}	C–H stretching vibrations of CH2 and CH3	
	1404 cm^{-1}	CH2 bending vibrations	
	1363 cm^{-1}	CH3 bending vibrations	
	1663 cm^{-1}	C=O stretching of acids and amides (amide I)	
	1555 cm 1 and 1458 cm^{-1}	N–H and C–N stretching of the amide II and III	
	1223 cm^{-1}	asymmetric stretching of C–O–C vibrations	
	1192 cm^{-1}	symmetric stretching of C–O–C vibrations	
	1042 cm^{-1}	S=O stretching vibration	
	627 and 528 cm^{-1}	C–N–C scissoring vibrations	
Hexadecyl-trimethylammonium bromide and dodecylamine treated *Penicillium chrysogenum* biomass	3423.8 cm^{-1}	NH2 asymmetric stretch mode of amines	Loukidou et al. (2003)
	2925.1 cm^{-1}	C–H groups stretching	
	1636.1 cm^{-1}	CO stretching mode, conjugated to a NH deformation mode (amide 1)	

Table 6 (continued)

Fungal biomass	IR band	Functional group stretching	Reference
	1559.7 cm^{-1}	NH deformation mode conjugated to C=N (amide 2)	
	1384.2 cm^{-1}	amide 3 or sulfamide band	
	1071 cm^{-1}	C–O stretching in carbonyl	
	1673 cm^{-1}	C=O stretching in carboxyl groups	
	1150 cm^{-1}	P=O stretching	
	1040–910 cm^{-1}	P–OH stretching	
	1050–970 cm^{-1}	P–O–C stretching	
Mucor rouxii	3398.3 cm^{-1}	N–H or O–H stretching vibrations	Majumdar et al. (2008)
	2920–2850 cm^{-1}	alkyl chains	
	1654.8 cm^{-1}	C=O stretching mode (amide 1)	
	1654.8 cm^{-1}	N–H bending (amide II)	
	1544.9 cm^{-1}	C–N stretching	
	1407.9 cm^{-1}	COO− of the carboxylate group	
	1078.1–995.2 cm^{-1}	phosphate group	
Arthrinium malaysianum	3422 cm^{-1}	–NH stretching in amides and O–H stretching vibration in alcohol and/or phenol	Majumder et al. (2017)
	2958 cm^{-1}	C–H stretching vibrations of –CH3	
	2927 cm^{-1}	C–H stretching vibrations of CH2	
	1404 cm^{-1}	C–N stretching	
	1239 cm^{-1}	C–H stretching in amide III and C–O stretching	
	1077 cm^{-1}	P–O–C and P–OH stretching	
Aspergillus oryzae	1089.58 cm^{-1}	C–N stretching of Aliphatic amines	Mohanty et al. (2016)
	775.24 cm^{-1}	N-H wag of Primary and Secondary amines	
	688.46 cm^{-1}	C=C stretch of alkynes	
	540.94, 464.76 cm^{-1}	CH2 vibrations of Polysaccharides	
	1377.89 cm^{-1}	C–O stretching of Alcohols, Carboxylic acid, esters, ethers	
	1249.65 cm^{-1}	C–N stretching of Aliphatic amines	
Termitomyces clypeatus	1299.79 cm^{-1}	P=O bands of polysaccharides	Ramrakhiani et al. (2011)
	1078.01 cm^{-1}	C–O bands of polysaccharides	
	1500 to 1650 cm^{-1}	primary, secondary and tertiary amines and ammonium salts of carboxylic acid	
	1403.92 cm^{-1}	sulfonyl, sulfonamide	

et al. 2012; Li et al. 2017; Karigar and Rao 2011; Irazusta et at. 2016 2018). Bannister et al. (1987) classified the SOD into two families based on their evolutionary homology and metal-binding cofactor at the active sites: copper- or zinc-containing SOD (Cu/ZnSOD) and manganese- or iron-containing SOD (Mn/FeSOD). Cu/ZnSOD and MnSOD are induced in the response of ROS toxicity. Jacob et al. (2004) reported that SOD activity increases with an increase in the incubation period in cadmium-treated ectomycorrhizal fungus *Paxillus involutus* which is essential in detoxification mechanisms of ROS. Teng et al. (2017) found a significant increase in activity of SOD, CAT, POD, glutathione reductase (GR), and glutathione-S-transferase (GST) and level of GSH and GSSG in *Penicillium janthinellum* BC109-2 under Zn stress. The increase in the activity of CAT, POD, SOD, POX, and PAL was also reported in *Trichoderma lixii* CR700, *A. flavus* CR500, and *Fusarium solani* (Kumar and Dwivedi 2019a, b; Kumar et al. 2019). The extracellular activity of glucose oxidase (GOD) was reported in bioleaching of Cd, Cu, Pb, Zn, Mn, and Cr (Deng et al. 2013). Extracellular GOD activity influences the excretion of metabolites by HMs (Ren et al. 2009). Bbakr1, a member of the aldo-keto reductase (AKR) family, homologous to 2,5-diketo-D-gluconic acid reductase, is involved in the development of *Beauveria bassiana* against Cr stress (Wang et al. 2018).

Non-enzymatic response to oxidative stress

Uptake of essential and non-essential metals is a well-known mechanism in the removal of HMs. The essential characteristic of live fungi in the removal of HMs is its tolerance and accumulation of a particular metal (Rehman et al. 2010). The tolerance of the fungi is maintained by many mechanisms. Other than enzymatic antioxidants, non-enzymatic antioxidants also are the major factor that provides tolerance ability to specific fungus for specific metal. However, it is often seen that in a single organism, more than one antioxidant is involved in the antioxidation mechanism which can be pronounced as multiple antioxidant systems. It has been also found that antioxidants vary with the types of pollutants (HMs) within the same organism. Glutathione (GSH) reduces Cd^{2+} toxicity and induces the production of metallothionein to increase the tolerance of the fungi (Singhal et al. 1987), while, in the yeast, glutathione (GSH)-metal complex formation and its export into the vacuoles of the cell is one of the major mechanisms of Cd(II) tolerance and detoxification (Li et al. 1997). Rehman et al. (2010) incubated *Candida tropicalis* in Cd(II) and glutathione-amended medium and found that intracellular oxidized glutathione levels raised from the control level; an increase in glutathione and non-protein thiol content was also observed. Thiol is an essential agent in cellular redox signaling and its control/management in fungi and other living organisms (algae and plant) (Moran et al. 2001; Pócsi et al. 2004). Increased production of thiol was also found in *A. flavus* CR700 under Cr(VI) exposure (Kumar and Dwivedi 2019a). The presence of Mn(II) induces manganese peroxide (MnP) which is involved in the detoxification of metal (Karigar and Rao 2011). GSH could also react with H_2O_2 in the presence of peroxidase (POD) enzyme and produces oxidized glutathione (GSSG) (Huang et al. 2017a, b; Zhang et al. 2016). In another report, it was found that GSH accumulated inside the cell and could be involved in the synthesis of metal sulfide (de Almeida et al. 2004). Li et al. (2017) reported that Cd improves the level of GSH content while Cr(VI) did not affect the level of GSH in *Pleurotus ostreatus* HAU-2. Delalande et al. (2010) suggested that GSH contains a two-tailed structure: one tail has thiol groups that can react with Cd and form cadmium-bis-glutathionate ($Cd\text{-}GS_2$) and another tail has γ-Glu residue which is not associated with Cd chelation. Oversynthesis of non-protein thiol, proline, and total phenolic content has been found under the stress of Cr(VI) in *A. flavus* CR500 and *T. lixii* CR700 (Kumar and Dwivedi 2019a, b). Total phenolic component and proline have also been reported in the plant as non-enzymatic antioxidants to relieve the oxidative stress by donating the H^+ in the neutralization of ROS. The non-protein thiol content was found as Cr(VI)- and arsenate-complexing agent in fungus (Kumar and Dwivedi 2019a, Chen et al. 2019; Wu et al. 2015).

Role of protein under HM stress

Oversynthesis of several specific proteins such as heat shock protein is also reported in fungi (Irazusta et al. 2012, 2018). They have an important role in detoxification and accumulation of HMs. Chaperone protein helped to protect *Candida fukuya-maensis* RCL-3 and *Rhodotorula mucilaginosa* RCL-11 against copper-induced oxidative stress (Irazusta et at. 2016, 2018). A detailed proteomic-based investigation of the Cu-tolerant *Penicillium janthinellum* strains GXCR and EC-6 has been done by Feng et al. (2017). They found that many proteins are in abundance such as heat shock proteins (Hsps), 60S ribosomal proteins (RPs)/ATP-dependent RNA helicases (ADRHs), 40S RPs/eukaryotic translation initiation actors, elongation factor 1, histone/26S protease regulatory subunit, actin, and proteasome/protein transport proteins. Palmieri et al. (2000) reported overexpression of 14-3-3 proteins in *Pleurotus ostreatus* under the exposure of Cu.

Role organic acid under HM stress

Organic acid secretion has been also reported to relieve the HM stress via binding/chelating of heavy metal in plants. Similarly, the synthesis of organic acid such as malic acid, oxalic acid, pyruvic acid, citric acid, gluconic acid, and succinic acid were detected in *Penicillium chrysogenum* in bioleaching of Cd, Cu, Pb, Zn, Mn, and Cr (Deng et al. 2013; Fomina et al. 2005; Rhee et al. 2014). These organic acid productions have been reported as extracellular and intracellular metabolites. Extracellular secretion mostly causes solubilization of metal and minerals from their surroundings. Extracellular organic acid production by fungi emphasizes its use in biomining purposes to extract metal from low graded ores. However, intracellular organic acid production causes intracellular precipitation of metal and also their translocation for compartmentation in vacuoles (Borovaya et al. 2015; Rhee et al. 2014). The intracellular production of these organic acids may also belong to their intracellular HM precipitation (Rhee et al. 2014).

Energy metabolism under HM stress

Several researchers have reported that metal stress increases the energy demand in fungi (Feng et al. 2017; Irazusta et at. 2016). Some metal transporter or hyper-accumulation processes are closely associated with energy metabolisms or ATP-driven mechanism (Visioli and Marmiroli 2013; Feng et al. 2017; Irazusta et al. 2018). A decrease in the level of glucose and D-fructose indicates that the demand for energy increases under Cu stress (Feng et al. 2017). Glycolysis, gluconeogenesis, and the citrate cycle (TCA) were greatly affected by Cu treatment in the *P. janthinellum* strain GXCR. Decreased in acetyl-CoA, carboxylase and fatty acid synthetase are found in *P. janthinellum* strains GXCR and EC-6 under the stress of Cu (Feng et al. 2017). Oversynthesis of alcohol dehydrogenase, enolase 1, phosphoglycerate kinase, and glyceraldehyde-3-phosphate dehydrogenase explains the increase in the demand for energy because these enzymes are related to the glycolytic pathway (Irazusta et al. 2018). The first responder of imbalanced homeostasis is the mitochondrion which acts as an important place for the Cu-dependent ATP production (Zischka and Lichtmannegger 2014). Mitochondrial cristae are greatly affected by Cu stress toxicity and cause deformity via peroxidation and inhibited the ATP transport outside of mitochondria (intercellular ATP deficit) (Zischka and Lichtmannegger 2014; Visioli and Marmiroli 2013).

Metal transportation

Metals generally occur in the environment, come into contact with organisms, and adhere to their surface. But after adherence to the surface, organisms accumulate the metal from outside to inside the cell via active (metabolic dependent) or passive mechanisms. In passive mechanism, the metal may come inside the cell via ion exchange, osmotic mechanism, etc, while in the case of active transport, it is driven by many types of transporting agents which are called a transporter. The transporter is also involved in the transport of the metal from the cytoplasm to the periplasm or vacuoles of the cell. Similarly, in fungi, many types of transporters have been reported for the transport of the HMs from outside to inside of the cell or from periplasm to cytoplasm or from cytoplasm to vacuoles or from inside to outside of the cell (in case of efflux pump). Cd-conjugated ATP-binding cassette (ABC) transporter, manganese transporter, iron transporter, copper transporter, metal transporting ATPase, and some other metal transporters are involved in metal transport from outside to cytoplasm and from cytoplasm to cell organelles (Bellion et al. 2006). Functionally ABC transporters are diverse and mediate ATP-dependent import and/or export of solute. Structurally, it revealed a transmembrane domain that contains a substrate or nucleotide-binding domain that binds and hydrolyzes ATP to drive the transport cycle (Verhalen et al. 2017). The copper transporters (CTR) are the small integral membrane proteins. It contains three transmembrane domains with the C-terminus and N-terminus located at the cytosol and extracellularly respectively (Tamayo et al. 2014). CTR1 and CTR3 are the efficient transporters found in the plasma membrane of *Saccharomyces cerevisiae* that obtain Cu from the environment, while CTR2 is found in the tonoplast which transports Cu into the cytosol (Marjorette et al. 2000; Puig and Thiele 2002). Copper-transporting ATPases belong to the HM P-type ATPase family (HMA) and possess eight transmembrane domains. These proteins are coupled with ATP hydrolysis for the efflux of metal cation from the cytoplasm (Tamayo et al. 2014). Siderophore production and a special group of proteins are involved in the uptake of Fe (Haas et al. 2008). Fungal siderophore is basically hydroxamates. A set of hydroxamate siderophore production was reported in *Laccaria bicolor* (Haselwandter et al. 2013). Putative ferrireductase, a protein present in *Rhizophagus irregularis*, can reduce Cu^{2+} and Fe^{3+}, which is taken up by Fe-oxidase and permease complex consisted high-affinity transporter, oxidase-dependent Fe^{2+} transporter (Tamayo et al. 2014). Vacuolar iron transporters are implicated in the transfer of metal from the cytoplasm to the vacuoles (Li et al. 2001). Zinc-iron-permease and cation diffusion facilitators are a family of proteins for the transportation of Zn (Eide 2006).

Transmembrane containing a histone-rich region is necessary for the selectivity of Zn for the fungi (Nishida et al. 2008). Cation diffusion facilitators transport the metal from the outside to the cytoplasm and from cytoplasm to the lumen of cell organelles and classified into three groups (Tamayo et al. 2014). The proton gradient of transmembrane is usually used by divalent metal transporters to facilitate the transport of many types of divalent metal cations (Tamayo et al. 2014). In *Saccharomyces cerevisiae*, four types of the transporter are involved in the uptake of Zn, Zrt1p (transport Zn from the low concentrated environment), Zrt2p (transport Zn from the high concentrated environment), Fet4p (involve in the uptake of Cu, Fe, and Zn), and Pho84p (involve in the transportation of phosphate and Zn) (Tangsombatvichit et al. 2015; Khouja et al. 2013). The Zhf1 and HcZnT1 from *Schizosaccharomyces pombe* and *Hebeloma cylindrosporum* respectively are localized on the endoplasmic reticulum membrane and are involved in Zn tolerance (Blaudez and Chalot 2011). Cu enhanced the many Cu-responding signaling pathways such as the calcium signaling pathway (CSP), insulin signaling pathway (ISP), NOD-like receptor signaling pathway (NOD), Hedgehog signaling pathway (HD), GnRH signaling pathway (GnRH), MAPK signaling pathway (MAPK), neurotrophin signaling pathway (NSP) in *Penicillium janthinellum* strain GXCR and EC-6 (Feng et al. 2017). Vaccaro et al. (2016) reported that proton motive forces drive the CDF protein or P-type ATPase to transport the HMs inside to the outside of the cell via multiple transportation steps such as from cytoplasm to periplasm and from the periplasm to the outside of the cell that is also called the active efflux mechanism.

Metal compartmentation

Metal localization in fungi has great importance in metal accumulation inside the cell of fungi. Cd proportion has been quantified in the cytosol and vacuoles of *Paxillus involutus* which are 20% and 30% respectively (Blaudez et al. 2000). Cd-conjugated glutathione (Cd-GSH) or Cd-conjugated PCs and/or Cd-conjugated MTs may be involved in the detoxification of Cd via ATP-binding and transport it into vacuoles which is a crucial step in Cd detoxification (Bellion et al. 2005). X-ray microanalysis revealed the Cd accumulation correlated with electron-dense accumulated sulfur in the vacuolar compartment which also indicated the involvement of thiolic compound in metal complexation (Ott et al. 2002). Compartmentalization or sequestration of metal depends on the ionic radius of metal and electronegativity (Teng et al. 2017). The soluble fraction containing organo-ligands such as sulfur-rich organic alkali, peptides, and organic acids which detoxify the metal by complexation is stored in vacuoles (Bhatia et al. 2005). Metal compartmentation in vacuoles is a well-known intracellular detoxification mechanism driven by metal transporter (Li et al. 2001; Blaudez et al. 2000). The vacuolar proton-pyrophosphatase (V-Ppase) pump and vacuolar proton ATPase (V-ATPase) pump energizes vacuolar uptake of metal in plants (Singh et al. 2016). The schematic presentation of metal compartmentation is shown in Fig. 2.

Metal chelating agents

Phytochelatins

Out of abovementioned mechanisms, biochelation, biocomplexation, biooxidation, etc. are also involved to remove HMs by fungi. Some chelating agents such as metallothionein (MT) (Vaseem et al. 2017) and phytochelatins (PC) (Jacob et al. 2016) are present inside the fungal cells and play an important role in detoxification of HMs. These chelating agents form complex compounds by binding with the metal ion which is usually secreted by fungi as secondary metabolites or can be accumulated inside the vacuoles of the cell (Vaseem et al. 2017). The PCs are the family of small cysteine-rich peptides which carry the –SH group having the capacity to bind metal ion. The PC synthesis catalyzed by phytochelatin synthetase (e.g., dipeptidyltranspeptidase, γ-glutamylcysteine dipeptidyl transpeptidase; EC 2.3.2.15) enzymes required HMs as an activating factor (Grill et al. 1989). GSH works as an activator for phytochelatin synthetase production which reduces the ROS into GSSG. Induction of ROS by the toxicity of HMs has been reported in many fungi (Xiang and Oliver 1998; Hirata et al. 2005; Kumar and Dwivedi 2019a, b). *Candida glabrata* produces PC in the response of Cd (Mehra and Winge 1991). Courbot et al. (2004) isolated thiol compound Cys and their derivates, γ-GluCys and glutathione, to PC (up to polymerization degree *n* = 8) from *Paxillus involutus* mycelium treated with Cd. Increases in glutathione and γ-GluCys in Cd-stressed *P. involutus* formed a stable complex compound of Cd and other thiophilic metals (e.g., Hg, Cu, and Zn). Specific permeases such as the Ycf1 membrane transporter of *S. cerevisiae* (Li et al. 1997) are involve in Cd-γ-GluCys2 transportation to vacuoles in *P. involutus* (Courbot et al. 2004). In *Penicillium janthinellum* EC-6 (a mutant strain), the synthesis of PC significantly increased under the stress of Cu that forms a complex PC-Cu (Feng et al. 2017).

Metallothionein

High cysteine containing the low molecular mass of polypeptide is metallothionein, first reported in the equine kidney (Ruta et al. 2017). Three metallothionein protein classes are recognized as class I which resemble equine kidney protein; class II has a different extensive sequence homology from class I protein (Howe et al. 1997). Poly(γ-glutamylcysteinyl)-glycin is the general structure of metallothionein (MT). These MTs are known to be widespread in fungi (Kneer et al. 1992). Howe et al. (1997)

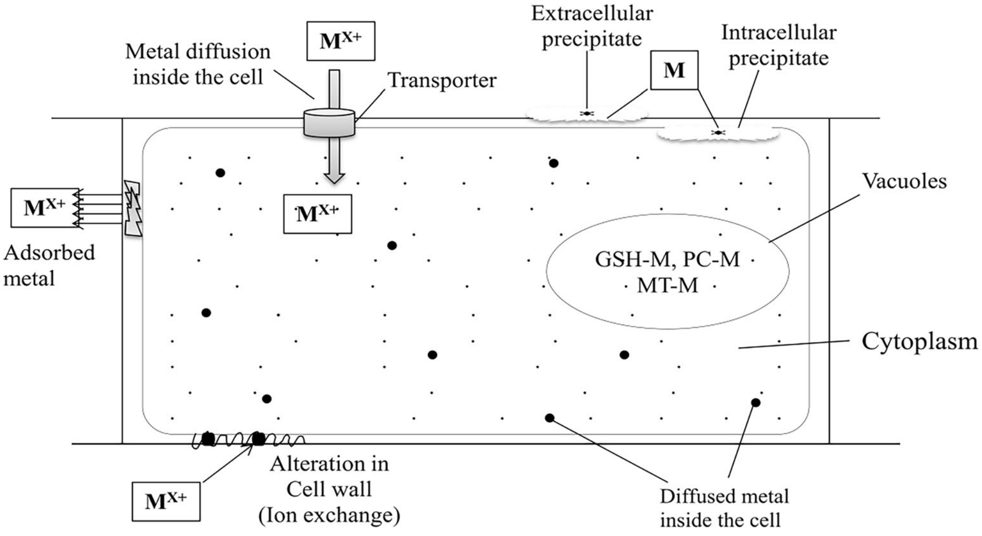

Fig. 2 Schematic diagram shows the possible metal accumulation site in a cell of the fungi. Dark black sphere (metal ion) diffused in cytoplasm and conjugated metal with glutathione (GSH-M), phytochelatin (PC-M), and metallothionein (MT-M) are transported in vacuole. M, metal ion

reported Cu-binding metallothionein in *Paxillus involutus* GPaxRSp2, *Paxillus involutus* Pax4, and *Laccaria laccata* (GLac4 and ELacl). In Brewer's yeast and *Candida glabrata*, MTs are reported for Cu tolerance (Jensen et al. 1996; Sutherland and Stillman 2014). Transpeptidase works as an intracellular metal sensor in the control of (y-EC)nG peptide formation by the metalloactivation mechanism. It was found in yeast that transpeptidase is involved in structural metal discrimination of Zn and Cu (Mehra and Winge 1991; Sutherland and Stillman 2014). In *Schizosaccharomyces pombe*, copper-binding component (y-EC)nG peptides of (y-EC)2G through (y-EC)4G devoid of sulfide have been reported (Reese et al. 1980). The absorption spectroscopy and luminescence measurement suggested the Cu(I)-thiolate cluster in peptides (Mehra and Winge 1991). The low-molecular-weight cysteine-rich protein found in *Neurospora crassa* in the presence of Cu is classified as MT because of the presence of N-terminal sequences of animal MT and Cys-X-Cys motif (Lerch 1980). Two domains exist in metallothioonein: α-domain containing 11 cysteine residues have the potential to react with four Cd^{2+} and Zn^{2+} or six Cu^{+2} ions while β-domains including 9 cysteines have potential to chelate three Cd^{2+}, three Zn^{2+}, or six Cu^{+} ions (Sutherland and Stillman 2014).

Melanin

The negatively charged hydrophobic dark-brown pigment containing a high molecular weight produced by some fungal species is known as melanin (Sandra et al. 2017; Eisenman and Casadevall 2012). Generally, it is found in the outermost layer of the cell wall linked with chitin; and, in some fungi, it is also located outside of the fungal cell in granulous form. Oxidative polymerization of compounds (indolic and/or phenolic compounds) such as glutaminyl-3,4-dihydroxybenzene (GDHB) or 3,4-dihydroxyphenylalanine (DOPA) or catechol or 1,8-dihydroxynaphthalene (DHN) are the major mechanisms involved in the formation of melanin (Eisenman and Casadevall 2012). The high antioxidant potential of melanin was reported in *Fonsecaea pedrosoi* which showed via reducing Fe(III) to Fe(II) (Cunha et al. 2010). Various functional groups (phenolic, carboxyl, alcoholic hydroxyl, carbonyl, methoxy groups, etc.) present in melanin are mainly responsible for the chelating potential of fungi (Butler and Day 1998; Sandra et al. 2017). Siegel (1987) reported that the melanin-rich fungal strain *Cladosporium cladosporioides* has more potential to biosorb Cd, Ni, Cu, Zn, and Pb compared with non-melanized *Penicillium digitatum* (Gonçalves et al. 2012). Melanin over producing *A. nidulans* mutant strain (MEL1) has more potential to biosorption of neodymium and lanthanum. Radio cesium (^{137}Cs) and radio cobalt (^{60}Co) significant uptake is reported in *A. alternate* and *Aspergillus pulverulents* (Mahmoud 2004). The antioxidant characteristic of melanin is reported by Hoogduijn et al. (2003). They found that melanin defends keratinocytes and melanocytes from the induction of DNA strand broken down by ROS (H_2O_2).

Siderophore

Chemically, siderophore is made up of alcoholates, hydroxamates, and α-hydroxycarboxylates which contain negatively charged oxygen atoms and can make a tight interaction with metal ions such as Fe^{3+} ion (Kurth et al. 2016). Nitrogen and sulfur are also present as bidentate ligands but they exhibited lower selectivity. These moieties are featured by siderophore which is capable to make a complex with metal ion other than ferric ion (Hider and Kong 2010). Siderophore is mostly involved in the uptake of ferric ion. In the presence of water, ferric ion reacts with water molecules and produces octahedral $Fe(H_2O)_6{}^{3+}$ complexes (Kurth et al. 2016). Hexadentate ligands (siderophore) can make a stable complex with Fe^{3+} ion. *Cupriavidus metallidurans* applied in metal-contaminated soil treatment in bioreactor produces citrate siderophore staphyloferrin B with a 16-fold reduction in HMs (Diels et al. 2009). Arsenic-contaminated soil washing with siderophore removed 92.8% of arsenic from the soil as compared with washing with a medium (Kurth et al. 2016). However, bacteria are mostly reported for the production of siderophore which is important in metal bioremediation. Some plants are dependent on bacterial siderophore for the uptake of ferric ion and they uptake ferric ion by direct uptake of bacterial metal chelates or chelate degradation, or ligand exchange reactions. Bioaugmented Cr-polluted soil with *Ralstonia metallidurans* and *Pseudomonas aeruginosa* increased Cr accumulation up to 5.4 times in maize plants (Braud et al. 2009). Dimkpa et al. (2009) found that the culture filtrate of *Streptomyces tendae* F4 containing siderophores improved the Fe and Cd uptake capacity in sunflower and increased its growth. It is investigated by Yun et al. (2001) that ferrireductase (Fre) protein might be involved in the uptake of Fe by siderophore.

Bioreduction

In the bioreduction mechanism, the toxicity of metals is reduced due to the reduction in their oxidation state which is driven by living organisms (Li et al. 2017). Chromium commonly exists in the environment in its stable form Cr(III) and Cr(VI); however, Cr(VI) is more toxic than its Cr(III) form (Ramırez-Ramırez et al. 2004; Romo-Rodríguez et al. 2015; Gu et al. 2015; Long et al. 2018). Its reduction in Cr(III) form mitigates its toxicity potential. *Aspergillus tubingensis* Ed8 produces glucose oxidase (GOX) in Cr(VI) reduction into Cr(III) which indicate that GOX enzyme is important for the transformation of Cr(VI) to Cr(III), and this transformation reaction is dependent on glucose, indicating that Cr(VI) reduction requires more energy (Romo-Rodríguez et al. 2015). It is also confirmed by oversynthesis of phosphoglycerate kinase, enolase 1, glyceraldehyde-3-phosphate dehydrogenase, and alcohol dehydrogenase under the presence of Cr(VI) that is commonly involved in the glycolytic pathway (Irazusta et al. 2018). Organic acids including citrate and salicylate enhanced the rate of Cr(VI) bioreduction which indicated that a decrease of medium pH is more favorable for Cr(VI) reduction (Coreño-Alonso et al. 2009; Romo-Rodríguez et al. 2015). Shi et al. (2018) reported the production of citric acid, oxalic acid, and maleic acid decreases the pH of the solution that leads to the higher reduction of Cr(VI) to Cr(III) by *Pisolithus* sp1. An increase in the ROS (H_2O_2) production is also associated with Cr(VI) reduction via a multiple-step mechanism by forming Cr(V) and Cr(IV) (as an intermediate product) and the final product of Cr(III) (Wani et al. 2018). This mechanism is called a multistep electron transfer reaction which may be enzyme-dependent or substrate-dependent (Qamar et al. 2011). Sometimes, these mechanisms extracellularly completed and do not dependent on the enzyme and driven by the functional group or negative charges present on the cell surface of the fungi (Cao et al. 2018; Yin et al. 2011; Dang et al. 2018).

Mitochondrial ferredoxin-NADP reductase Yah1 oversynthesized under the stress of Cr(VI) may be involved in the reduction of Cr(VI) (Irazusta et al. 2018). The chromate reductase enzyme is reported in several fungal and bacterial species that are responsible for the reduction of Cr(VI) to Cr(III) via electron transfer mechanism donated from NADH or electron-donating agents (Irazusta et al. 2018; Kumar and Dwivedi 2019a, b). Wani et al. (2018) hypothesized two types of mechanisms for the reduction of Cr(VI): direct mechanism and indirect mechanism. Direct mechanism includes Cr(VI) reduction under aerobic and anaerobic conditions while indirect mechanisms include other mechanisms such as extracellular Cr(VI) reduction, membrane-bound Cr(VI) reduction, cytochrome c (Cyt-c) dependent reduction and intracellular Cr(VI) reduction, etc. In the case of growing fungi, bioreduction is mostly metabolic dependent, but in the case of dead fungal biomass, it happened mostly extracellularly or through surface-attached reaction. Electrostatic attraction and one-electron transfer reaction mechanisms are reported by many researchers for the reduction of Cr(VI) by dead fungal biomass (Pradhan et al. 2017). It is investigated by Yun et al. (2001) that the ferrireductase (Fre) protein might be involved in the uptake of Fe by siderophore. Fre1p, a plasma membrane, is necessary for the uptake of Fe inside the cell of the fungi and plants from their growth medium or environment (Radisky and Kaplan 1999). The reductase-abundant plasma membrane of *S. cerevisiae* containing an Fre1 protein exhibited a comparable activity towards Fe^{3+} and Cu^{2+} and one-electron acceptor activity was found by paraquat (methyl viologen), INT (iodophenyl nitrophenyl tetrazolium chloride), and TTC (triphenyltetrazolium chloride) (Hassett and Kosman 1995).

Mycoprecipitation

Bioprecipitation is one of the main mechanisms which is involved in the removal of HMs by microbes from wastewater (Maisa et al. 2018). In the case of fungi, it can be pronounced as mycoprecipitation which is the part of bioprecipitation. The main anionic species involved in bioprecipitation are PO_4^{2-}, CO_3^{2-}, S^{2-}, OH^-, $C_2O_4^{2-}$, O^{2-}, Cl^-, etc. Bioprecipitation can be categorized into two types: (1) extracellular bioprecipitation and (2) intracellular bioprecipitation. In intracellular precipitation, metal ion comes inside the cell through the fungal cell wall and precipitate (sable/insoluble compound) as their minerals by reacting with respective anionic species, while in extracellular precipitation, metal ion, extracellularly synthesized into their precipitate where anionic species may be donated by the fungus or may be provided from their surrounding medium, while the fungal cell surface provides a base for the reaction to take place. In intracellular precipitation, precipitate products mostly adhere to the intracellular surface of the cell, while in extracellular precipitation, the precipitate product may occur on the fungal cell surface or diffuse in the surrounding medium after precipitation. Liang et al. (2015) reported phosphate, sulfate, oxide anion involvement for removal of lead and found lead phosphate ($Pb_3(PO_4)_2$), anglesite ($PbSO_4$) ,and pyromorphite ($Pb_5(PO_4)_3Cl$), the lead oxides massicot and litharge (PbO) as a lead precipitate. The phosphate ion is also reported for the precipitation of uranium (U) that forms uranium complex compounds such as meta-ankoleite, chernikovite, bassetite, and uramphite (Liang et al. 2016). *Aspergillus niger* produces uranyl acetate hydrate (organo-uranyl complex) mineral from the low-grade ore of uranium (Maisa et al. 2018). Sutjaritvorakul et al. (2016) reported zinc oxide (ZnO) formation in a fungus isolated from the zinc mining site. Li et al. (2015) studied Ca and Sr precipitation by fungus and found $CaCl_2$ and/or $SrCl_2$, calcite($CaCO_3$), strontianite ($SrCO_3$), vaterite in different forms ($CaCO_3$, $(CaxSr_{1-x})CO_3$), and olekminskite ($Sr(Sr,Ca)(CO_3)_2$) as bioprecipitate. Sulfide and phosphate of Cd were found by Borovaya et al. (2015) and Kumar et al. (2019) in fungal-mediated Cd precipitation. *Paecilomyces javanicus* precipitated the lead as plumbonacrite ($Pb_{10}(CO_3)_6O(OH)_6$), cerussite ($PbCO_3$) and lead oxalate (PbC_2O_4) (Rhee et al. 2014). Dhami et al. (2017) also reported Pb co-precipitation into lead carbonate, Plumbonacrite, Shannonite ($Pb_2O(CO_3)$), vaterite and aragonite and Sr into Strontianite, Strontium calcium carbonate ($SrO_5CaO_5(CO_3)$), carbocernaite along with calcite by two calcifying fungal isolates *Aspergillus* sp. UF3 and *Fusarium oxysporum* UF8.

Biovolatilization

Biovolatilization basically deals with the biological volatilization of metal/loid from the water and soil into the environment. Biovolatilization is broadly reported for the volatilization of As and Hg by microorganisms (bacteria, fungi, and algae) and plants. In the case of As, methylation is the basic mechanism that converts the non-volatile As-species to volatile As-species. The methylation of As was firstly observed in the fungus *Scopulariopsis brevicaulis* involving As(V) reduction into As(III) followed by the oxidative addition of a methyl group ($–CH_3$) (Challenger 1945). Challenger (1945) proposed the pathway of As methylation where As(V) ($AsO(OH)_3$; arsenic acid) is first reduced to As(III) ($As(OH)_3$; arsenious acid) and then bio-methylated to monomethylarsonic acid ($AsO(OH)_2(CH_3)$) → dimethylarsinic acid ($AsO(OH)(CH_3)_2$) → trimethylarsineoxide ($AsO(CH_3)_3$) → arsenobetaine ($(CH_3)_3As^+(CH_2)COO^-$), and other multifarious As-compounds such as arsenoribosides (AsRib). Recently, these compounds also have been reported in many other fungi such as *Penicillium* sp., *Aspergillus* sp. (Guimarães et al. 2019), and *Rhizophagus irregularis* (Li et al. 2018a, b, c) that interlinked with the methylation pathway as proposed by Challenger (1945). In addition, some microorganisms also degrade or/and synthesize As-compounds into volatile As (such as arsine (AsH_3), monomethylarsine ($AsH_2(CH_3)$), dimethylarsine ($AsH(CH_3)_2$), and trimethylarsine ($As(CH_3)_3$). This mechanism has been also reported by Guimarães et al. (2019) in *Penicillium* sp. and *Aspergillus* sp. at the time of As-volatilization from potato dextrose broth medium. However, methylation and biovolatilization commonly occurred in the ecosystem (contaminated with As) and majorly contributed to As global flux (Wang et al. 2014; Mestrot et al. 2013).

Hg which is one of the toxic metals and is volatile can also be biovolatilized by microorganisms. Bacterial as well as fungal volatilization of Hg is frequently reported in many studies that play an important role in the decontamination of the Hg-polluted site (Urík et al. 2014; Wang et al. 2018; Chang et al. 2020). Generally, bacteria and archaea utilize the *mer* operon which is capable of enzymatic reduction of Hg(II) or methyl mercury (MeHg) to less toxic Hg(0), volatile species of Hg (Boyd and Barkay 2012; Giovanella et al. 2016). In fungi, the mechanism of biovolatilization of Hg is not well characterized. However, in a recent report, it is found that *mer* genes (*merA*) are upregulated in the exposure of Hg(II) in *Penicillium* spp. DC-F11, a potential isolate for the volatilization of Hg (Chang et al. 2020). They have also analyzed the activity of mercuric reductase that is responsible for the reduction of Hg(II) to Hg(0). Thus, the *mer* operon is basically involved in enzymatic reduction of Hg(II) to Hg(0) as well as its volatilization. Some other fungal species such as *Candida albicans*, *Saccharomyces cerevisiae* (Yannai et al. 1991), *Scopulariopsis brevicaulis* (Boriová et al. 2014), *Aspergillus niger*, and *Cladosporium* sp. (Urík et al. 2014) also have been reported for volatilization of Hg, but no other clear Hg volatilization pathway has yet been observed in fungi. Some other metal/loid such as Se (Selenium), Sb (Antimony), Tl (Thallium), and Bi (Bismuth) are also reported for volatilization by fungi (Boriová et al. 2014). Despite this, sometimes, fungi change the less toxic form of metal/loid into its high toxic form. Yannai et al. (1991) tested the tolerance ability of *Candida albicans* and *Saccharomyces cerevisiae* towards Hg ($HgCl_2$) and reported that *Candida albicans* and *Saccharomyces cerevisiae* are unable to grow above 0.75 μg/mL. Further, they investigated the end product of Hg at the tested concentration (below 0.75 μg/mL) and found that an amount of Hg (proportional to Hg tested concentration) is transformed in organo-mercury (methyl mercury) compound. Methyl mercury, a highly toxic species of Hg, can inhibit the growth of fungi as well as other organisms.

Methylation

The synthesis and transfer of the methyl group is a vital metabolic process and widely distributed (Bentley et al. 2002). Basically, the C, O, N, and S atom of organic compounds serve as methyl group acceptors in the metabolic process. Metal and metalloids are also reported in many studies as methyl group acceptor and resultant into methylated end products. However, the term "biomethylation" considers the formation of both either a volatile or non-volatile methylated compound of metals and metalloids. The methylation of As is widespread, occurring in bacteria, fungi, algae, and plants. As methylation was first proposed in fungus *S. brevicaulis* by Challenger (1945). In As methylation, As(V) first reduced in As(III) followed by oxidative addition of a methyl ($–CH_3$) (earlier discussed in "Biovolatilization"). A similar pathway has been proposed for antimony (Sb) methylation; first, it proposed Sb methylation in the fungus *S. brevicaulis* and *P. notatum* for the methylation of phenylstibonic acid ($C_6H_5SbO(OH)_2$) to phenyldimethylstibine ($C_6H_5SbO(CH_3)_2$) via reduction of Sb(V) to Sb(III) followed by methylation (Challenger 1945). Later, some other fungal species were reported for methylation of Sb such as *Cryptococcus humicolus* (Hartmann et al. 2003) and *Phaeolus schweinitzii* (Andrewes et al. 2001). Andrewes et al. (2001) reported that *P. schweinitzii* efficiently transforms the antimony (III) compounds potassium antimony tartrate and antimony trioxide (Sb_2O_3) to non-volatile dimethylantimony and trimethylantimony species. Mercury is another metal reported for its methylation by bacteria and fungi. In bacteria, clear Hg-methylation pathway, genes responsible for Hg-methylation and Hg-transporting agents have been reported (Regnell and Watras 2019). Fungi such as *Coprinus comatus*, *C. radians*, *Candida albicans*, and *Saccharomyces cerevisiae* have been reported for Hg-methylation potential (Fischer et al. 1995;

Yannai et al. 1991). But in fungi, the mechanism of Hg-methylation is least known.

Biooxidation

Manganese peroxidase is a heme enzyme extracellularly produced by the lignin-degrading fungus (basidiomycetes) that can oxidize Mn^{2+} to oxidant Mn^{3+} in a multiple-step electron transfer reaction (Have and Teunissen 2001). Extracellular protein involvement in Mn oxidation in anamorphic ascomycete strain KR21-2 and *L. discophora* SS-1 has been reported by Miyata et al. (2004). The proteins such as p-phenylenediamine and 2,2′-azinobis (3-ethylbenzothiazoline-6-sulfonic acid) are the extracellular Mn oxidizer. The peroxide-oxidized enzyme catalyzes Mn(II) into Mn(III) in the presence of a suitable Mn(III) chelator. Purified laccase enzyme isolated from *Stropharia rugosoannulata* can catalyze the Mn(II) into Mn(III) (Schlosser and Hofer 2002).

Other mechanisms

Many known and unknown other mechanisms may be also involved in the tolerance and accumulation of HMs in fungi; ion exchange is the major interactive manner among some divalent metal ions and the extracellular polymeric substances (EPS) (Sheng et al. 2010). It was found that the binding between the metal ions (divalent; Ca^{2+}, Ni^{2+}, and Mg^{2+}) and EPS is one of the most important intermolecular interactions behind microbial aggregate structures. The simultaneous release of Ca^{2+} and Mg^{2+} into the solution during the metal removal mechanism by microbial aggregates indicates the ion exchange involvement (Yuncu et al. 2006). However, strong binding capacity is also seen in neutral and extreme acidic eukaryotic biofilms for heavy metals (Co, Ni, Zn, Cu, As, Cd, Cr, Hg, and Pb) which might be produced by colloidal materials, such as protein, or affecting the ionic values of metal (e.g., the transformation of Hg^{2+} to Hg0 or transformation of Cr(VI) into Cr(III)) (Choi et al. 2009; Neu and Lawrence 2010). There are some specific transport systems involved through the membrane and carriers may consist of all the metabolically coupled and H+ gradient–driven transport system. They play an important role in the metal efflux pump systems. The metal efflux pump maintains the salinity inside of the cell and their surroundings. Adriaensen et al. (2006) found enhanced Zn efflux which may act as a tolerance mechanism in *Suillus bovines*. The GSH as discussed above is reported for the binding of HMs.

Genes involved in HM tolerance and detoxification

Exploration of the basic molecular mechanisms of tolerance and adaptation of fungi in HM stress environment is an important field of scientific interest. Gene expression has an imperative role in the biological process which establishes the growth and development of fungi as well as HM tolerance in HM stress condition. In plants, many types of sets of gene expression have been triggered under HM stress. Different types of stressors induce the expression of a set of the gene in microbes and plants in order to link the signaling pathway with HMs and other stress tolerance (He et al. 2013; Singh et al. 2016). The regulatory genes and functional genes are the two groups of genes expressed under stress conditions. Various transcription factors (TFs) encoded by groups of genes are called the regulatory gene group. It can regulate many stress-responsive genes separately or cooperatively and make up a gene system. However, the metabolic compounds such as amines, alcohol, sugar, enzymes, etc. that play an important role in the tolerance of HMs encoded by a group of genes are known as the functional gene group (Singh et al. 2016).

Flores-Alvarez et al. (2012) reported *CHR-1* gene expression under Cr(VI) exposure in *Neurospora crassa* that encoded the CHR-1 protein (homologous to ChrA protein), sensitive upon Cr(VI) exposure and promotes its accumulation inside the cell. The expression of glutathione-S-transferase (GST) encoding six *GintGst* genes found in an arbuscular mycorrhizal fungus *Glomus intraradices* in the exposure of Cd, Zn, and Cu (Waschke et al. 2006) which confirm its role in the adaptation of *G. intraradices* in Cu-, Cd-, and Zn-contaminated environment. However, Shen et al. (2015) identified 24 GST genes in *Exophiala pisciphila*. All these *EpGSTs* were upregulated by Pb stress but some of them were differentially expressed under the stress of Cd, Cu, and Zn. Metallothionein (MT) is a systolic peptide reported for binding of HMs via cysteinyl-thiolate bonds and participate in metal homeostasis. MT family gene expression belongs to the functional gene group and is reported in many fungal species in the exposure to heavy metal: *Neclu_MT1* gene induced by Cd in *Heliscus lugdunensis* (Loebus et al. 2013), Cu-specific MT genes (*CMT1* and *CMT2*) expressed underexposure of Cu in *Cryptococcus neoformans* (Palacios et al. 2014), *LbMT1* gene upregulated by Cu and Cd in *Laccaria bicolor* (Reddy et al. 2014), Cu-dependent expression of *HcMT1*and *HcMT2* genes in *Hebeloma cylindrosporum* (Ramesh et al. 2009), and transcription of AsMT1s and AsMT3 in *Amanita strobiliformis* inducible with the treatment of Ag and Cu and Zn and Cd respectively (Hložková et al. 2016).

Recently, Bakti et al. (2018) reported *PcaA* gene expression in *A. fumigatus* induced underexposure of Cd which is associated with the induction of GFP-PcaA fusion protein. This protein specifically produced underexposure of Cd neither Cu nor Zn or Fe and localized in the membrane as found in confocal microscopic observation and strongly correlated with the detoxification of Cd. However, Bakti et al. (2018) also studied the role of AfYap1 (ortholog of the yeast Yap1 transcription factor) in metal sensing by *A. fumagatus* Af293 (Wild Type) and they found that AfYap1 is involved in the sensing of Cd and Cu both. The Cd and Cu have also upregulated the *GintABC1* gene in *Glomus intraradices* that encoded the GintABC1 protein which belongs to the sub-family of ABC transporter and possibly involved in Cu and Cd detoxification (González-Guerrero et al. 2010). In a recent study, Li et al. (2018a, b, c) investigated Cd tolerance in *Pleurotus eryngii* which differentially expressed 15 unigenes. These differentially expressed genes (DEGs) are specifically upregulated upon Cd exposure which is mainly related to heat-shocked protein (HSP) genes including three HSP 70 genes, one HSP 9 gene, one HSP 20, one HSP 60, and one HSP 78. Some other unigenes such as "carbohydrate-binding module family 13 protein," "3-beta-hydroxy-delta 5-steroid dehydrogenase activity," "uncharacterized aromatic compound mono-oxygenase," and "mannose-6-phosphate isomerase" are some that were upregulated in Cd stress. Further, they were added NO with Cd stress and found an increase in the biomass of *P. eryngii*. They found in transcriptomic analysis that putative oxidoreductase, transferase, reductase, dehydrogenase genes, and TFs such as "GTPase activator activity," "GTP binding," "transcription factor complex," "enzyme activator activity," and "ATP binding" are upregulated significantly that enhance the Cd tolerance capacity in *P. eryngii*. These studies confirmed that there are sets of gene expression in fungi that are upregulated under HM stress and interlinked with metabolic activity and development of fungi. However, single HM–induced gene expression may vary from species to species, and also in the same fungal species, different HMs may induce a various set of genes expression which might be specific for each HM. These expressed sets of genes are strongly associated with tolerance and detoxification mechanisms of HMs in fungi and very essential for fungi to survive in HMs stressed environmental conditions.

Effluent treatment process development

pt?>Fungi have a great potential application for the bioremediation of effluent treatment because it has high metal removal efficiency with simple and quick biomass separation after effluent treatment. Presently, both forms of fungi are reported for their metal removal efficiency: dead form and live or viable or growing form. Authors have highlighted the advantages of the dead form of the fungi for industrial applications. Dead fungal biomass is immune to the toxic effect of HMs, no need for supply or availability of nutrients, unaffected under effluence pH and temperature, easily storable for a long time, and no need for specific conditions to maintain their growth (Soares and Soares 2012; Fernández et al. 2018).

The metal removal efficiency of fungi in growing form is high but its application in the treatment of wastewater needs a more appropriate environment, because in the open environment, controlling factors such as temperature is a tough task that affects the growth and metal removal efficiency of the fungal isolate. In natural conditions, fungi accumulate the metal inside the cell or adsorb it on its cell surface but the metal could not get degraded like organic pollutants. However, HM-laden biomass is considered hazardous substances so, after the treatment of wastewater it is required to remove the fungal biomass from treated wastewater. Therefore, in situ treatment approaches such as biostimulation and bioaugmentation can't be preferred for HMs treatment. Where providing oxygen or required nutrients to on-site present microbe is called biostimulation, and the addition of foreign microbes into the contaminated sites is known as bioaugmentation (Rahman and Singh 2020). Thus, after the selection of metal-resistant suitable fungal isolate, there is a need for development and design of the bioremediation process to get the best HM removal efficiencies by the fungal isolate from wastewater and separate the fungal biomass from the treated wastewater. Biofiltration and bioreactor are the most effective technological approaches which are being applied in wastewater treatment.

Biofilter

Biofilters are stripping columns with immobilized microbes (bacteria, fungi, and algae) either dead or viable form on porous carrier materials (Boopathy 2000; Ali 2013). It is a highly superficial setup for the removal or detoxification of HMs from wastewater. This system is accomplished with one or more than one fungal species attached to the inert surface. In this system, biosorption, bioprecipitation, redox reaction, bioaccumulation, biovolatilization, etc. are associated with the removal of HMs (mechanism discussed in "Heavy metal tolerance and removal mechanism in fungi"). The biofilters provide strength to fungi to remove HMs from wastewater. The biosorption capacity of *Candida utilis* and *Aspergillus niger* dead biomass was investigated by Ali (2013) as a biofilter. The bed height was 2 cm. Biofilter contains *Aspergillus niger* biomass could remove 89%, 90%, and 91% of Cr, Ni, and Pb respectively, while *Candida utilis* removed 81%, 83%, 80% of Cr, Ni, and Pb respectively at the pH 6, residence time 10 min and flow rate 9 ml/min. In another study, in an aerobic biofilter, *Penicillium citrium* EPAMIG 0086 and *A. brasiliensis* EPAMIG 0084 tested for removal of Cu, Mn, and Zn. *Penicillium citrium* EPAMIG 0086 removed 44, 62 and 48% and *A. brasiliensis* EPAMIG 0084 removed 21.7, 51, and 41.6% of Cu, Mn, and Zn respectively (Pereira et al. 2014).

Bioreactor

Bioreactor is considered the most suitable and applicable approach for lab study to large-scale wastewater treatment. A bioreactor is mostly used to provide suitable conditions (pH, temperature, agitation rate, nutrients supply, retention time, etc.) to the pollutants catalyzing microorganism for efficient removal of HMs. The selection of appropriate bioreactors is always closed with different operational conditions such as hydrodynamic, mass transfer, and growth condition of microbes. Different types of bioreactors have been used in HM removal by fungi. Commonly used bioreactor types are described below in subsections.

Stirred tank reactors

This type of reactor can be used in batch or continuous mode and as its name the design of this type of reactors is equipped with a stirrer. The stirrer is used for the mixing of medium with supplied air from the bottom of the reactor. The feeding ability of the tank to reach the reaction volume and its simplicity is ab advantage of stirred tank reactors (STRs). STRs have some other advantages such as simple and easy in operation and repetition of the experiment, easy to measure the operational parameters (pH and dissolved oxygen), pellets size, and shape-controlled by agitation speed. The disadvantages of this reactor are impractical at a large scale (> 500 m^3), requires high energy for agitation, and excessive agitation causes damage to fungal pellets (Moreira et al. 2003; Hlihor et al. 2014). Sepehr et al. (2012) investigated the Cr(III) removal ability of *Aspergillus niger*. They reported 88% removal of Cr(III) without any growth medium supplementation. However, after adding a growth supplement under optimized condition, *A. niger* can remove 96% of Cr(III).

Fixed-bed reactors

In this type of reactor, the biosorbent is positioned in a fixed bed on a column, similar to a biofilter. The HM-contaminated wastewater is passed through the column. Fixed-bed reactors (FBRs) are used for the biosorption of HMs from wastewater and the fungal biomass is encapsulated, entrapped, and bonded on polymeric substances or fibrous material to stabilize on column (Rosca et al. 2015). This reactor has more advantages such as utilizing large particles for biomass immobilization, simple in construction and operation, increase the life of the biosorbent, high recyclable possibility of the biosorbent, adjustable hydraulic retention time, and a high possibility for metal recovery, while the disadvantage includes regeneration is required when fungal biomass reached adsorption equilibrium, requiring more than one column for continuous use (Fernández et al. 2018). Migahed et al. (2016) placed six bacterial (belongs to the genera *Vibrio*, *Serratia*, *Bacillus*, and *Paenabacillus*) and two fungal (*Trichoderma viride* and *Fusarium oxysporum*) biomass in mixture forms as a biomass consortium on a column of fix-bed mini-bioreactor and investigated its HM removal performance. At the pH 6.0 and flow rate of 5 ml/min, they recorded 98% removal of Cr(VI) and 55% removal of Pb(II). In another study, HMs removal capability of *Pycnoporus sanguineus* was investigated using FBR and efficient removal of Pb^{2+}, Cu^{2+}, and Cd^{2+} (Zulfadhly et al. 2001).

Bubble column reactors

Bubble column reactors (BCRs) belong to the multi-phase reactor category which is an elongated non-mechanically agitated type of reactor and air provided by gas distributer from the bottom. Proper mixing of the gas and liquid phases is required for the best performance of BCRs. This reactor is most suitable for fungi application in wastewater treatment, because it does not cause mechanical damage and prohibit the formation of fungal pellets, so fungal mycelia are well dispersed in the medium and provide more contact surface area and increase the HMs removal efficiency of the fungi (Rodríguez-Porcel et al. 2007; Kantarci et al. 2005). This system required little maintenance and low operational cost. This reactor has many other advantages such as no mechanical agitation, low energy input, excellent heat and mass transfer property, no mechanical damage to applied fungi, and scale-up is easy (Kantarci et al. 2005). There are some disadvantages associated with this reactor including short gas phase residence time, the fluid flow pattern is undefined inside the reactor and no-uniform mixing. The tannery waste treatment capability of *P. citrinum* and *T. viride* has been examined using BCRs (Zapana-Huarache et al. 2020). *P. citrinum* effectively reduced effluent content of COD (chemical oxygen demand) and sulfide and removed Cr(VI) by 80%. *T. viride* also successfully reduces the effluent content TSS (total suspended solid), COD and sulfides, but removed Cr(VI) only by 20% after 120 h of incubation period. BCR is also used for the growth of *Aspergillus niger* to maximize the production of organic acid for enhanced bioleaching of Ni and V (Vanadium) from power plant residual ash (Rasoulnia and Mousavi 2016).

Airlift reactors

Airlift reactors (ALRs) are pneumatically agitated and basically designed to avoid mechanical agitation, to ensure increased oxygen transfer rate, and to offer the smallest energy requirement for aeration. The continuous recirculation and mixing of liquid and gaseous phase is also an important part of this reactor to assure at the time of designing to achieve maximum HMs removal by the reactor. This reactor does not use mechanical agitation and cause no/less damage to applied multicellular organisms; therefore, this reactor is also more suitable for the use of fungi in HM removal and wastewater treatment (Kanai et al. 1996; Merchuk and Gluz 1991). The major advantages of this type of reactors are no moving parts, high heat and mass transfer, low power consumption, rapid mixing, homogeneous shear, increased oxygen solubility, high homogenization efficiency, easy sterilization, low shear stress to cells, and low contamination risk. There are some disadvantages also associated with this reactor such as incompatibility with viscous broths, less liquid volume required for proper operation, dead zone inside the reactor, and inadequate mixing at high biomass density (Erika et al. 2015). Morales-Barrera and Cristiani-Urbina (2015) investigated the Cr(VI) reduction ability of the fungus *Hypocrea tawa* using a concentric airlift bioreactor (draft-tube airlift bioreactor). They recorded a 100% reduction of Cr(VI) from the medium containing 4.54 mM Cr(VI) concentration. Negi et al. (2020) investigated the selenite removal capability of *Asergillus niger* KP pellets using ALRs and reported 94.3% at the concentration of 10 mg/L and hydraulic retention time of 72 h.

Factors affecting removal of heavy metal

There are some important factors that are closely related to mycoremediation. The pH, temperature, time, concentration of pollutant, adsorbent dose, and shaking rate are factors which affect the HM remediation.

pH and heavy metal remediation

The pH of the solution is the most influencing parameter in the mycoremediation process in both cases, by growing fungi and by fungal biomass. It affects the removal capacity by affecting the following properties of fungal adsorbent and solution:

- Fungal cell viability (in case of growing fungi).
- Solubility of metal.
- Availability of active site (Functional group) on the fungal adsorbent.
- Interaction (repulsion or attraction) between the fungal adsorbent and metal ions by H^+ isoionic effect.

In the case of growing fungi, with the increase (basic) and decrease (acidic) in the pH from their optimum condition, the growth of the fungi is affected which leads to lower sorption of HMs. Metal accumulation by growing fungi is the metabolic dependent mechanism; thus, by the change in the pH of the medium, the removal rate will be affected. *Aspergillus* spp. showed higher copper and nickel removal capability at pH 4 (Pundir et al. 2018). Pundir et al. (2018) reported that biosorption is inhibited below pH 3.0. Reduction in the biosorption was due to the generated repulsion forces between metal cations and positively charged metal-binding active sites or ligands on the surface of fungal biomass (Al-Homaidan et al. 2015). Pundir et al. (2018) found that a decrease in the removal rate of metal at higher pH value (above pH 5) is due to the metal hydroxide formation. It is found in the fungus that at higher pH, the negative charge on the surface of the fungus is more frequent that makes strong relations with a metal ion. However, it is also affected by the dissociation of surface functional groups (Tian-Wei et al. 2004; Mohsenzadeh 2014; Rawat et al. 2019).

In the case of dead fungal biomass, in the adsorption phenomenon, pH plays an important role, and with an increase and decrease in the pH of the solution, adsorption is negatively affected. Li et al. (2018a, b, c) investigated *Auricularia polytricha*, *Flammulina velutipes*, *Pleurotus eryngii*, and *P. ostreatus* dead biomass in adsorption of Cu(II), Zn(II), and Hg(II) and reported that adsorption was increased from 5.64 to 77.39% with decreasing the solution pH. Dead biomass of Artist's Bracket fungus is reported most effective at lower pH (pH 2) in adsorption of Cr(VI) (Pourkarim et al. 2017). Amin et al. 2016 applied *Pleurotus eryngii* in the removal of Hg (II) and reported high removal ability at pH 7. They found that at pH less than 5.0, the metal-binding cell surface ligands such as hydroxyl group or other lone pair carrier groups like carbonyl is strongly coupled with the hydronium ions (H_3O^+) that limit the availability of ligands for metal ions biosorption due to repulsive forces; this repulsion may become stronger with the decrease in pH. Hence, there arises an antagonism between H_3O^+ ions and Hg ions. The functional groups such as COOH, OH, NH_2, and PO_4^{3-} on the fungal cell surface have a major role in the sorption of HMs ions and they showed diverse behavior by the change in the pH of the medium (Chergui 2007). The pH of the medium considerably affected the chemical characteristics of the biomaterial and their surface functional groups (such as COOH, PO_4^{2-}, and NH_2) (Liu et al. 2009).

Temperature and heavy metal remediation

The effect of temperature depends on the nature of the adsorption reaction. In the case of HM adsorption by the dead fungal biosorbent, if the adsorption reaction is endothermic than with an increase in temperature, the adsorption rate will be increased, e.g., fungal (*Pencillium fellutinum*) dead biomass composite with bentonite (FBC) shows the endothermic reaction in the removal of Ni and Zn (Rashid et al. 2016), but if the adsorption reaction is exothermic than with an increase in the temperature, adsorption rate will decrease such as Artist's Bracket decreasing its removal capacity (Pourkarim et al. 2017). However, in live fungi, the optimum temperature for the growth of fungi usually varies between 25–35 °C, and the removal rate basically depends on the growth of the fungi (Prasad et al. 2018; Kumar and Dwivedi 2019a). At lower and higher temperatures, enzymatic mechanisms get affected that reduce the metabolic rate of the fungus; ultimately, the growth and biomass productivity get hampered (Pundir et al. 2018; Kumar and Dwivedi 2019b). The optimum temperature for the growth of edible and other fungi was reported to be ranged from 25 to 35 °C (Pani 2010; Prasad et al. 2018) while *Aspergillus* sp. can grow between 10 and 40 °C temperature (Srivastava and Thakur 2006).

According to adsorption theory, the adsorption decreases on rising the temperature as molecules absorbed earlier on a surface tend to desorb from the surface at the higher temperatures (Iftikhar et al. 2009; Rashid et al. 2016). *Penicillium janthinillum* strain GXCR immobilized with polyvinyl alcohol (PVA)-sodium alginate (SA) beads used for adsorption of Cu, Pb, and Cd from water and the adsorption was unaffected at temperature ranging from 15 to 40 °C for Cu and Pb while maximum removal of Cd was found at 25 °C (Cai et al. 2016). Usually, metal bioadsorption using fungal biomass reduced by an increase in temperature particularly at elevated temperature due to the reason that elevated temperature cannot only lead to distortion and damage of surface functional groups (active sites) present on biosorbent (Wang and Chen 2006) but also influence the integrity of cell membranes, the wall configuration of the microbial cell, the stability of the metal-microbe complex, and the ionization characteristics of chemical moieties of the cell wall (Godlewska-Żyłkiewicz 2006). A rise in thermal energy of the adsorbing species leads to a lower removal rate (Pourkarim et al. 2017). With an increase in temperature from 30–51 °C, the removal capacity of fungal (*Pencillium fellutinum*) dead biomass composite with bentonite (FBC) was increased in the removal of Ni, Zn and decreased after 51 °C (Rashid et al. 2016). Due to the deteriorating of attraction forces between the surface functional group of the adsorbent and metal ions, the adsorption rate can be decreased (Ho et al. 2005). The strong affinity between the active site and metal ions at moderate temperature may be due to the re-orientation of fungal cell wall components and the chemical moiety ionization on the cell wall (Al-Qodah 2006; Shroff and Vaidya 2011).

Heavy metal removal and time

Mycoremediation is a time-dependent process in the removal of heavy metal, while fungal biomass showed rapid adsorption reaction (Salvadori et al. 2015; Amin et al. 2016; Pourkarim et al. 2017). In the case of fungal biomass, adsorption reaction is completed from minute to hours whereas remediation of HMs with growing fungi is a time-taking process and it may take some hours to days. Cai et al. (2016) studied immobilized live conidia of the *Penicillium janthinillum* strain GXCR with polyvinyl alcohol (PVA)-sodium alginate (SA) and reported that at a time of 100 min, the removal of Cu, Pb, and Cd was higher than that at the lower time. The highest removal efficiency of Cr and Cu reported in about 30 min by dead and dried biomass of Artist's Bracket and *Lepiota hystrix* biomass (Pourkarim et al. 2017; Kariuki et al. 2017), while for Hg(II), the maximum removal was within 5 min (Amin et al. 2016). The adsorption mechanism depends on the availability of the functional group, and after coming into contact with pollutant, the active site of the surface of bioadsorbent is rapidly saturated and that is why after a duration of time, the removal of the pollutant will be constant or decrease due to the desorption phenomenon (Babu et al. 2012; Hajahmadi et al. 2015; Melvin et al. 2015; Mondal et al. 2017; Sriharsha et al. 2017). It is explained by Rashid et al. (2016) that the adsorption mechanisms complete in two stages: the first one is the early fast phase (short time) followed by the second slower phase (long time) that prolonged until reaching equilibrium (Fig. 3). After equilibrium, the increase in time duration did not show any incremental change in the adsorption potential and decreases the adsorption capability at the latter stage, due to the difficulties faced by ions at the time of occupying the residual vacant active sites present on the surface of the adsorbent. The decrease in adsorption potential of fungal biomass with an increase in period may be due to intraparticle diffusion at the time of the second phase of adsorption (Noreen et al. 2013; Ullah et al. 2013; Rashid et al. 2016). Gupta and Balomajumder (2015) explained the mechanism behind dual adsorption phases. Initially, in the first phase, the active sites on the surface of the adsorbent are vacant and freely accessible to bind the metal ions, and in the second phase, the residual active sites are worn out and there might be a repulsion force that occurred between the pollutants and bulk phase. The repulsion may also exist between the adsorbed solute particle on the adsorbent surface and the remaining dissolved solute particles, because both carry the same charges and this repulsion force slows down the attraction between the active functional group and solute particle which decreases the adsorption after the second phase.

In the case of growing fungi, after incubation, with an increase in time duration, fungal biomass increased which leads to an increase in removal efficiency, because with increase in the amount of biomass, the availability of active sites increased, and on another hand, accumulation of HMs inside the cell via metabolic activity also increases the rate of removal. Pundir and Dastidar (2015) reported an exponential growth of *Aspergillus* spp. within 12–48 h in the presence of different initial concentrations of Cu. Vaseem et al. (2017) reported maximum removal capacity of growing macro fungus *Pleurotus ostreatus* at 17 to 20 days after incubation for

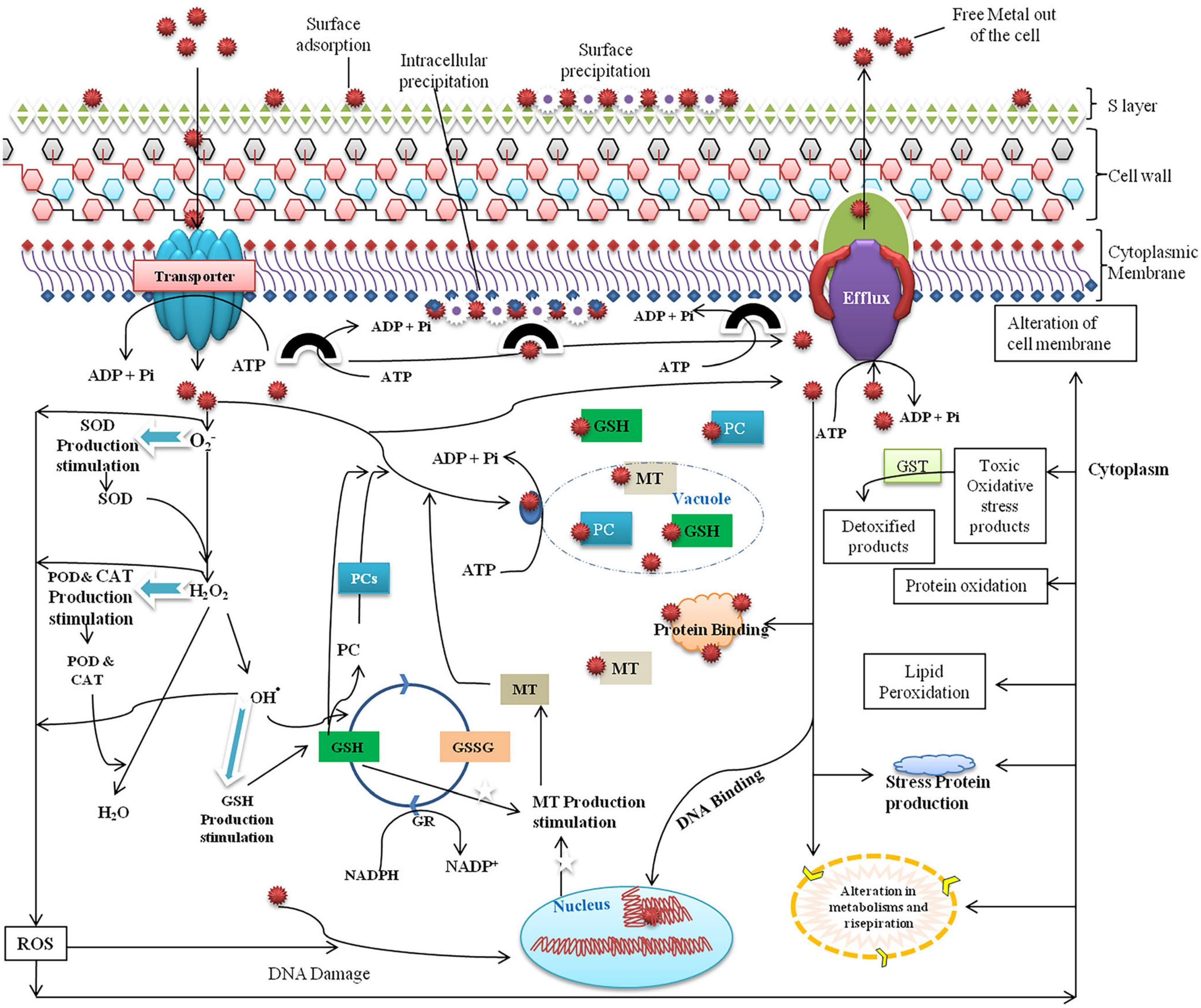

Fig. 3 Heavy metal sorption mechanism in fungi, figure (schematic representation) shows the hypothesized metal ion (red sphere) stress response or tolerance mechanisms in fungi. Metal interact with surface cell wall and may adsorb on the surface or uptake by cell inside with the help of transporter. After coming inside of the cell, metal stress produces superoxide anion (O_2^-) which stimulate the production of superoxide peroxidase (SOD) and SOD react with O_2^- and coverted it into H_2O_2. Hydrogen peroxide stimulates the production of peroxidase (POD) and catalase (CAT). POD and CAT catalyzes H_2O_2 into H_2O. The remaining H_2O_2 convert into OH (hydroxyl radical) which is most active agent of reactive oxygen species (ROS) and stimulate the production of glutathione (GSH). GSH and/or metal stimulate the metallothionein (MT) and phytochelatin (PC) production, bind metal ion, and also react with OH and form oxidized glutathione (GSSG). Glutathione reductase (GR) reduces GSSG into GSH. MT, PC and GSH involved in metal chelation may transport inside vacuole with the help of transporter. ROS causes alteration in metabolisms and respiration, DNA damage, protein oxidation, lipid peroxidation, alteration of cell membrane, and sometimes cell death. Diffused metal ion in the cytoplasm causes binding of protein, DNA, and –SH- and –COOH-containing molecules and alteration of cell metabolisms and respiration

different metas (Mn, Zn, Ni, Cu, Co, Cr, Fe, and Pb) from coal washery effluent at different concentrations, while Gola et al. (2018) reported the highest removal within 120 h for Cr(IV) and Zn(II) by growing cell *Beauveria bassiana.*

HM removal and initial metal ion concentration

The initial concentration of the solutes is the effective variant which directly affects the adsorption rate. It is important in both cases, remediation by growing fungi and by fungal biomass. In the case of growing fungi, with an increase in the concentration of heavy metals, firstly, removal rate is increased, but after reaching their optimum concentration, the removal rate decreases. The first phenomenon that occurred may be due to available active sites on the surface of growing fungi and increase in interaction between HMs and growing cell fungi which favor maximum removal. On the other hand, metal accumulation was controlled by time, growth, and metabolic rate factor that also favor the metal removal. But the higher concentration of HMs causes toxicity to the growing fungi which leads to slower sorption and removal rate by affecting the metabolic rate and growth of the fungus. Samadi et al. (2017) reported that the presence of lead increases the production of fungal biomass in mostly filamentous forms in the first and last stages of cultivation. The fungus *Lentinus cladopus* was cultivated in the presence of different metal (Fe, B, Mn, Mo, and Zn). It was observed that the amount of produced biomass decreased with increasing the concentration of iron and boron from 1 to 2 mg/L, while the biomass concentration was increased by increasing the concentration of zinc, manganese, and molybdenum in the same range (Arti and Guleria 2013). The mycelial pellets of *Penicillium simplicissimum* impregnated with powdered biochar (MPPSIPB) were used in the removal of Cr(VI) from an aqueous medium, and it is reported that at 100 mg/L, the removal of Cr(VI) by MPPSIPB was 95.0% (Xu et al. 2015). They concluded that the presence of biochar powder not only can protect mycelial pellets from the toxicity of Cr(VI) but also can enhance the removal rate of Cr(VI).

In the case of fungal biomass (dead and treated), influence in removal rate occurred the same as growing fungi, first, with an increase in the concentration of HMs which quickly saturate the active site (Christoforidis et al. 2015), but after reaching equilibrium, the removal rate decreases. An increase in removal rate increases the availability of metal ions to saturate the available active sites or due to the concentration gradient of the solution and fungal biomass (Zang et al. 2017; Saravanan et al. 2015). The lower metal concentration gradient causes a decrease in transport due to the enhancement in the diffusion rate (Chen et al. 2012). But after reaching equilibrium concentration, a decrease in removal rate may be due to the unavailability of active sites on adsorbent and repulsion between adsorbed HMs and remaining HMs in the solution. Uzunoğlu et al. (2014) reported maximum removal at 100 mg/L for the removal of Cu(II) by *Sargassum acinarum* (seaweed). Zang et al. (2017) reported maximum adsorption capacity of *Auricularia auricula* at 200 mg/L concentration of Cr(VI) in the effluent, while Saravanan et al. (2015) applied mixed biosorbent of custard apple seeds and *Aspergillus niger* in the removal of Cr(VI) and Ni(II) and reported that with an increase in the concentration of the metal, the specific removal rate of mix biosorbent decreases.

Amount of fungal biomass and HM removal

The dose of the fungal adsorbent is an important factor in adsorption studies. The higher doses of adsorbent lead to an increase in the interaction of HMs with adsorbent and it also increases the availability of active sites. Xu et al. (2015) reported that the removal rate of Cr(VI) ion increased from 20.1% to 88.5% with the rise in the amount of mycelial pellets from 2 to 10 g/L and observed that the number of active sites increased with the rise the in the amount of biosorbent. Change in the removal rate with change in dose of fungal adsorbent was reported in some other studies due to similar effect as above explained; however, the used pollutant and adsorbent were different in all studies (Sathvika et al. 2015; Saravanan et al. 2015; Mondal et al. 2017).

Agitation rate and flow rate effect on HM removal

Generally, the agitation rate may affect the removal rate by fungi or fungal biomass, because adsorption or accumulation of pollutants with fungi or any other remediation agents depends on their interaction with pollutants. If the interaction rate is more between pollutant and remediation agents then the rate of removal of the pollutant will be high, and it also depends upon the pollutant nature and adsorbent characteristics. The agitation rate can influence the interaction rate between adsorbent and heavy metal, so it affects the removal. It is well known that heavy pollutants, after a duration of time, settle down on the bottom of the pot which may lead to slower interaction. Due to less interaction between fungal biosorbent and HM ion, the removal rate may slow down. Jadhav and Hong (2014) applied *Aspergillus niger* 34770 in the removal of tin and reported maximum removal rate at shaking speed 150 rpm and similar results were reported in other studies (Ting et al. 2000; Manorama et al. 2016). Mondal et al. (2017) reported that the shaking rate increased the adsorption capacity of Cr(VI) by *Aspergillus niger* and they found maximum adsorption at a shaking rate of 500 rpm. They explained that the enhancement in adsorption at a higher shaking rate is probably due to the thinning of boundary layer thickness near the adsorbent surface (Hanafiah et al. 2009; Choudhary et al. 2014). However, Mondal et al. (2017) found that the concentration of metal ions possibly increased at a higher agitation rate that increases the availability of metal ion to adsorb or accumulate inside the cell. After an optimum agitation rate, the removal rate may become constant or decrease which might be due to desorption at a higher shaking rate, decrease in concentration of metal ions after adsorption, decrease in the availability of active sites, the repulsion between adsorbed and remain metal ions of the solution, decrease in the attraction force between adsorbent and metal ion, and decrease in the growth of the fungus without base or physical damages at high speed.

Flow rate is the major function of a continuous experiment which affects the interaction rate and contact time between fungi and metal ions. Zang et al. (2017) reported that with increasing flow rate from 20 to 40 mL/min, uptake capacity of modified and immobilized *Auricularia auricular* spent substrate in fixed-bed column decreases from 6.755 to 5.201 mg/g. The fast flow rate which was unable to provide sufficient time for metal ions to diffuse inside of the pore of the bioadsorbent delayed the equilibrium stage from their schedule (Kumar et al. 2011; Zang et al. 2017). However, microbial consortia of bacteria and fungi showed optimum removal at the flow rate of 1–5 mL/min (Migahed et al. 2017) and almost similar results (2.5 mL/min) were recorded with glutaraldehyde-alginate-fungi biocomposite (Aftab et al. 2014). Studies recommended a slow flow rate should be preferred to attain better removal in order to provide an adequate interaction time between the pollutants and used bioadsorbent (Migahed et al. 2017; Zang et al. 2017). This hypothesis also regulates the removal of pollutants by growing fungi.

Conclusion and future aspects

No doubt, heavy metals are the major pollutants of the environment that have serious issues to human health and the environment. The conventional treatment technologies have many disadvantages, so bioremediation is one of the alternatives to these technologies that can give an efficient and sustainable approach for the treatment of HMs contaminated wastewater. From the metal treatment perspective, several fungal species have been explored that have the potential to treat the HM-contaminated wastewater. Much of the studies have focused on single or binary metal-contaminated wastewater, but the studies that target more than two metals are very little in the public domain. The fungal consortium also gives appreciable results. However, multiple metal-contaminated sites are the best source for the isolation of metal-tolerant fungus. These contaminated sites also contain many types of pollutant other than HMs, including nitrate, phosphate, sulfates, fluoride, polyaromatic hydrocarbons, pesticides, etc. and studies have reported the capability of many fungal species to remove these pollutants (one or more of them). So, fungal application in the simultaneous treatment of HMs with other pollutants is a novel approach and potential application in wastewater treatment. Many of the metal tolerant fungal species show a mutual relationship with plants that can also be used in the crops to reduce the accumulation of HMs in the grains.

From the technological perspective for large-scale wastewater remediation, HM-tolerant fungal-plant mutual relation can also be applied in the constructed wetlands for wastewater treatment, very less studied at the present. The technologies such as biofilter and bioreactor containing fungi (either utilizing in viable form or dead form) have great potential in large-scale application for the treatment of HM-contaminated wastewater. These bioremediation techniques are highly efficient in batch as well as in continuous mode. However, the continuous mode will be more effective with a viable form of fungal application because of the self-replenishing ability of fungi.

HM tolerance is the basic characteristic of fungi for their utilization in bioremediation. Table 2 shows that most HM-tolerant fungi belong to the class ascomycetes, but the link between them on HM tolerance needs more scientific concern. Challacombe et al. (2019) highlighted the similarities of some ascomycetes to survive in the arid environment that can be followed as a model study to get insights on HM tolerance similarities between ascomycetes fungi. Further, the pathway of Hg methylation and molecular signaling of HMs in fungi are not fully explored. A set of genes are involved in tolerance and accumulation of HMs via regulating different types of protein, PCs, MTs, amino acids, transporter, etc. that have an imperative role in metal homeostasis inside the cell. So, overexpression of these regulating and functional genes via genetic engineering may give highly efficient fungal isolate for HM decontamination such as AfYap1 overexpression in *A. fumagatus* Af293 (Wild Type) involved in sensing of Cu and Cd. Through genetic engineering, the utilization of pathogenic fungus can also be avoided and the remediation efficiency of microbes can be improved, it has great potential in the future. Furthermore, the mechanisms that deal with tolerance and removal of HMs by fungi give unexpected results but its full potential remains to be exploited.

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