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REVIEW

Heavy metals and soil microbes

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Abstract Heavy metal pollution is a global issue due to health risks associated with metal contamination. Although many metals are essential for life, they can be harmful to man, animal, plant and microorganisms at toxic levels. Occurrence of heavy metals in soil is mainly attributed to natural weathering of metal-rich parent material and anthropogenic activities such as industrial, mining, agricultural activities. Here we review the effect of soil microbes on the biosorption and bioavailability of heavy metals; the mechanisms of heavy metals sequestration by plant and microbes; and the effects of pollution on soil microbial diversity and activities. The major points are: anthropogenic activities constitute the major source of heavy metals in the environment. Soil chemistry is the major determinant of metal solubility, movement and availability in the soil. High levels of heavy metals in living tissues cause severe organ impairment, neurological disorders and eventual death. Elevated levels of heavy metals in soils decrease microbial population, diversity and activities. Nonetheless, certain soil microbes tolerate and use heavy metals in their systems; as such they are used for bioremediation of polluted soils. Soil microbes can be used for remediation of contaminated soils either directly or by making heavy metals bioavailable in the rhizosphere of plants. Such plants can accumulate 100 mg g^{-1} Cd and As; 1000 mg g^{-1} Co, Cu, Cr, Ni and 10,000 mg g^{-1} Pb, Mn and Ni; and translocate metals to harvestable parts. Microbial activity changes soil physical properties such as soil structure and biochemical properties such as pH, soil redox state, soil enzymes that influence the solubility and bioavailability of heavy metals. The concept of ecological dose (ED_{50}) and lethal concentration (LC_{50}) was developed in response to the need to easily quantify the influence of pollutants on microbial-mediated ecological processes in various ecosystems.

Keywords Soil microbial biomass · Metal pollution · Bioremediation · Biosorption · Bioavailability · Rhizosphere · Anthropogenic · Ecosystem · Phytoremediation

Introduction

Heavy metal pollution is widespread in the environment. Heavy metals are those elements with density greater than five and constitute more than 35 % of the elements in the periodic table. Some of them like zinc (Zn), iron (Fe), copper (Cu), molybdenum (Mo), manganese (Mn) are important in plant and animal nutrition in a very low concentration. They participate in redox processes and osmoregulation and act as cofactors of enzymes (Silver and Phung 2005). The use of metals by both prokaryotic and eukaryotic microbes for structural and/or catalytic functions is a well-known phenomenon (Gadd and Griffiths 1978; Gadd 1990; Rosen 2002; Khan et al. 2009; Novarro-Noya et al. 2010; Gounou et al. 2010). A typical example of microbial utilization of heavy metals is depicted in Figs. 1 and 2. In Fig. 2, the organisms use the metals to enhance their growth and metabolism.

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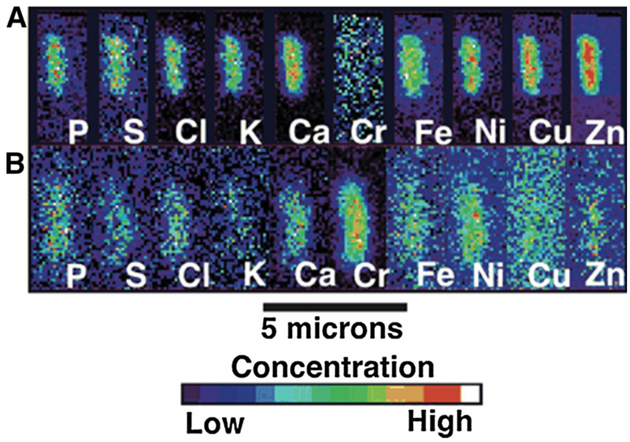

Fig. 1 False-colour micro-XRF maps of qualitative spatial distributions and concentration gradients of elements in and around planktonic *P. fluorescens* microbes harvested before (**A**) and after (**B**) exposure to potassium dichromate [Cr(VI)] solution (1000 ppm) for 6 h (Kemner et al. 2004)

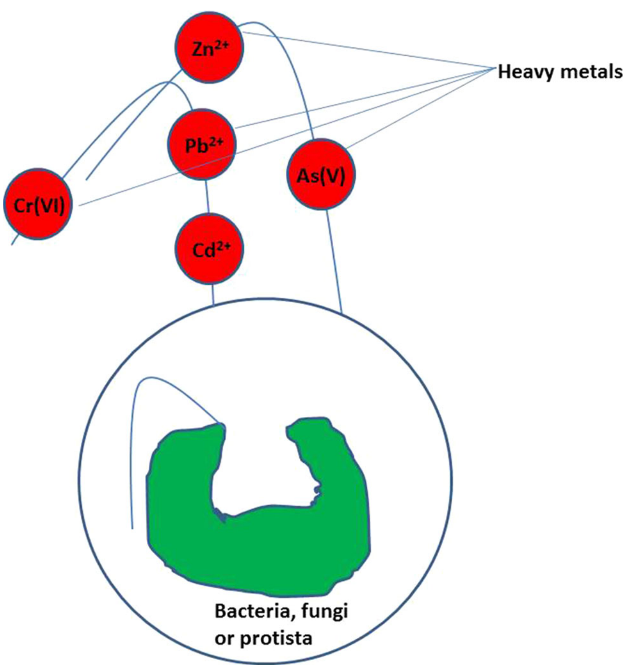

Fig. 2 Microbial utilization of heavy metals through ingestion and subsequent removal or detoxification of the heavy metals. The microbes ingest, solubilize and assimilate the metal into its biological system

However, beyond a certain threshold level, they are all regarded as poisonous and deleterious to plant and animal health. Some heavy metals have no essential function in the life cycle of living organisms (e.g., mercury (Hg), cadmium (Cd), lead (Pb)). They can damage cell membranes; disrupt enzymatic and cellular functions; damage the structure of DNA; modification of protein structure and replacement of essential elements (Bruins et al. 2000; Göhre and Paszkowski 2006). Heavy metals may therefore impair the life cycle of living organisms. This is attributed to their long biological half life, toxicity and non-biodegradability (Alloway 1995; Adriano 2001).

Soil microbes are integral and essential components of the ecosystem (Harris 2009). There is complex interaction between various components of the soil ecosystem including microbial biomass and soil chemical contaminants such as heavy metals and radionuclides (Kabata-Pendias 2001). Besides soil properties like pH (Fierer and Jackson 2006), soil type (Wu et al. 2008; Bach et al. 2010), salinity (Rajaniemi and Allison 2009) that significantly influence the soil microbial biomass, their activities and dynamic behaviour may be governed by the level and type of chemical contaminants such as heavy metals. However, some microorganisms like bacteria, protista and fungi can degrade heavy metal compounds and transform the end product into part of their metabolism with the aid of specialized enzymes. During the process, the heavy metal is either removed or transformed into nontoxic compound. Metal mobility and bioavailability have been shown to be reduced by soil microbes through biosorption and bioprecipitation (Zhuang et al. 2007; Pajuelo et al. 2011). These mechanisms also help in immobilization of heavy metals in the soil (Méndez and Maier 2008). Figure 3 shows a microbial transformation of Fe(III) to Fe(II) and immobilization of heavy metals. These and other mechanisms of heavy metal immobilization and sequestration by soil microbes shall be discussed in details. Human activities constitute the major source of heavy metals pollution while their solubility, movement, retention and availability are mainly controlled by the soil chemical matrices. High metal concentrations in living tissues of organisms have resulted to severe organ impairment, neurological disorders and eventual death.

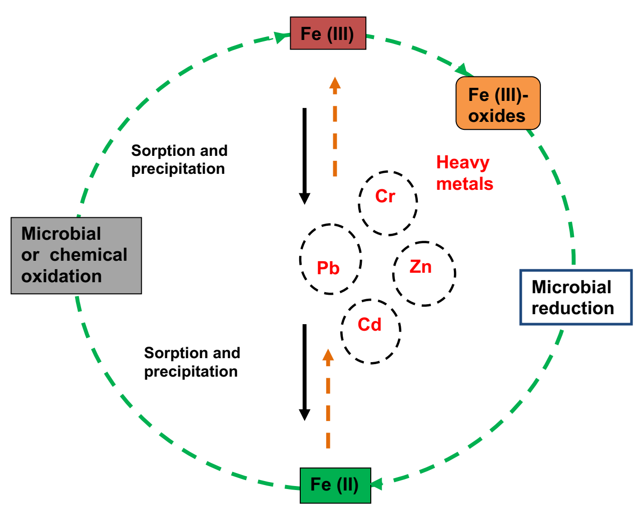

Fig. 3 Diagrammatic illustration of the iron cycle and its involvement in heavy metal immobilization. Modified from Burkhardt et al. (2010)

Heavy metals in the environment

Sources of heavy metals pollution

Heavy metals are derived from two major sources: natural and anthropogenic. Anthropogenic contamination of the environment with heavy metals is the most widely distributed and most deleterious. This is probably as a result of their instability and solubility and hence bioavailability (Abdu et al. 2011a). Human activities such as smelting, mining, agricultural activities such as mineral fertilizer and sewage sludge application and pesticide use, industrialization, metal-containing waste disposal and military activities such as weapon testing are varieties of anthropogenic heavy metal contamination sources. Building materials like paints, cigarette smokes, metallurgy or smelting, aerosol cans and sewage discharge are all anthropogenic sources of heavy metals (Abdu 2010). Colouring of plastics during manufacturing is achieved through addition of pigments containing heavy metals. Coating of cutleries, industrial and hand tools, aeroplane parts, automobile and truck parts with heavy metals such as Cd are common anthropogenic sources of pollution (Kirkham 2006). The use of Cd as luminescent dials and rubber curing also contribute to heavy metal pollution (Adriano 2001). Wearing and tearing of automobile parts is a major exposure route of heavy metals to the environment. Cadmium can be released from automobile tires as it wears which can be transported into the sewage system through run-off (Kirkham 2006) or as particulate matter into the atmosphere.

Weathering and pedogenesis are the major natural sources of heavy metals. Mineral ores like galena, cerussite, cassiterite and arsenopyrite can undergo dissolution through chemical weathering thereby releasing heavy metals contained in their structure (Abdu 2010; Abdu et al. 2011b). Heavy metals are constituents of primary and secondary minerals through the process of inclusion, adsorption and solid solution formation termed as coprecipitation (Sposito 2008). Acid rain and dew are also natural sources of heavy metal pollution (Nriagu 1990). Atmospheric dust storms, wild forest fires and volcanic eruptions are input routes for natural heavy metal pollution (Naidu et al. 1997). The effect of pedogenic heavy metal pollution may override that of anthropogenic sources especially when the parent material contains high level of heavy metal (Brown et al. 1999).

Availability and movement of heavy metals in soil

Soil chemical component is the major determinant of heavy metal movement and availability in the soil. Hydrous oxides and hydroxides of iron, aluminium and manganese are major soil chemical components contributing to heavy metal mobility in the soil (Tack et al. 2006). The large affinity of the crystalline and amorphous form of these metal oxides and hydroxides for heavy metals influences the movement and sorption of metals in soil (Abdu 2010). The binding effect of organic matter on soil components also influences the availability of heavy metals (Naidu et al. 2003). The diverse functional groups in organic substances which often dissociate easily under alkaline condition also affect the availability of toxic heavy metals in the soil. Formation of metal–organic compounds in the soil is achieved through the interaction of humic substances with sesquioxides such as oxides of Fe, Al and Mn. Heavy metals occluded in the oxides of these metals are often referred to as relatively active fractions (Shuman 1985). Agbenin (2002), however, observed inhibitory effect of soil organic matter on crystallization of heavy metal occluded in Mn and Fe oxides in soils of the Nigerian savanna.

The chemistry of the aqueous soil phase exerts a profound influence on metal mobility. Acidic conditions tend to increase the mobility of heavy metals as a result of proton competition and decreased negative binding sites (Horckmans et al. 2007). Conversely, at elevated soil pH heavy metals such as Pb may be precipitated as insoluble hydroxides. However, the functional groups present in organic matter may dissociate under alkaline conditions thereby increasing bioavailability of organic matter-bound heavy metals (Fine et al. 2005). Competition for metal cations by organic complexing ligands and soil colloidal surface especially at elevated pH also increases heavy metal mobility and bioavailability in soil (Abdu 2010). This might be attributed to the pH-dependent dissolution/precipitation and redox reactions of the hydrated metal oxides in the soil (Tack et al. 2006). Soil pH is often the most important soil chemical properties influencing heavy metal mobility in the soil. It exerts a strong influence on metal solubility, adsorption and desorption processes and on metal speciation in the soil–solution interface. Christensen (1984) observed a twofold increase in heavy metal concentrations in soil solution due to a unit increase in soil solution pH. Bioavailability is a term used to describe the release of a chemical from a medium of concern to living receptors such as plant roots (Adriano 2001) and microbes. In relation to heavy metals, it is defined as the fraction of a metal in the soil that is accessible to the food chain, plants (Misra et al. 2009) and other components of the soil microbial biomass. Mycorrhizal fungi under symbiosis can increase the adsorptive surface area of plant roots thereby influencing heavy metal uptake (Alloway 1995). Wang et al. (2009) reported modification of heavy metal movement and fixation as a result of root excretion of organic acids that form complexes and chelates with metal ions.

The effects of root exudate on soil microbial population and diversity and on the chemistry of the rhizosphere may also alter the mobility and retention of heavy metals (Giller et al.1998).

Dehydration and re-crystallization of precipitates of hydrous metal oxides with time known as metal ageing often reduce the mobility of the metal associated with these oxides. The same process was observed by Lock and Janssen (2003) to reduce heavy metal bioavailability in soil with time.

Effect of heavy metals on the ecosystem

The persistence and long biological half life of heavy metals coupled with their ubiquitous nature in the environment make them a nuisance to the ecosystem. The fate of metal contaminant in an ecosystem depends on chemical properties of the metal, abiotic factors within the ecosystem and interaction with the biotic environment. These can result into either degradation, transformation into another phase or bioaccumulation (Timothy et al. 1999), which will then be hazardous. The major effect of heavy metal on the ecosystem is biomagnifications in the tissue of living organisms. The effect of heavy metal pollution on an ecosystem starts with active or passive uptake of heavy metals by primary producers (phytoplankton). Primary consumers feed directly on the phytoplankton while secondary consumers feed on either or both the primary producers and primary consumers. As we advance up the trophic level, higher consumers and top predators will eventually be affected. Different toxic effects of heavy metals to different components of the ecosystem have been reported. Toxic effects of lead on organisms include reduced growth and reproduction, impairment of blood chemistry by inhibiting heme formation (Eisler 1988), lesions and behavioural changes (Timothy et al. 1999). Reduction in muscle condition with eventual alteration in feeding activities was observed in hawks under elevated lead exposure (Osborn et al. 1983). The most severe effect of lead poisoning is death. Recently, in northern Nigeria a case of over 800 deaths of people mostly children has been reported as a result of lead poisoning through mining activities. Heavy metals accumulate in mammals, especially in the kidney, liver and reproductive organs. Effect of cadmium in humans includes renal dysfunction (Kirkham 2006), pulmonary emphysema and the notorious Itai–Itai (‘ouch–ouch’) disease (Yeung and Hsu 2005) which results in painful bone demineralization (osteoporosis) (Kirkham 2006) and resulted to the death of hundreds of people in Japan. Heavy metal pollution has been reported to significantly reduce human life expectancy in Romania (Lăcătuşu et al. 1996). In Turkey, high occurrence of upper gastrointestinal cancer has been correlated with heavy metal pollution (Türkdoğan et al. 2003). Jarup (2003) reported Cd and Pb to be associated with the aetiology of a number of cardiovascular, kidney, blood, nervous system and bone diseases in man.

Elevated concentrations of heavy metals in soils have been shown to decrease soil microbial biomass, diversity and activities. However, certain soil microorganisms are used for remediation of heavy metal-polluted environments. This is as a result of certain physiological mechanisms they exhibit which enable them to tolerate and utilize heavy metals in their systems. They also aid in making heavy metals bioavailable in the rhizosphere of plants that are used in phytoremediation.

Heavy metals and soil microbial biomass

Toxicity of heavy metals to soil microbes

The soil microbial biomass population is under tremendous pressure due to contamination by a variety of toxic substances such as pesticides, heavy metals and organic pollutants such as sewage sludge and waste water of environmental origin (McGrath et al. 1988; Chaudhary and McGrath 1996). A review about toxicity of heavy metals to microorganisms and microbial processes in agricultural soils has been given by Giller et al. (1998).

Soil microbes utilize some heavy metals as electron donors or acceptors during the process of metabolism. In such case, high amount of the metal is employed by the microbes without manifestation of toxicity. Such metals are usually those with variable oxidation states like chromium, vanadium, arsenic, selenium, copper, iron and manganese. Despite the utilization of heavy metals by soil microbes, microorganisms have been the most sensitive of all living soil organisms to heavy metal stress (Giller et al. 1998). High level of metal pollution has been reported to inhibit the activity of soil microorganisms through accumulation of organic matter at the surface soil layer (Strojan 1978; Freedman and Hutchinson 1980). Adverse effects of heavy metals on soil microbial activities have been reported as early as the 1910s, but severe consequence of metal pollution on microbial diversity, processes and the ecosystem became more glaring in the 1960s–1970s (Giller et al. 1998). The first documented report of heavy metal toxicity on soil microbial activities was the work of Lipman and Burgess (1914).

Mechanism of the toxicity of heavy metals to soil microbes

Microorganisms in less heavy metal-polluted soils were found to utilize higher amount of carbon for assimilation with smaller amount released as CO_2 in the dissimilation process, than in polluted soils. The synthesis of microbial biomass in heavy metal-polluted soils was found to be less effective than in non-polluted soils due to the stress caused by heavy metals (Smejkalova et al. 2003). In polluted environments, microorganisms require more energy to survive due to unfavourable conditions. Therefore, a higher portion of consumed carbon by the microorganisms is released as CO_2 and a smaller part built into organic components (Smejkalova et al. 2003). The pollution causes more pressure on sensitive microbes and thus changes the diversity of soil microflora representative groups of microorganisms (Zaguralskaya 1997).

There have been reviews on the effect of heavy metals on microorganisms such as that of Trevors et al. (1986) that have dealt with mainly in vitro studies of biochemical and physiological mechanisms. Some others studied the effects of metals on microorganisms (Giller et al. 1998, 2009; Abdousalam 2010). Heavy metals influence the microbial population by adversely affecting their growth, morphology, biochemical activities and ultimately resulting in decreased biomass and diversity (Roane and Pepper 1989). They can damage the cell membrane, alter enzymes specificity, disrupt cellular functions and damage the structure of the DNA (Rathnayake et al. 2010). Toxicity of heavy metals could occur through the displacement of essential metals from their native binding sites or through ligand interactions (Bruins et al. 2000). It could also occur as a result of alterations in the conformational structure with oxidative phosphorylation and osmotic balance (Bruins et al. 2000). A summary of heavy metals toxicity to plants and soil microorganisms is represented in Figs. 4 and 5.

Effects of heavy metals on microbial diversity

Ecotoxicological studies have shown a decreased microbial population and alteration of the microbial diversity and structure as a result of heavy metal toxicity (Brookes and McGrath 1984; Frostegard et al. 1993; Leita et al. 1995; Witter and Dahlin 1995; Kandeler et al. 1996; Knight et al. 1997; Chaudri et al. 1993, 2000; Megharaj et al. 2003; Barajas-Aceves 2005; Linton et al. 2007; Giller et al. 2009).

Significant inhibition of carbon (C)–biomass occurred in soils highly contaminated by heavy metals (Smejkalova et al. 2003) which corroborated data obtained by Brookes and McGrath (1984) who observed only half content of biomass in soil-contaminated heavy metals compared to uncontaminated soils. Dias et al. (1998) even observed higher than 80 % inhibition of C–biomass by heavy metals, just as Abdousalam (2010) observed microbial biomass C to sharply decrease with Cd and Ti, whereas the addition of Pb did not have any significant inhibitory effect on the level of microbial biomass C. Similar significant negative effects on microbial biomass and its metabolic activities have been described in many other studies such as that of Brookes (1995). Thus, it has become clear and obvious that metal-contaminated soil can have its microbial diversity and population adversely affected.

The observed effects of heavy metals on microbial biomass were related to the total concentration of heavy metals or to the water-soluble concentration (Hund-Rinke and Kordel 2003). However, because bacteria are present within colonies in the soil (Harris 1994), they often may not be exposed to the equilibrium solution, activity of heavy metals (Hund-Rinke and Kordel 2003). Water-soluble heavy metals are thought to be more available to organisms and thus may be considered to be better indicator for microbial biomass dynamics (Anand et al. 2003).

Contamination of soil with high rates of Cd was observed to cause a significant decrease in the number of oligotrophic bacteria, oligotrophic sporulating bacteria and copiotrophic and copiotrophic sporulating bacteria in the soil (Wyszkowska and Wyszkowski 2002). In a study by Ahmad et al. (2005) pollution of the soil with salts of Cu, Cd, Cr, Hg, Mn, Ni, Pb and Zn under laboratory conditions showed sensitivity of aerobic heterotrophic bacteria to metal groups like Ni and Cd, followed by Cu, Cd, Hg, Mn, Cr and Zn. These authors also reported symbiotic nitrogen fixers showing higher sensitivity to metal groups like Cd, Pb, Hg followed by Cu, Cr, Mn and Zn. Actinomycetes were found to be most sensitive. They observed that metal toxicity to be concentration and time dependent (Ahmad et al. 2005).

Copper toxicity was observed to decrease the number and diversity of Collembola (Filser et al. 1995), it was also reported to decrease microbial biomass (Baath 1989), and it inhibits the activities of cyanobacteria (Pipe 1992). It was also reported by Fritze et al. (1996) to have decreased soil respiration activity. Arsenic was observed to decrease plant root activity while lead decreased microbial activity (Turpeinen 2002). Similarly, Rasmussen and Sorensen (2001) reported a decreased microbial diversity as a result of mercury toxicity. Cadmium, Zn, Cu, Pb, Cr and Ni were all reported to decrease bacteria population, inhibited phosphatase, urease and dehydrogenase activities in a metal-polluted soil (Gao et al. 2010).

Adaptation to and utilization of heavy metals by microbes

Microbes utilize heavy metals and exhibit different tolerance in their utilization in the soil. Soil microbial biomass plays indirect roles in phytoremediation of heavy metals by indirectly acting in the plants rhizosphere and influence

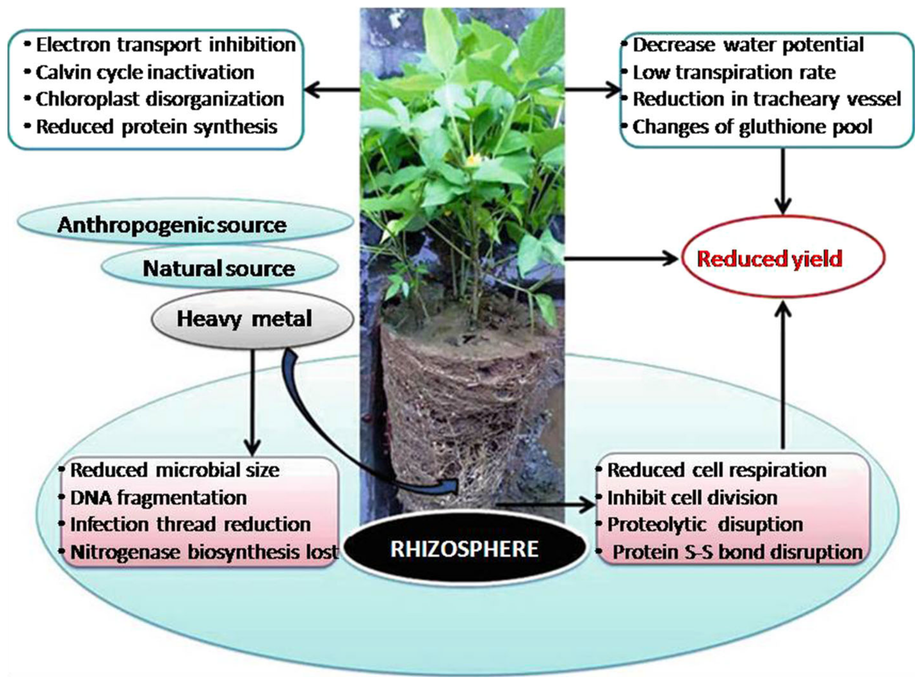

Fig. 4 Toxic effect of heavy metal on various stages of plant metabolism. (Adapted from Ahmad et al. 2012 with permission)

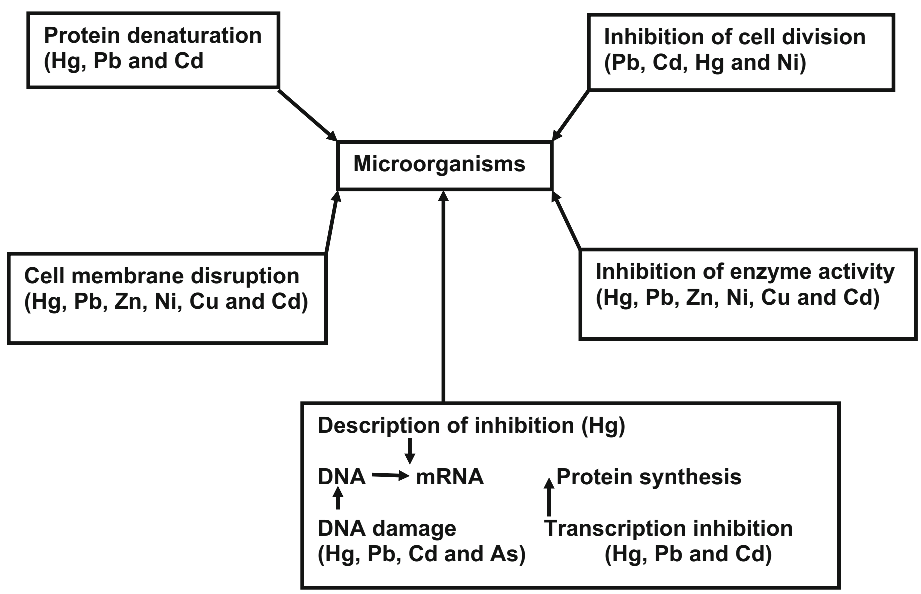

Fig. 5 Mechanisms of heavy metal toxicity to soil microbes. (Adapted from Turpeinen 2002)

chelated or complexed metals into soluble forms that are readily available for plant uptake. Naees et al. (2011) found a certain bacteria (Burkholderia spp.) to increase the bioavailability of Pb and Cd and increase their uptake by maize and tomato plants.

Soil microbes have devised several mechanisms to combat and mitigate the effect of heavy metal toxicity on their survival. Microbes are equipped with genes that enable them accumulate heavy metals beyond a certain limit and also possess the ability to modify or transform heavy metals into less toxic forms. Such microbes can survive and reproduce in a heavy metal-contaminated environment. Scientists have taken advantages of these specialized genes in organism in the field of bioremediation. Soil fauna and flora have used the following strategies or mechanisms to adapt and survive heavy metal-polluted environments:

Tolerance

This refers to the ability of microorganisms to survive and thrive under conditions of heavy metal stress while still maintaining normal physiological, reproductive and biochemical functions. Tolerance of soil biota towards heavy metals involves different mechanisms and involves binding of the metal by the cell wall or proteins; formation of insoluble metal complexes, volatilization and removal from the soil. This tolerance depends on the sensitivity of microorganisms to certain heavy metals in the soil. It also depends on the level of organization of the soil biota and goes by the order of soil macrofauna being more sensitive than microfauna which are in turn more sensitive to the microflora (Fig. 6). Kandeler et al. (2000) found a sensitivity of microbial enzyme functions and increasing metal levels. While several studies show the negative effects of heavy metals on soil microbial biomass and enzyme activities, elevated levels of Pb in monocultures had no effect on biomass C, urease and acid phosphatase activities (Yang et al. 2007). The same study suggests that the coexistence of plant species under elevated levels of Pb increases the functional diversity of soil microbes and increases urease activity and hence decreases the negative effect of Pb to soil biota (Yang et al. 2007). Vig et al. (2003) emphasized that the effect of Cd bioavailability and toxicity on biota varies with time, soil type, speciation, ageing, Cd source, organisms and the environmental factors.

Tolerance and uptake capacities have been identified as essential characteristics of organisms that enable their use in bioremediation (Macaskie and Dean 1989). Several studies have reported tolerance of micro- and macroorganisms to heavy metal toxicity (see, for example, Gadd and Griffiths 1978; Rehman and Anjum 2010). Tolerance of organisms especially plants to excessive concentration of heavy metals may be through the prevention of uptake into the root (by complexation with root exudates) or limited translocation from the root to the shoot, an adaptive mechanism referred to as exclusion, and it may be through the process of detoxification which is an internal tolerance mechanism and occurs either by vacuolar compartmentation of the metal or binding (Tarradelas et al. 2005; Rama Rao et al. 1997). This mechanism prevents internal cellular injury and is mainly through the production of varieties of metal chelating organic compounds (Tarradelas et al. 2005) and binding of heavy metals to rhizodermal cell walls, thus avoiding heavy metal uptake (Göhre and Paszkowski 2006). It could also be by biochemical tolerance like enzymatic adaptations (Baker and Walker 1990). A typical heavy metal sequestration mechanism in the rhizosphere is shown in Fig. 7. Other mechanisms are regulation of metal uptake and transformation into less toxic forms (Rama Rao et al. 1997; Gharieb and Gadd 1998).

The relationship of microorganisms to heavy metal pollution is complex and contradictory in case of sewages sludge application to the land (Smith 1991), some positive and negative interactions between metals upon their toxic effects on microorganisms have been reported by Abdou-salam (2010), and there is enormous disparity as to which heavy metal concentrations are toxic (Baath 1989). Microorganisms interact with metals in many ways, and several metals are essential to microorganisms because they are electron acceptors or cofactors in enzymes, whereas other metals are toxic (Collins and Stotzky 1992). Muhlbachova and Simon (2003) showed the activity of the microbial pool to differ among contaminated soils and that in long-term contaminated soils it may not be necessarily lower even in the presence of toxic elements (Muhulbachova and Tlustos 2006). Artificial contamination of soils of known physicochemical characteristics with metal salts and enumeration of the surviving indigenous populations, in a short-term study, revealed the occurrence of microbes in a particular soil sample with intrinsic ability to tolerate metals (Ahmad et al. 2005). An earlier observation also revealed that heavy metal tolerance by a particular group of bacteria or an individual isolated in artificial media supplemented with heavy metals was high (Ahmad et al. 2001; Hayat et al. 2002).

The tolerance of certain soil bacteria to heavy metals has been proposed as an indicator of the potential toxicity of heavy metals to other forms of biota in soils (Olsen and Thornton 1982; Hassen et al. 1998). The bacteria *E. coli* is known to bind heavy metals like Cd and Cu through metal-binding peptides and membrane-associated proteins like LamB (Gadd 2000). Two gram-positive isolates of bacteria; *Paenibacillus* sp. and *Bacillus thuringiensis* were identified as tolerant (Rathnayake et al. 2010). When the metal tolerance of both was compared, *Paenibacillus* sp. showed the highest sensitivity to Cu, whereas *Bacillus thuringiensis* showed the highest sensitivity to Cd and Zn. These findings reveal the potential of *Paenibacillus* sp. in developing biosensor to detect Cu in environmental samples (Rathnayake et al. 2010). This also involves several genes encoding metal uptake transporter and trafficking proteins like Nramp3, RAN1 and AtHMA3 (Thomine et al.

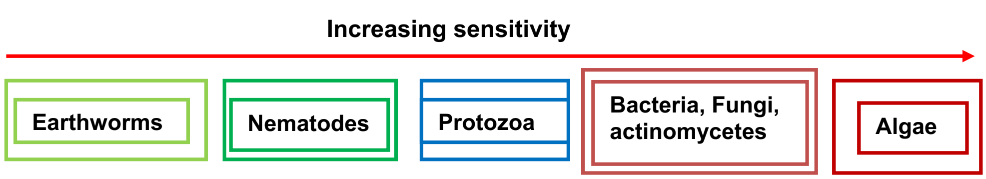

Fig. 6 A schematic representation showing sensitivity of soil organisms to heavy metals. Adapted from Vig et al. (2003)

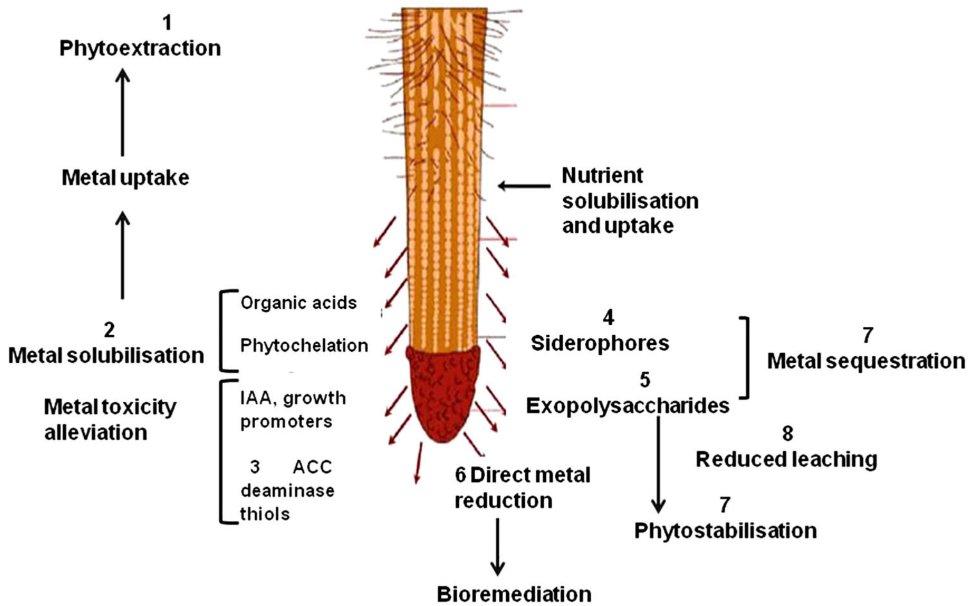

Fig. 7 Mechanisms of heavy metal sequestration and detoxification in the rhizosphere. *1* The use of hyperaccumulating plants to remove organic and inorganic contaminants from soil by concentrating them in the harvestable parts. *2* Transformation of metals into easily adsorbable form by organisms. *3* Plant growth promoters: IAA; Indole Acetic Acid, ACC; 1-Aminocyclopropane-1-Carboxylate. *4* Highly specific metal ligands and chelates produced by bacteria and fungi that regulate iron availability and assimilation in the rhizosphere. *5* Metal-binding organic compounds produced by microorganisms. *6* Mobilization of metals through direct reduction and oxidation processes by consortium of soil bacteria. *7* Complexation or immobilization of metals in a nontoxic form. *8* Solubilization and subsequent leaching of metal compound such as metal sulphide by *Thiobacillus* species. (Adapted from Kamaludeen and Ramasamy 2008 with permission)

2000; Hirayama et al. 1999; Gravot et al. 2004). Bioavailability of Cd, Pb and associated toxicity to soil biota, however, varied with time, soil type, speciation, ageing, Cd and Pb sources, organisms and environmental factors (Abdousalam 2010).

Redox transformations of heavy metals in the soil environment have been shown to aid microbial mobilization of toxic metals (Oremland et al. 1991; Gadd 1993; Phillips et al. 1995; Chang et al. 1999; Gharieb et al. 1999; Smith and Gadd 2000; Hobman et al. 2000; Lovley 2000; Gadd 2004). This is very clear as most redox reactions occurring in the soil environment require anaerobic bacteria as source of electron. This can, however, cause high metal availability through soil acidification especially when iron-oxidizing bacteria reduce iron pyrites to ferrous sulphate ($FeSO_4$) and sulphuric acid (H_2SO_4) (Giller et al. 1998). Moreover, some microbes use heavy metals through redox reaction as source of energy and growth and play a vital role in biogeochemical cycling of the metal ions (Spain and Alm 2003), for example, biomethylation of mercury (Hg(II)) to very toxic gaseous methyl mercury, and of lead to dimethyl lead by some certain bacteria species (Pongratz and Heumann 1999). It is still not very clear as whether microbial transformation of heavy metals through redox reaction is mainly for detoxification or for the benefit of the microbes during growth (Spain and Alm 2003). The possibility of a symbiotic relationship between soil microbes and polluted environments has been clearly demonstrated. Anaerobic sediments were found to accumulate arsenite in a microbe-mediated arsenic reduction by Brannon and Patrick (1987). Similar observation was made by Harrington et al. (1998) who reported microbial reduction of arsenate to arsenite. Certain sulphate-reducing bacteria have been demonstrated to contribute in the oxidation and reduction of certain toxic heavy metals and thus play a vital role in the cycling of such metals (Harrington et al. 1998). In general, microbial activities can either increase metal bioavailability and potential toxicity by solubilizing them, or reduce their bioavailability by immobilize them (Spain and Alm 2003).

Bioremediation

Bioremediation involves the use of microorganisms, green plants and vegetations in ameliorating or detoxifying the pollution that results from heavy metals. Microorganisms that have the capability of growing in heavy metal-polluted environment and also have a significant metal uptake are used in bioremediation (Shakoori et al. 2004). Microbial biomass of bacteria, fungi and yeast has been used severally in bioremediation (Shakoori and Qureshi 2000; Feng and Aldrich 2004; Rehman et al. 2007; Morales-Barrera and Cristiani-Urbina 2008). The use of microbes in remediation is through the process of reducing and immobilizing toxic metals (Francis and Dodge 1998). It has been shown that microbes in the family Geobacteraceae have been used in remediation of contaminated aquifer sediments with uranium through reduction (Holmes et al. 2002) and also in technetium reduction (Lloyd et al. 2000).

Hyperaccumulator plants that accumulate heavy metal beyond recommended level into their tissue without showing physiological symptoms (Baker and Brooks 1989; Baker et al. 1991; Entry et al. 1999) are also used in phytoremediation. For a plant to qualify as a hyperaccumulator, it must be able to accumulate more than 2 % of heavy metals (100 mg g^{-1} Cd and As; 0.01 % dry wt.), (1000 mg g^{-1} Co, Cu, Cr, Ni; 0.1 % dry wt.) and (10,000 mg g^{-1} Pb, Mn and Ni; 1 % dry wt.) and translocate them to the harvestable part (Reeves and Baker 2000; Watanabe 1997). In addition to these, the plant must have significant amount of root surface area (Prasad and Freitas 2003) and shoot biomass. It must be easy to handle with low maintenance cost (Prasad and Freitas 2003) and easily disposable without further contamination of the environment. Besides hyperaccumulating heavy metals in their tissues, they also survive the toxicity by total avoidance of the metal (Khan et al. 2009).

Salt et al. (1998) described six phytoremediation processes, viz. asses of phytoremediation, viz. phytostabilization, phytoextraction, rhizofiltration, phytovolatilization, phytodegradation and plant removal of pollutants from the air. Several plant species that accumulate and tolerate heavy metals otherwise known as hyperaccumulators have been used in the detoxification of metal-polluted soils. About 400 species of plants including fungi, weeds, and food crops to ornamentals have been identified to hyperaccumulate heavy metals (Prasad and Freitas 2003). Such plants may be native of metalliferous soils or not. Table 1 lists the common hyperaccumulator plants with the potential heavy metal tolerance as reported in the literature. Heavy metal hyperaccumulator plants are dominated by Asteraceae, Brassicaceae, Caryophyllaceae, Cyperaceae, Cunoniaceae, Fabaceae, Flacourtiaceae, Lamiaceae, Poaceae, Violaceae, and Euphorbiaceae families (Prasad and Freitas 2003). Though most of them are specific to contaminants, some still have the capability to hyperaccumulate more than one heavy metal (Table 1).

Water hyacinth grown in wastewater and soil of landfills may contain some microbes which may play some roles in phytoremediation of metals and nitrogen (Mehmood et al. 2009). Aspergillus niger, Azotobacter, Thiobacillus thiooxidans (A. ferrooxidans) play a vital role in bioremediation of metals and nitrogen compounds (Simmonds 1979; Pelczar Jr. et al. 1986; Frattini et al. 2000; Allegretti et al. 2006 and Pathak et al. 2009). The technique of phytoremediation is cheap and environmentally friendly; however, the problem still lies on how to dispose the plants after harvesting without further contamination of another environmental component. Incinerating the harvested biomass will definitely release the metal content into the atmosphere similar to incorporating them deep into the soil through leaching and eventual contamination of groundwater. The proposed disposal options of Salt et al. (1995) which include composting, air drying, ashing and compressing in a landfill could still be a source of contaminating the ecosystem.

Another major drawback of phytoremediation is low heavy metal removal rate by plants (McGrath et al. 2002; Rattan et al. 2002). Most hyperaccumulator plants are shallow rooted (Khan et al. 2009) and can therefore extract metal to a certain shallow soil depth.

Soil microbial population exists in different hierarchical order and performs different biochemical roles according to their organizational level and structure. Soil microbes used for bioremediation of heavy metal-polluted soils are mainly in the micro and mesolevels.

Components of microbial population

Components of soil microbial biomass

Soil biota makes up the biotic component of the soil systems and exists as living organisms that are either visible or so tiny to the human vision. They are made up from different levels of organization from cellular, tissue and systematic levels. Soil organisms play diverse roles in soil physical and biochemical processes. The activities of each group of organism depend on their sizes as well as their functional diversity within the soil habitat which led to their classification into functional groups. They are classified into functional group that includes ecosystem engineers, litter transformers, predators, decomposers, microregulators, soil borne pest and diseases and prokaryotic transformers (Swift et al. 2008). Soil organisms in these functional groups fall under major target groups of macrofauna, mesofauna and soil microbial biomass (microflora and microfauna). Characterization of the soil biota into target groups allows further discussion on the diversity and roles they play in the soil system.

Macrofauna

Macrofauna comprises mainly of soil animals that are 1 cm long and have a diameter greater than 2 mm. Macrofauna are the most conspicuous of the three target groups and are soil animals often referred to as the ‘soil ecosystem engineers’ (Lavelle et al. 1999) and play a significant role in

Table 1 Plant species exhibiting resistant to high dosage of heavy metals and with potential of phytoremediation

Plant	Metal	References
Brassica juncea	As, Cd, Cu, Pb, Hg, Zn, Cr, Ni, Se	Kumar et al. (1995), Salt et al. (1995), Zaidi et al. (2006), Watanabe (1997), Ebbs et al. (1997), de Souza et al. (1999), Mudgal et al. (2010)
Vetiveria zizanioides	Pb, Zn	Chen et al. (2000), Zhou et al. (2007)
Cardaminopsis halleri	Pb	Dahmani-Muller et al. (2000)
Spartina alterniflora	Pb	Windham et al. (2001)
Cynodon dactylon	Pb	Madejon et al. (2002)
Sorghum halepense	Pb	Madejon et al. (2002)
Helianthus annuus	Pb, Cd	Boonyapookana et al. (2005), Kirkham (2006)
Hemidesmus indicus	Pb	Sekhar et al. (2004), Chandra et al. (2005)
Pteris vittata	As, Pb	Ma et al. (2001), Caille et al. (2004), Wang et al. (2011)
Pteris cretica	As	Zhao et al. (2002)
Pteris umbrosa	As	Zhao et al. (2002)
Pteris longifolia	As	Zhao et al. (2002)
Alyssum sp.	Ni	
Hordeum vulgare L.	Cu, Cd, Zn	Ebbs and Kochian (1998)
Avena sativa L.	Cu, Cd, Zn	Ebbs and Kochian (1998)
Medicago sativa	Cu, Pb, Cr, Ni	Gardea-Torresdey et al. (1998)
Thlaspi caerulescens	Cd, Zn, Ni	Lombi et al. (2001), Goel et al. (2009), Mudgal et al. (2010)
Lycopersicon esculentum	Cd, Ni	Madhaiyan et al. (2007)
Phytolacca acinosa Roxb.	Mn	Xue et al. (2004)
Avena sativa	Cd and Pb	Pishchik et al. (2009)
Padina sp.	Cu, Pb	Sheng et al. (2004)
Sargassum sp.	Cu, Pb	Sheng et al. (2004)
Bidens pilosa	Pb	Salazar et al. (2016)
Tagetes minuta	Pb	Salazar et al. (2016)

soil structural formation. Their tunnelling and burrowing activities in mechanical mixing and bioturbation stabilize soil aggregates which in turn influences air and water movement (Swift et al. 2008; Ayuke 2010), and in the transformation and distribution of organic materials. Many macrofauna acts as litter decomposers and soil predators in their functional diversity. Examples of soil macrofauna are earthworm, termites, ants, beetles, millipedes, centipedes and large arachnids.

Mesofauna

Soil mesofauna are composed of animals whose sizes range 0.2–2 mm who function as predators and litter decomposers. They ingest organic matter and other soil microbes such as bacteria and fungi. This in turn influences the overall soil ecosystem performance by altering the population of microbes who mediate in the decomposition of organic matter (Emmerling et al. 2002). Examples of soil mesofauna include collembolan, enchytraeidae, acari (mites), protura, pauropoda, some nematodes and larval forms of macrofauna. There are evidences that suggest the significant role of mesofauna such as Collembola and enchytraeids in soil aggregate stability, water and air movements in compacted soils, and in the development of finely structured soils (Emmerling et al. 2002).

Microorganisms

Soil organisms can be grouped as microfauna and microflora whose sizes are less than 0.2 mm and are actively involved in different microbial processes in the soil. Soil fertility in natural agroecosystem depends on the microbial processes such as mineralization of organic nitrogen (N), carbon (C), sulphur (S) and phosphorus (P), transformation of soil organic matter and N_2 fixation, all of which are executed by soil microbial biomass (Brookes 1995). In decomposition of organic soil materials, alternate assimilation and release of N and C by soil microbes are involved (Mary et al. 1996), and the rate is often driven by the nature of the plant material and their corresponding C:N ratios. Cyanobacteria or blue-green algae resemble higher plants in their intracellular structure and have a significant importance to agricultural soils due to their ability to fix N. In recent years, the use of algae in bioremediation of wastewater in eutrophication studies is rapidly gaining grounds (Vig et al. 2003). Certain bacteria and fungi, pseudomonas, achromobacter, flavobacterium, streptomyces, aspergillus and arthrobacter form the free living organisms that thrive in the rhizosphere. They are known to solubilize phosphate and heavy metals and make it bioavailable (Dommergues et al. 1980; Naees et al. 2011). Metal detoxification mechanism by soil macro- and microorganism is represented in Fig. 8.

Microbial activities affect the soil's physicochemical and biological properties such as soil structure, pH, soil redox state, soil enzymes that influence the solubility and bioavailability of heavy metals in the soil.

Soil microbial parameters

Microbial parameters have been used as useful indicators to heavy metal contamination in soils (Kizilkaya et al. 2004). These parameters can be either microbial activities such as carbon (C) and nitrogen (N) mineralization, respiration, biological N fixation, measurable soil enzymes or the measure of the size of soil microbes at different functional levels or the total population as a whole (Brookes 1995). Different contamination studies make use of various combinations of microbial parameters as indicators of heavy metal pollution (Table 2). Giller et al. (1989) observed a decrease in effective symbiotic N fixation in clover plants in heavy metal-contaminated soils while Brookes et al. (1986) observed a decrease in N fixation and growth of blue-green algae in the presence of heavy metals. Several studies indicate a decrease in microbial population in heavy metal-polluted soils (Brookes and McGrath 1984; Giller et al. 1989; Chander and Brookes 1991) while others focus on the decrease in the activities of soil enzymes due to the presence of heavy metals in excess of a critical EU level (CEC: Commission of European communities 1986). According to Brookes (1995), combining microbial activities and measurements of microbial population rather than a single parameter provides a more useful indication of heavy metal presence in soil pollution studies. From their study, Kandeler et al. (1996) observed a decrease in microbial biomass and enzyme activities with increasing concentrations of heavy metals. The authors also discovered that enzymes associated with N, P and S cycling are more sensitive and having decreased activities in the presence of heavy metals. Decreased microbial biomass and activities were observed with increasing metal stress in the studies of Kuperman and Carreiro (1997), Yao et al. (2003) and Wang et al. (2007). Castaldi et al. (2004) and Kizilkaya et al. (2004) also observed a decrease in microbial population, respiration, reduced enzyme activities in soils polluted with heavy metals. All these studies show that soil microbial parameters can be useful bioindicators of heavy metal pollution in the soil although the mechanisms of how microbial response to heavy metals still remains an area of major challenge (Giller et al. 2009), in addition to the dynamics in microbial population, diversity of species and criteria used for toxicity assay (Vig et al. 2003). Soil microbial biomass that influences microbial processes in the soil includes and is not limited to respiration, C and N mineralization, soil enzymes, and microbial diversity/soil microbial biomass.

Microbial indices and soil physical and biochemical properties

Soil microbial biomass has been identified as a major soil component regulating nutrient transformation and storage (Fritze et al. 1996). Different microbial parameters were found to be good indicators of soil contamination by heavy metals (Smejkalova et al. 2003). Specific groups (spore forming, oligotrophic) microorganisms are better used as indicators of heavy metals contamination instead of total counts of bacteria, and other characteristics react to increasing concentrations of heavy metals are C-biomass and $C_{biomass} : C_{ox}$ (Smejkalova et al. 2003). Colony-forming units (CFU) of total bacteria and micromycetes decreased with increasing heavy metals concentrations, but the decrease in CFU was most significant in the case of oligotrophic and spore forming bacteria (Smejkalova et al. 2003). Two of the most common categories of bioindicators are microbial biomass and microbial activity (Cameron et al. 1998). Microbial biomass can be a sensitive indicator of longer-term declines in total soil organic matter that results from agricultural intensification and land disturbance (Sparling 1992; Weigand et al. 1995). Heavy metal contamination of soils can have marked and persistent effects on microbial biomass (Brookes and McGrath 1984). Measures of biological activity rely on quantifying substrate use (Bardgett et al. 1994) or mineralization (Groot and Houba 1995). The biological activity in soils is usually evaluated by measuring CO_2 evolution, and results obtained from different studies on the influences of heavy metals on CO_2 evolution in contaminated soils by addition of sewage sludge have been at variance (Abdousalam 2010). Soil respiration and microbial biomass can be useful indicators of soil contamination, combining the two measurements to give amounts of CO_2 evaluated per unit of biomass (μg CO_2–C/g soil) (Abdousalam 2010).

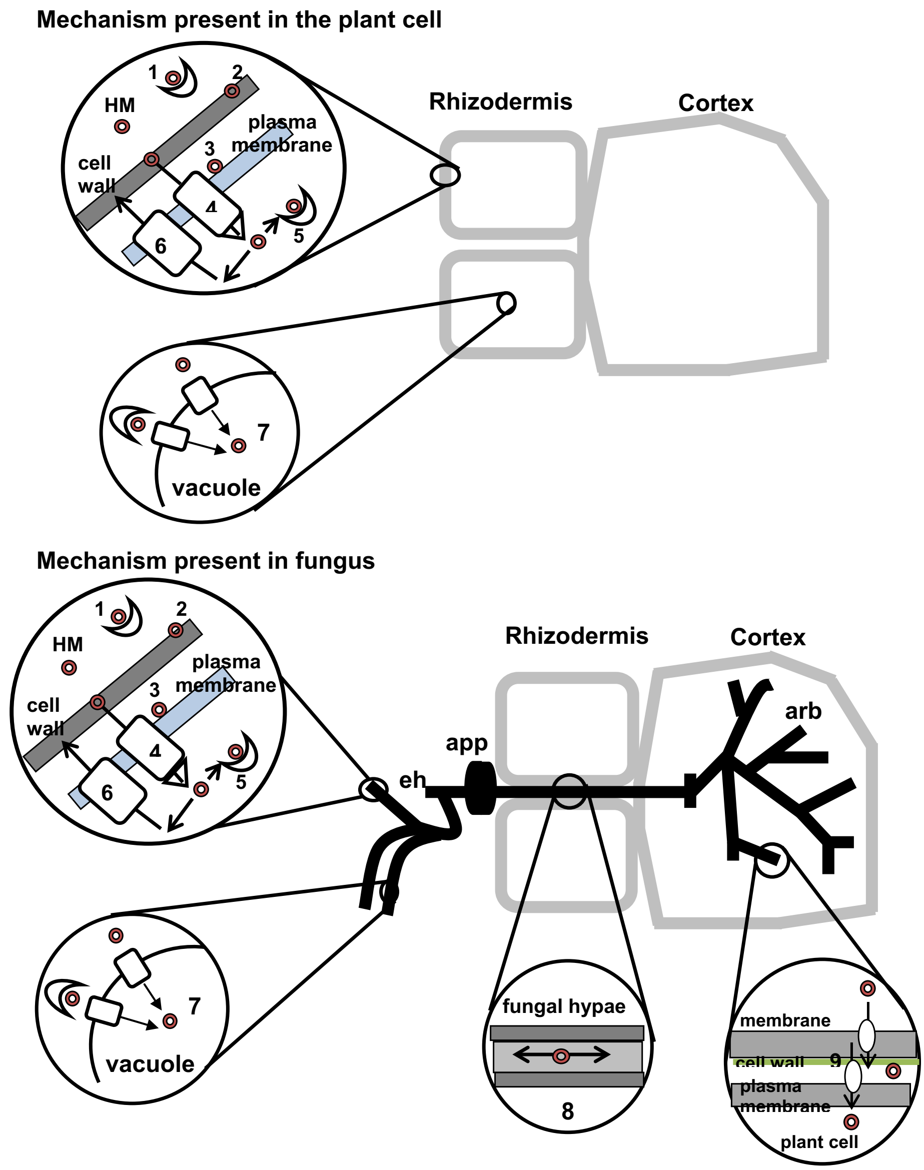

Fig. 8 Mechanism of heavy metal detoxification by plants and fungi in soils. *1* Chelating agents that bind metals in the soil. *2* Binding of heavy metal to cell wall components in plants and fungi. *3* The plasma membrane as a living, selective barrier in plants and fungi. *4* Specific and non-specific metal transporters and pores in the plasma membrane of plants and fungi. *5* Chelates in the cytosol, e.g., metallothioneins (plants and fungi) and metal-specific chaperons. *6* Export via specific or non-specific active or passive transport from plant or fungal cells. *7* Sequestration of heavy metal in the vacuole of plant and fungal cells. *8* Transport of heavy metal in the hyphae of the fungus. *9* In arbuscules, metal export from the fungus and import into plant cells via active or passive transport. (Adapted from Göhre and Paszkowski 2006 with permission)

Enzymatic activities can sensitively reflect the biological situation in the soil, and several reasons establishing enzymatic analyses to be good indicators of soil quality have been enumerated by Dick et al. (1996) and Smejkalova et al. (2003); (i) they are strongly connected with important soil characteristics such as organic matter, physical properties, microbial activity or biomass; (ii) they occur earlier than other characteristics; (iii) they involve relatively simple methods compared to other important parameters of soil quality. There have been considerable interests in studying enzyme activity in soils (Burns 1978) because such activities may reflect the potential capacity of a soil to perform certain biological transformations of importance to soil fertility (Subhani et al. 2001). A number of studies have measured the activities of enzymes in relation to heavy metals in soils such as Baath (1989), Schuller (1989), Bardgett et al. (1994) and Gao et al. (2010). Generally, enzyme activities in soils have been shown to decrease drastically in response to increasing heavy metal pollution (Subhani et al. 2001; Gao et al. 2010). Heavy metals inhibit enzymatic activities in 3 ways: (1) through complexation of the substrate, (2) by combining with the protein-active groups of the enzymes or (3) by reacting with the enzyme–substrate complex (Dick 1997; Moreno et al. 2003). However, the addition of low metal sludge increased the activities of dehydrogenase, phosphatase and beta-Glucosidase (Chander and Brookes 1991). This was attributed to an enhanced microbial activity in the soils, stimulated by the addition of nutrients in the sludge with the heavy metals below toxic level.

Table 2 Soil microbial parameters used in different studies

Soil microbial parameter	References
Microbial biomass C	Kandeler et al. (1996), Kuperman and Carreiro (1997), Yao et al. (2003), Kizilkaya et al. (2004), Simona et al. (2004), Yang et al. (2007), Wang et al. (2007)
Respiration	Kandeler et al. (1996), Yao et al. (2003), Kizilkaya et al. (2004), Simona et al. (2004)
N Mineralization	Kandeler et al. (1996)
Nitrification	Kandeler et al. (1996)
Soil bacterial diversity	Salazar et al. (2016)
Microbial diversity index	Yang et al. (2007), Wang et al. (2007)
Cmic/Corg ratios	Yao et al. (2003), Simona et al. (2004)
Nmic/Cmic ratios	Yao et al. (2003)
Metabolic quotient	Yao et al. (2003)
Enzymes	
Dehydrogenase	Kandeler et al. (1996), Kizilkaya et al. (2004), Simona et al. (2004), Yang et al. (2007)
Urease	Kandeler et al. (1996), Kizilkaya et al. (2004), Simona et al. (2004), Yang et al. (2007)
Xylanase	Kandeler et al. (1996)
Cellulase	Kandeler et al. (1996)
B-Glucosidase	Kandeler et al. (1996), Kuperman and Carreiro (1997), Simona et al. (2004)
Protease	Kandeler et al. (1996), Simona et al. (2004)
Arginine deaminase	Kandeler et al. (1996)
Nitrate reductase	Kandeler et al. (1996)
Acid phosphatase	Kuperman and Carreiro (1997)
Alkaline phosphatase	Kandeler et al. (1996), Simona et al. (2004), Yang et al. (2007), Wang et al. (2007)
Phospholipase	Kandeler et al. (1996)
Arylsulphatase	Kandeler et al. (1996)
Catalase	Kandeler et al. (1996)
N-acetylglucosaminidase	Kuperman and Carreiro (1997)
Sulphatase	Simona et al. (2004)

Significant inhibition of enzymatic activities by a high level of soil contamination has been observed; heavy metals mainly inhibit enzymatic reactions through either complexing with substrate or blocking the fundamental groups of enzymes or reacting with complex enzyme–substrate (Smejkalova et al. 2003).

One general criterion used to determine microbial activity and biomass in soil is dehydrogenase activity, an indicator potential non-specific intracellular enzyme activity of the total microbial biomass (Subhani et al. 2001). It serves as an indicator of the microbiological redox systems and may be considered as a good measure of microbial oxidative activities in soils. It has been used as an indicator for active microbial biomass and is adversely affected by the presence of heavy metals (Subhani et al. 2001).

Microbial activities affect the soil's physical properties such as soil structure and biochemical properties such as pH, soil redox state, soil enzymes that influence the solubility and bioavailability of heavy metals (Dommergues et al. 1980; Kara et al. 2008).

Toxic limits of heavy metal to soil microorganisms

Soil quality upper control limits for heavy metals need to be based on their effects on soil microorganisms or important soil microbial processes (Abdousalam 2010). The importance of this is supported by observation by Brookes (1995) that significant effects of heavy metals on both microbial biomass and activity occur at concentrations around or below current soil metal limits based on their effects on plants and animals. Unfortunately, results from research into the effects of metals soil microorganisms tend to be contradictory and there are yet no general agreement and scientifically defensible critical limits to soil metal-based microbial effects (Abdousalam 2010), and are unlikely to be for some time. One of the problems to be encountered in defining metal limits is the need to assess soil metal bioavailability rather than total soil metal concentrations (Naidu et al. 2006). It has been suggested that determination of free metal ions in soil solution may put many presently contradictory studies on the effect of metals on soil microbial activity into a unified framework for interpretation, and the issue clearly needs resolving if we are to develop a reliable, meaningful measurement of soil metal contamination for use in a dynamic assessment scheme (Cameron et al. 1998). The concept of ecological dose (ED_{50}) and/or lethal concentration (LC_{50}) was developed in response to the apparent need to easily quantify the influence of pollutants on microbial-mediated ecological processes in various ecosystems. It has been used by several authors to quantify the effect of heavy metals on enzymatic activities in the soil (Moreno et al. 1999, 2001; Renella et al. 2003; Yang et al. 2006; Ribeiro and Umbuzeiro 2014; Hoppe et al. 2015). ED_{50} and LC_{50} have been defined as the concentration that inhibits a microbe-mediated ecological process by 50 % (Babich et al. 1983; Gao et al. 2010).

Conclusion

Microbial activities play a vital role in soil productivity and sustainability as it underpins a number of fundamental soil properties (Subhani et al. 2001). The turnover and mineralization of organic substances, nutrient transformations and cycling of organic wastes in soils are all dependent on the metabolic functions of soil microorganisms. Therefore, the role of microbial activity in the development and functioning of soil ecosystem is inevitable and changes in soil microbial activity may be an indicator of extremely sensitive changes in the soil health (Pankhurst et al. 1995). Contamination of soils with heavy metals can adversely affect the size of the soil microbial biomass and various measures of soil microbial activity such as nitrogen mineralization and nitrogen fixation (Brookes and McGrath 1984), thus adversely affecting the ecosystem.

There is yet to be a general agreement and scientifically defensible critical limits to soil metal-based microbial effects. The concept of ecological dose (ED_{50}) was developed into overcome the apparent need to easily quantify the influence of organic and inorganic pollutants on microbial-mediated ecological processes in various ecosystems. Data presented in this review provide a foundation for future studies on the exploitation of soil microbes in the bioremediation of contaminated environments.

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