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Heavy metals stress and defense strategies in plants: An overview

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Abstract
Soil pollution by heavy metals is the most important problem nowadays because toxic contaminants like As, Cd, Cr, Cu, Fe, Mn, Ni, Pb, Zn etc. are released in the natural ecosystem due to anthropogenic activities like advancements in agriculture, industrialization and urbanization process. It has become a serious problem worldwide because heavy metals are noxious, persistent and non-biodegradable which adversely affect crop yields, soil biomass and soil fertility. Although some of these metals are essential micronutrients responsible for many regular processes in plants, their excess, however, can have detrimental effects and can directly influence the plant growth, metabolism, physiology and senescence. This study discusses the toxic effects caused by various metals and also overview the plants defense strategies to combat the heavy metal stress.

Keywords: Defense strategy, effects on plant, heavy metals, oxidative stress, reactive oxygen species

Introduction
Heavy metal (HM) stress is one of the major abiotic stress leading to hazardous effects on living beings including plants. The term HM includes only the elements with specific gravity above 5 g cm^{-3} but frequently biologists use this term for a vast range of metals and metalloids which are toxic to plants such as Lead (Pb), Copper (Cu), Iron (Fe), Manganese (Mn), Nickel (Ni), Zinc (Zn), Cobalt (Co), Cadmium (Cd), Chromium (Cr), and Arsenic (As) etc. All heavy metals are non-biodegradable, that is, they cannot be purged out naturally from the environment via any possible natural means, although some of them are reported to be immobile, that is, they cannot move from the place where they are accumulated, while there are others that are termed as mobile, that is, they can be taken up by plants root system via diffusion, endocytosis or through metal transporters. Metals like (Arsenic, Mercury, Chromium, Cadmium and Lead etc.) are non-essential and potentially highly toxic even at lower concentrations. The rate of accumulation and plant's tolerance to heavy metals vary from specie to specie, with some becoming toxic at a faster rate. Some of the HMs, such as (Nickel, Copper, Zinc, Cobalt, Iron, Manganese and Molybdenum) are at lower concentrations act as essential micronutrients that are critically involved in the functional activities of large numbers of proteins involved in sustaining growth and development of plants. Depending on the location, type of metals, their concentrations in soil ranged from trace to as high as 100,000 mg kg^{-1} (Blaylock and Huang, 2000) [17].

Defense strategy of plants against heavy metals stress
High level of HMs can cause serious harm to plant growth and development, photosynthesis, water balance, and nutrient capture (Sharma and Dubey, 2005) [53]. However, some plant species can still survive, grow and reproduce in environment polluted with heavy metals (HMs), indicating that they developed various inherent and extrinsic defense mechanism for tolerance or detoxification whenever confronted with the stressful condition caused by the high concentrations of HMs. As a first step towards dealing with metal intoxication, plants adopt avoidance strategy to preclude the onset of stress via restricting metal uptake from soil or excluding it, preventing metal entry into plant root (Viehweger, 2014) [70]. This can be achieved by some mechanisms such as immobilization of metals by mycorrhizal association, metal sequestration, or complexation by exuding organic compounds from root Dalvi *et al.*, (2013) [22]. At next stage, if these strategies fail and HMs manage to enter inside plant tissues, tolerance mechanisms for detoxification are activated which include metal sequestration and compartmentalization in various intracellular compartments (e.g., vacuole) Patra *et al.*, (2004) [59], metal ions trafficking, metal binding to cell wall, biosynthesis or accumulation of osmolytes and osmoprotectants, for example, proline, intracellular complexation or chelation of metal ions by releasing several substances, for example, organic acids, polysaccharides,

phytochelatins (PCs), and metallothioneins (MTs) Dalvi *et al*., (2013) [22] and eventually if all these measures prove futile and plants become overwhelmed with toxicity of heavy metal (HM), activation of antioxidant defense mechanisms is pursued Manara (2012) [45]. One of the most efficient mechanism that plants use to protect themselves is to increase the activity of antioxidative enzymes and metabolites Kumari (2009) [38]. Liu *et al*., (2008) [42] reported a significant increase in the activity of antioxidative enzyme sauch as superoxide dismutase (SOD), catalase (CAT), guaiacol peroxidase (POX), Gtutathione reductase (GR), Dehydroascorbate reductase (DHAR) and non-enzymatic metabolites such as ascorbate (AsA) and glutathione (GSH) in Sedum alfredii under Pb stress.

Effects of heavy metal on plants

Like all living organisms, plants are often sensitive both to the deficiency and to the excess concentration of some heavy metals. The heavy metals available for plant uptake are those present as soluble components in the soil solution or those solubilized by root exudates Blaylock and Huang (2000) [17]. As metals cannot be broken down, when concentrations within the plant exceed optimal levels, they adversely affect the plant both directly and indirectly and some of the direct toxic effects caused by high metal concentration include inhibition of cytoplasmic enzymes and damage to cell structures due to oxidative stress Jadia and Fulekar (1999) [29]. Indirect toxic effect is the replacement of essential nutrients at cation exchange sites of plants Taiz and Zeiger (2002) [68]. The negative influence of heavy metals on the growth and activities of soil microorganisms also indirectly affect the growth of plants. Reduction in the number of beneficial soil microorganisms due to high metal concentration may lead to decrease in organic matter decomposition leading to a less fertility of soil. Enzyme activities are very much useful for plant metabolism, hampered due to heavy metal interference with activities of soil microorganisms.

Plants faced with heavy metal toxicity have visible symptoms such as stunted growth, chlorosis, root browning, decline and death (Ozturk *et al.,* 2008, 2015b) [56]. Heavy metal stress inactivates or denatures various important enzymes and other proteins, and interferes with substitution reactions of essential metal ions from biomolecules. This reaction disturbs the integrity of membranes, resulting in alteration of basic plant metabolic reactions such as photosynthesis, respiration and homeostasis (Hossain *et al.*, 2012) [27]. Moreover, it stimulates the production of reactive oxygen species such as superoxide radical ($O_{.}^{-2}$), hydroxyl radical (OH^{-}) and hydrogen peroxide (H_2O_2). Another cytotoxic compound called methylglyoxal has also been reported to increase during heavy metal stress. These highly reactive species leads to lipid peroxidation, especially of the cellular membranes causing them to leak, damaging of biomolecules and also cleavage of DNA strands collectively known as oxidative stress Ahmad *et al.,* (2012) [5].

Effect of copper on plants

Copper is an essential metal for normal growth and development within the certain limits after that it is potentially toxic to the plants. Copper is considered as a micronutrient for plants Kabir *et al*., (2009) [35] and plays an important role in CO_2 assimilation and ATP synthesis Mohnish and Kumar (2015) [15]; furthermore, it is also an important constituent of plastocyanins and cytochrome oxidase, both of which are vital components of both photosynthetic and respiratory systems; nevertheless, Cu in excess can cause oxidative stress in plants, which in turn leads to the an extensive damage to the membranes and macromolecules and have an effect on various different biochemical pathways and DNA (Yadav 2010) [74]. Plants under Cu stress show various noticeable symptoms such as chlorosis and inhibited growth, in addition to ion leakage and retarded root growth (Bouazizi *et al.*, 2010) [19]. Neelima and Reddy (2002) [64] studied copper effects in seeds of *Solanum melongena* and found that Cu excess adversely affects the germination, length of seedlings and number of roots of the plant. In case of black bindweed (*Polygonum convolvulus*) the plant mortality, biomass and seed production is reduced due to copper toxicity Mohnish and Kumar (2015) [15]. In bean (*Phaseolus vulgaris*) and root malformation and reduction seen Jyotish *et al*., (2015) [34] under the Cu stress.

Effect of zinc on plants

Zinc (Zn) is an essential element required by the plant for its normal growth and development. Zinc played an important role in many physiological functions such as carbohydrate synthesis, auxin and protein metabolism, enzymatic reactions; pollen formation, chlorophyll production. Zinc deficiency causes leaf discoloration called chlorosis tissue of the veins to turn yellow and also lead to severe yield loss of crops (Aziz *et al.*, 2016) [13]. However, Zn is required in trace amounts only, and its excess can lead to Zn toxicity with dire consequences. Zn toxicity also induces accumulation of other heavy metals such as copper (Cu) and manganese (Mn) in root and shoot Nagajyoti *et al*., (2010) [51, 52]. Moreover, Zn toxicity can lead to phosphorous (P) deficiency appearing as purplish red color leaf symptom (Lee *et al.*, 1996) [39]. They have roots which are thickened, blunt and have restricted cell elongation and division. Zinc in excess reduces the germination, chlorophyll, carotenoid, sugar, amino acid and growth of cluster beans (*Cyamopsis tetragonoloba*) Manivasagaperumal *et al.*, (2011) [46]. Whereas, in pea (*Pisum sativum*) reduces chlorophyll, photosynthesis and plant growth Mohnish and Kumar (2015) [15]. In rye grass (*Lolium perenne*) it reduces the growth, nutrient content and photosynthetic energy conversion Bonnet *et al*., (2000) [18].

Effects of cadmium on plants

Plants grown in soil containing high levels of Cd show visible symptoms of injury reflected in terms of chlorosis, growth inhibition, browning of root tips and finally death Guo *et al*., (2008). Cd accumulation leads to Fe deficiency and in turn affects the photosynthesis. Photosynthesis is also affected due to reduced chlorophyll synthesis and inhibition of enzymes involved in CO_2 fixation. In general, Cd has been shown to interfere with the uptake, transport and use of several elements (Ca, Mg, P and K) and water by plants Das *et al.*, (1997) [23]. Bagheri *et al*., (2013) [14] reported numerous impacts of Cd stress, which vary from induction of oxidative stress to stunted growth. Cadmium treatment shows significant inhibitory effects on fenugreek plants (Alaraidh *et al.,* 2018) [6]. Qureshi *et al.*, (2010) [61] observed that Cd stress caused reduced photosynthetic efficiency of plants resulting into poor health and stunted growth. Similarly, decrease in dry mass in *Cicer arietinum* by Rana and Ahmad (2002) [62]. Also Elsayed *et al.*, (2017) [25] found that under the Cd stress the number of leaves, leaf area, root length, shoot length, fine root biomass, coarse biomass and shoot biomass were significantly reduced in *Sesamum indicum L.*Yang *et al.*, (2016) [75] concluded that the chlorophyll content in the leaves of rice reduced by 60% as compared to control with 10 µM of Cd treatment. Jiang *et al.,* (2016) [33] reported that the significant increase in MDA content by the increased lipid peroxidation under Cd treatments as compared to the control in *L. japonica.* Allah *et al.*, (2015) reported Cd induced H_2O_2 production in *Helianthus annuus*.

Effects of mercury on plants

Mercury acts as a toxic element for the plants and has no beneficiary effect at all Hameed *et al.,* (2017) [26]. Contamination of soils by Hg is often due to the addition of this heavy metal as part of fertilizers, lime, sludges, and manures. The dynamics between the amount of Hg that exist in the soil and its uptake by plants is not linear and depends on several variables (e.g., cation-exchange capacity, soil pH, soil aeration, and plant species). Mercury can persist in soil for a long period of time as it is absorbed into the clay, sulfides and organic matter. Mercury is chelated and precipitated as carbonate, hydroxide, sulfide and phosphate. It is converted to methylated form by an anaerobic bacterium than it gets absorbed into the plant and shows phytotoxic effects Tangahu *et al*., (2011) [69]. It can also affect the mitochondrial and chloroplast activity by interfering with electron transport chain and inducing oxidative stress along with membrane degradation and biomolecules oxidation Nagajyoti *et al*., (2010) [51, 52]. Studies conducted by Malar *et al.*, (2015) [44] have revealed at genomic template stability of plants is highly affected when treated with mercury. The reason was that mercury ions lead to disruption of cellular functions and blockage of normal growth and development. In rice (*Oryza sativa*) excess of mercury decreases plant height, reduces tiller and panicle formation, yield reduction and increase of its bioaccumulation in shoot and root of seedling Kibra (2008) [37]. Further, in tomato (*Lycopersicon esculentum*) show reduction in germination percentage, reduced plant height; reduction in flowering and fruit weight and finally resultant chlorosis appears on the whole plant Shekar *et al.,* (2011) [64].

Effects of chromium on plants

Chromium is known to be a toxic metal that can cause serve damage to plants and animals. Chromium induced oxidative stress involves induction of lipid peroxidation in plants that causes severe damage to cell membranes. Oxidative stress induced by high concentration of chromium initiates the degradation of photosynthetic pigments causing decline in photosynthesis and growth Asati *et al.,* (2016) [9]. Seed germination is the first physiological process affected by Cr, the ability of a seed to germinate in a medium containing Cr would be indicative of its level of tolerance to this metal Peralta *et al*., (2001) [60]. Cr toxicity causes chlorosis, growth retardation, wilting of top and injury of roots Ozturk *et al*., (2015b) [55]. It also affects the activities of many enzymes and hence producing reactive oxygen species Yadav (2010) [74]. In tomato (*Lycopersicon esculentum*) chromium toxicity resultant decrease in plant nutrient acquisition Moral *et al*., (1996) [50]. Wherein, onion (*Allium cepa*) shows the inhibition of germination process and reduction of plant biomass Nematshahi *et al*., (2012) [54]. Moreover, in wheat (Triticum sp.) Reduction of shoot and root growth were noticed Panda and Patra (2000) [58].

Effects of lead on plants

Lead (Pb) is a non-redox active metal having a low melting point. It can affect the plant, physiologically, ultra-structurally and biochemically. The nonspecific symptoms of Pb toxicity are stunted growth, chlorosis and reduced root lengths. Once entered into the cell, Pb changes cell membrane permeability, hormonal changes, inhibition of various enzymes containing sulfhydryl group, reduction in water content and disturbed mineral nutrition. In seedlings, Pb toxicity causes retarded growth and inhibits germination. Plants faced with lead toxicity have their photosynthetic pathways adversely affected as it disrupts ultrastructure of chloroplast and blocks synthesis of essential pigments including chlorophyll and carotenoids. Pb causes ROS production and oxidative stress within plant cells, these ROS readily attacks the biological structures and biomolecules and result in metabolic dysfunctions Clemens (2006) [20]. Plant activates the anti-oxidative defense system, which includes both enzymatic and non-enzymatic anti-oxidants in response to oxidative stress induced by Pb Ashraf *et al*., (2017) [10]. A high lead level in soil induces abnormal morphology in many plant species. For example, lead causes irregular radial thickening in pea roots, cell walls of the endodermis and lignification of cortical parenchyma Paivoke (1983) [57]. In maize (*Zea mays*) reduction in germination percentage; suppressed growth; reduced plant biomass; decrease in plant protein content has been noticed Hussain *et al.,* (2013) [28]. Whereas in Portia tree (*Thespesia populnea*) Reduction in number of leaves and leaf area; reduced plant height Kabir *et al*., (2009) [35]; decrease in plant biomass and in Oat (*Avena sativa*) Inhibition of enzyme activity which affected CO2 fixation Jyotish *et al.,* (2015) [34].

Effects of cobalt on plants

Cobalt, a transition element, is an essential component of several enzymes and co-enzymes. Cobalt (Co) naturally occurs in the earth's crust as cobaltite [CoAsS], erythrite [$Co_3(AsO_4)_2$] and smaltite [$CoAs_2$]. It has been shown to affect growth and metabolism of plants, in different degrees, depending on the concentration and status of cobalt in rhizosphere and soil. Cobalt interacts with other elements to form complexes and the cytotoxic and phytotoxic activities of cobalt and its compounds depend on the physicochemical properties of these complexes, including their electronic structure, ion parameters (charge-size relations) and coordination. Phytotoxicity study of Co in barley (*Hordeum vulgare L.*), oilseed rape (*Brassica napus L.*) and tomato (*Lycopersicon esculentum L.*) has recently shown the adverse effect on shoot growth and biomass Li *et al*., (2009) [40]. In addition to biomass, excess of Co restricted the concentration of Fe, chlorophyll, protein and catalase activity in leaves of cauliflower. Further, high level of Co also affected the translocation of P, S, Mn, Zn and Cu from roots to tops in cauliflower. In raddish (*Raphanus sativus*) Reduction in shoot length, root length, and total leaf area; decrease in chlorophyll content; reduction in plant nutrient content and antioxidant enzyme activity; decrease in plant sugar, amino acid, and protein content has been noticed Jayakumar *et al*., (2007) [30-33]. Mung bean (*Vigna radiata*) reduction in antioxidant enzyme activities; decrease in plant sugar, amino acid, and protein content Jayakumar *et al.,* (2008) [30]. Tomato (*Lycopersicon esculentum*) Reduction in plant nutrient content Jayakumar *et al*., (2013) [32].

Effects of nickel on plants

Nickel is an essential nutrient for plants. However, the amount of Ni required for normal growth of plants is very low when its concentration exceeds certain limit in the soil than it toxic to the plants. The increase to toxic levels is due to application of fertilizers, smelting, mining, sewage disposal and burning of fuel Aziz *et al*., (2015) [12]. Plants growing in Ni toxic soil have symptoms of necrosis, chlorosis, nutrient deficiency, disturbed function of cell membrane. Ni stress also disrupts the water balance of the plant, and a decline in water content of monocot and dicot plants has been reported. The decrease in water content is often seen as an indicator of Ni toxicity Yadav (2010) [74]. The Ni toxicity also leads to a reduction in the growth of plants and their photosynthetic ability. It also induces the oxidative stress, inhibits the nitrogen metabolism and enzymatic and mitotic activities, and interferes with the uptake of other metals. In pigeon pea (*Cajanus cajan*) nickel decreases chlorophyll content and stomatal conductance; decrease enzyme activity which affected Calvin cycle and CO_2 fixation Sheoran *et al*., (1990) [66]. Due to nickel Rye grass (*Lolium perenne*) reduction in plant nutrient acquisition; decrease in shoot yield; chlorosis Khalid and Tinsley (1980) [36]. Inhibition of root growth due to this heavy metals in rice (Oryza sativa) Lin and Kao (2005) [41].

Effects of iron on plant

Iron as an essential element for all plants has many important biological roles in the processes as diverse as photosynthesis, chloroplast development and chlorophyll biosynthesis. Iron is mainly involved in the process of plant photosynthesis. Iron is a major constituent of the cell redox systems such as heme proteins including cytochromes, catalase, peroxidase and leghemoglobin and iron sulfur proteins including ferredoxin, acontiase and superoxide disumutase (SOD) Marschner (1995) [48]. Although most mineral soils are rich in iron, the expression of iron toxicity symptoms in leaf tissues occurs only under flooded conditions, which involves the microbial reduction of insoluble Fe^{+3} insoluble Fe^{+2} Becker and Asch (2005) [16]. Iron toxicity in tobacco, canola, soybean and Hydrilla verticillata are accompanied with reduction of plant photosynthesis and yield and the increase in oxidative stress and ascorbate peroxidise activity Sinha *et al*., (1997) [67]. The appearance of iron toxicity in plants is related to high Fe^{+2} uptakes by roots and its transportation to leaves and via transpiration stream. The Fe^{+2} excess cause free radical production that impairs cellular structure irreversibly and damages membranes, DNA and proteins Arora *et al*., (2002) [7]. Iron toxicity is not common, but some plants do secrete acids from the roots, which lowers soil pH. These plants can take up too much iron, leading to toxicity.

Effects of manganese on plants

Manganese (Mn) is an essential plant mineral nutrient, playing a key role in several physiological processes, particularly photosynthesis. Manganese deficiency is a widespread problem, most often occurring in sandy soils, organic soils with a pH above 6 and heavily weathered, tropical soils. Mn is readily transported from root to shoot through the transpiration stream, but not readily remobilized through phloem to other organs after reaching the leaves Loneragan (1988) [43]. Necrotic brown spotting on leaves, petioles and stems is a common symptom of Mn toxicity Wu (1994) [71]. Another common symptom is known as ‘‘crinkle leaf’’, and it occurs in the youngest leaf, stem and petiole tissue. It is also associated with chlorosis and browning of these tissues Wu (1994) [71], Elamin, O.M and Wilcox (1986a). In the broad bean (*Vicia faba*) Mn accumulation in shoot and root; reduction in shoot and root length; chlorosis Arya and Roy (2011) [8]. Otherside in spearmint (*Mentha spicata*) Mn decrease the chlorophyll a and carotenoid content; increase accumulation of Mn in plant roots Asrar *et al*., (2005) [11]. Moreover, Mn in pea (*Pisum sativum*) reduces chlorophylls a and b content; reduction in relative growth rate; reduced photosynthetic O2 evolution activity and photosystem II activity Doncheva *et al*., (2005) [24]. However, in tomato (*Lycopersicon esculentum*) Mn slower plant growth; decrease in chlorophyll concentration Shenker, (2004) [65].

Effects of arsenic on plant

Arsenic is known for its toxic effects on plants, animals, chromosomes, genes etc. In plants it adversely affects the growth and yield. Abedin *et al.*, (2002a and 2002b) [2, 3, 4] has confirmed that, when plants were exposed to excess arsenic either in soil or in solution culture, they exhibited toxicity symptoms such as: inhibition of seed germination, decrease in plant height, depress in tillering, reduction in root growth, decrease in shoot growth, lower fruit and grain yield, and sometimes, leads to death. However, little is known about the effect of arsenic on photosynthesis; the basis of plant bio-chemical system. In tomato (*Lycopersicon esculentum*) arsenic reduces fruit yield, decreases the leaf fresh weight Barrachina *et al*., (1995) [15] Whereas, in canola (*Brassica napus*) arsenic causes stunted growth, chlorosis and wilting Cox *et al*., (1996) [21]. Further, arsenic in rice (*Oryza sativa*) reduces seed germination, seedling height, leaf area and dry matter production Marin *et al*., (1993) [47] and Abedin *et al*., (2002) [2, 3, 4].

Conclusion

Plants grow on heavy metal polluted soils resultant in reduction in growth due to changes in their physiological and biochemical activities. In current review, the various detrimental consequences of plant exposure to HM stress and some diverse defense strategies employed by plants against HM stress were discussed. Heavy metals such as Fe, Cr, Mn, Cu, Pb, Ni, Co, Cd, Zn, Hg and arsenic are for long being accumulated in soils through industrial waste and sewage disposal etc. Although some of these metals are essential micronutrients responsible for many regular processes in plants but their excess, however, can have deleterious effects and can directly influence the plant growth, metabolism, physiology and senescence.

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