



Toxicity of heavy metals and metal-containing nanoparticles on plants[☆]



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ABSTRACT

Plants are under the continual threat of changing climatic conditions that are associated with various types of abiotic stresses. In particular, heavy metal contamination is a major environmental concern that restricts plant growth. Plants absorb heavy metals along with essential elements from the soil and have evolved different strategies to cope with the accumulation of heavy metals. The use of proteomic techniques is an effective approach to investigate and identify the biological mechanisms and pathways affected by heavy metals and metal-containing nanoparticles. The present review focuses on recent advances and summarizes the results from proteomic studies aimed at understanding the response mechanisms of plants under heavy metal and metal-containing nanoparticle stress. Transport of heavy metal ions is regulated through the cell wall and plasma membrane and then sequestered in the vacuole. In addition, the role of different metal chelators involved in the detoxification and sequestration of heavy metals is critically reviewed, and changes in protein profiles of plants exposed to metal-containing nanoparticles are discussed in detail. Finally, strategies for gaining new insights into plant tolerance mechanisms to heavy metal and metal-containing nanoparticle stress are presented. This article is part of a Special Issue entitled: Plant Proteomics – a bridge between fundamental processes and crop production, edited by Dr. Hans-Peter Mock

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1. Introduction

Heavy metals are defined as elements having a specific gravity above five and commonly include toxic metals such as aluminum (Al), cadmium (Cd), copper (Cu), chromium (Cr), lead (Pb), and zinc (Zn), and metalloids, including arsenic (As) and boron (B), which are detrimental for plant growth and development [1]. Nieboer and Richardson [2] divided toxic metals in different classes based on binding capacity with different functional groups. Anthropogenic activities have major impacts on the global and regional cycles of most trace elements and often lead to environmental contamination and accumulation of toxic metals in the food chain [3]. During the last century, heavy metal emissions into the environment have dramatically increased as a result of industrial activity, release of contaminated sewage sludge from wastewater treatment facilities, and widespread use of heavy metal-containing agrochemicals [4,5]. Nriagu and Pacyna [3] reported that the annual total toxicity of all heavy metals mobilized by human activities exceeds the combined toxicity of all radioactive and organic waste produced each year.

Abbreviations: ROS, reactive oxygen species; TCA, tricarboxylic acid; RuBisCO, ribulose-1,5-bisphosphate carboxylase oxygenase; PS, photosystem; MAPK, mitogen activated protein kinase.

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Heavy metal bioavailability largely depends on soil characteristics and the growing plant species [6,7]. Plants require certain metals, particularly Zn, iron (Fe), and Cu, for the proper functioning of various metal-dependent enzymes and proteins. However, several metals, such as As, mercury (Hg), Cd, and Pb, are non-essential and potentially toxic to plants [8]. Plants take up heavy metals from the soil or water through the root system by both active and passive transport processes [9]. The specific ion carriers that are responsible for the influx of essential elements, including Zn^{2+} , Fe^{2+} , and calcium (Ca^{2+}), also facilitate the cellular influx of heavy metal ions [10,11]. After their uptake, heavy metals can be translocated from the plant roots to the aerial parts through the xylem [12]. All plant species display basal heavy metal tolerance, which is primarily mediated by the sequestration and efflux of metal ions [13].

The use of agrochemicals is a major source of heavy metal contamination posing an overwhelming risk to the environmental health. Among the agrochemicals, phosphate fertilizers are the main source of trace elements [14]. Extreme high concentrations of Cd in these phosphate fertilizers are a point of concern. Various studies indicated that the repeated application of agrochemicals caused the accumulation of heavy metal ions like Cd, Pb, and Zn in the agricultural soil [15]. Transport of heavy metals from the fertilizers to the plant parts is an alarming fact. Satpathy et al. [16] reported that Mn and Cd were accumulated in the rice shoot from the applied fertilizers. The transfer of metals from the soil to the rice plants was significant for Pb, Cd, Cu, Cr, Mn, and Zn. Ongoing usage of these agrochemicals with the heavy metal components is a major threat that needs to be addressed.

Plants primarily respond to heavy metal stress by accumulating their ions in different organs. Based on this responsive strategy, plants are divided into two groups: hyper- and non-accumulating plants [17]. The ability of plants to accumulate heavy metals is the basis of phytoremediation, which is a plant-based strategy used to clean-up metal-contaminated soils [18]. After entry into cells, heavy metal ions bind to chelators and chaperones, which are involved in trafficking and their delivery to metal-requiring proteins and organelles [13]. Heavy metal ions bind to the protein groups and are able to replace specific cations from binding sites, resulting in the inactivation of enzymes and reactive oxygen species (ROS), which cause oxidative damage to proteins, lipids, and nucleic acids [19].

The application of high-throughput 'omics' techniques, such as transcriptomics, proteomics, and metabolomics, is a promising approach to identify the plant molecular mechanisms and pathways involved in tolerance to different abiotic stresses, including exposure to heavy metals. In the last decade, the production and industrial application of nanoparticles has dramatically increased [20]. However, because nanoparticles frequently contain heavy metals, the possible entry of the materials into ecosystems and the food chain is a major point of concern [21]. Nanoparticles are able to enter plant tissues through the root system [22] and affect cells either directly or indirectly depending on particle size [23]. Nanoparticles cause both positive [24,25] and negative effects in plants [26]. Although a few proteomic studies have investigated the effects of nanoparticles on the plants [24,27,28,29,30,31], more extensive studies on the effects of nanoparticles on plant biological pathways are needed. In this review, recent trends and advances in the field of proteomics aimed at enhancing our understanding of plant responses to heavy metal toxicity are presented. Transport of the heavy metal ions from the soil into the cell and sequestration inside the cell are discussed in detail. In addition, the findings from various proteomic studies that have examined plant responses to heavy metals and metal-containing nanoparticles stresses are discussed.

2. Proteomic analysis of plants under heavy metal toxicity

2.1. Aluminum

Al is not essential for crop growth and development; however, Al toxicity is primarily caused by Al^{3+} which is a major limiting factor for crop growth in acidic soils [32]. Al ions are extremely toxic to plants at high concentrations [33]. Toxic levels of Al inhibit the growth and reduce the yields of Al-sensitive crops by disrupting various cellular processes and components by binding with phosphate, sulfate, and carbonyl functional groups [34,35]. Physiological studies indicate that plants use two main strategies to resist Al toxicity: blocking Al^{3+} uptake and detoxifying cellular Al through the formation of harmless complexes with organic ligands, which are then sequestered to specific organelles [36,37]. Comparative proteomic analysis and bioinformatic techniques are effective tools for revealing the molecular mechanisms underlying responses to abiotic stress [38].

Soybean is sensitive to Al toxicity [39]. Comparative proteomic analysis has revealed that Al induces tolerance-related proteins in the tolerant cultivar; whereas, proteins related to stress responses are increased in the sensitive cultivar [40]. In the Al-tolerant soybean cultivar, the increase in ROS scavenging is related to the increased abundance of proteins involved in sulfur metabolism. In addition, the levels of ABC transporter ATP-binding proteins help in transferring Al away from the roots [41]. In response to Al toxicity, the cysteine synthase and glutathione reductase played an important role in the soybean adaptation to heavy metal stress [42]. Glutathione-S-transferase was increased under the Al stress in soybean [40]. The antioxidation and detoxification enzymes played an important role in Al tolerance in rice, soybean, and tomato [43,42].

Rice is the most Al-tolerant species [44]; however, exposure of rice to Al causes severe yield reductions [45]. Comparative proteomic studies investigating mechanisms of Al tolerance in rice revealed that

the relative abundance of vacuolar H^+ -ATPase was increased in Al-tolerant rice cultivars compared to Al-sensitive cultivars, whereas structural proteins were decreased in both cultivars [46]. In addition, Al toxicity in rice caused an increase in antioxidative, carbohydrate, and nucleotide anabolism-related proteins in the resistant cultivar, whereas a number of pathogenesis and carbohydrate catabolism-related proteins were increased in abundance in the sensitive cultivar. A subsequent study demonstrated that activation of the glycolysis/gluconeogenesis shunt appeared to be a rapid and effective way to balance the levels of available energy to prevent an intracellular energy shortage resulting from the elevated cellular levels of Al [47].

In wheat, exposure to Al increased proteins including S-adenosylmethionine synthase, oxalate oxidase, malate dehydrogenase, and cysteine synthase [48]. In barley, a comparative proteomic study revealed that proteins involved in energy, cell growth, protein synthesis, protein destination/storage, transport, signal transduction, and disease/defense were increased in the tolerant cultivar in response to Al toxicity [49]. The identified proteins were associated with Al tolerance and demonstrated that Tibetan wild barley is a novel genetic resource. In *Arabidopsis thaliana*, the proteins related to tricarboxylic acid (TCA) cycle, glycolysis, reactive oxygen quenching, detoxification, and signal transduction pathways played a role in mediating plant response towards Al stress [50] (Table 1). Understanding the mechanism of action of Al at the molecular level is important for the development of stress-tolerant crop.

2.2. Cadmium

Cd is a highly toxic trace element that is released into the environment through industrial processes and the application of phosphate fertilizers [51]. Although Cd has no biological function, it adversely affects plant growth and development through the induction of oxidative stress [52]. Plants rapidly intake Cd^{2+} through the roots via metal transporters [9], and is then transported to the leaves [53]. Cd exerts its toxic effects by inhibiting ROS-detoxifying enzymes through an affinity for protein sulfhydryl groups, leading to oxidative stress [54]. Biologically, Cd is chemically similar to Zn, Fe, and Ca and can thus replace these elements in the prosthetic groups of many proteins [55].

The effects of Cd stress on various plant species have been examined at the protein level. Among the examined plant species, sunflower displays high tolerance towards Cd. Lopes Júnior et al. [56] reported that the differentially abundant proteins identified in response to Cd treatment were mainly involved in energy, disease, and defense-related functions. However, photosynthesis was reported to be the main process affected by Cd stress in sunflower [56]. In *Vigna radiata*, Cd stress primarily affects proteins associated with nutrient metabolism, though proteins involved in transcription and translation regulation, biosynthesis metabolism, antioxidant pathways, molecular chaperones, and stress responses were also increased [57]. In soybean, Cd stress increases the abundance of proteins related to glycolysis and the TCA cycle [58]. Increasing the abundance of glutamine synthetase and molecular chaperones functions as a plant defense strategy against Cd stress [58].

The toxic effects of short-term Cd exposure in *Populus nigra* revealed that the proteins related to stress responses, photosynthetic carbon metabolism, and energy production were changed under stress condition [59]. In the aquatic plants *Eichhornia crassipes* and *Pistia stratiotes*, exposure to Cd affected both physiological and metabolic properties [60]. In addition, many stress-resistance factors, such as proline, and proteins, particularly heat shock proteins, were found to be involved in the protection and repair of functional proteins. In addition, a number of antioxidant enzymes involved in the detoxification of ROS were increased in response to Cd stress. In tobacco, Cd exposure altered the levels of proteins related to metabolism, photosynthesis, stress responses, signal transduction, protein synthesis/processing, transport, and cell structure [61].

In *Arabidopsis halleri*, Cd and Zn exposure increased the abundance of several photosynthesis-related proteins, indicating that the accumulation

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