Naturally Occurring Heavy Metal Hyperaccumulators

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1. Introduction

Heavy metals are a group of elements with a high density, i.e., above 5 g/cm^3 [1]. These include metallic elements (Mn, Zn, Cu, Hg, and Cd) and metalloids (Se and As). These elements may be biogenic, i.e., essential for proper plant functioning, since they regulate the processes of photosynthesis, respiration, nitrogen metabolism (Fe, Zn, Cu, and Co, among others), or toxic, that cause diseases and disrupt many plant processes [2][3]. Soil trace metal sources can be classified as natural and anthropogenic. Naturally occurring soil metals result from rock weathering or volcanic eruptions and are less bioavailable compared to sources of anthropogenic origin. Man contributes to high heavy metal soil concentrations through mining, agriculture (fertilization), metallurgy, or fuel combustion and transport [4][5]. Not only do these sources seriously threaten humans, but also animals and plants. Heavy metals can contribute, among other things, to protein synthesis changes and ATP production disorders, which can cause serious pathological changes, including cancer. Soil heavy metals inhibit rhizospheric microorganism development, which decreases their degradation efficiency as well as organic compound transformation. When microorganism growth is inhibited, plant pathogen resistance decreases, as does plant development [6]. Fortunately, certain plants can establish in areas with a high heavy metal content. These plants have characteristics that enable them to survive adverse conditions, including a tolerance to high soil heavy metal concentrations [7]. This emphasizes the importance of understanding the mechanisms by which plants absorb high metal concentrations, as well as their depollution of contaminated soils.

2. Naturally Occurring Heavy Metal Hyperaccumulators

A hyperaccumulator is a plant which can absorb and accumulate heavy metals in its above-ground sections (especially the leaves) at values exceeding specific metal thresholds [4]. These values are reportedly 10–500 times higher than in other plants, and hyperaccumulators exhibit no phytotoxic symptoms [2][8]. Trace metals can be taken up by the plant at different rates, depending on, among other things, soil pH, soil organic matter content, metal type, and whether other soil ions are present (which can be antagonistic) [3]. The main plant tolerance mechanism is based on metal uptake avoidance, or on uptake and neutralization through specific plant processes [9]. Plants reportedly take up and accumulate large amounts of heavy metals as an allelopathic defense strategy against competing plants; metal accumulation can also serve as a defense against drought or as a defense strategy against herbivores and pathogens [4] (**Table 1**).

Table 1. Types of plant strategies allowing them to adapt to the presence of heavy metals.

#	Type of Strategy	Description
1	**Strategy for avoiding heavy metal uptake**	• The formation of symbioses with rhizospheric microorganisms which stimulate plant growth under stress conditions [7]. • Developing mechanisms which prevent heavy metals from entering the root cells by releasing substances into the soil that immobilize metals [8]. • The formation of a rhizosphere oxidation zone which oxidizes metals, thus reducing their solubility and availability [9]. • A rhizospheric pH change, whereby an alkaline environment reduces metal availability [10]. • Reduction in cell wall permeability, which forms a barrier against protoplast metal penetration [11]. • Cell wall modification by creating surface components (callose, lignin, cutin) or by increasing the wall's metal accumulation capacity [12].
2	**Strategy of plant tolerance to heavy metals (ion uptake and neutralization)**	• Change in expression of genes encoding tonoplast transporters, responsible for metal ion uptake and sequestration, contributes to an activity reduction [13]. • Binding of metal ions (involved in metabolism) by proteins—chaperones and their transport to cellular compartments which use the ions, e.g., incorporating them into enzymatic molecules [14]. • Chelation of heavy metals into the cytosol by metallothionine classes I and II, organic acids, and the amino acids (histidine), glutathione (GSH), phytochelatin (PC), and nicotianamine (NA), followed by transfer of complexes to the vacuole or cell wall [15]. • The production of heat-shock proteins (HSP), with a regenerative function, that efficiently and quickly repair damage [12].

Many studies on hyperaccumulators have confirmed the above-mentioned defensive plant mechanisms. Transcriptomic studies on *Arabidopsis halleri* have shown that excessive metal accumulation is associated with an increased expression of more than 30 genes, while in *Noccaea caerulescens*, the Zinc Transporter 1 (ZnT1) increases in expression [14].

All these mechanisms allow plants to adapt to stress factors. However, it is possible that heavy metal ions can be unbound and not transported, e.g., to a vacuole, and thereby remain in metal-sensitive areas [1]. Under such conditions, the plant may form reactive oxygen species (ROS) which cause oxidative stress. Excess ROS can damage and reduce antioxidant pathway activity, while in chloroplasts, excess ROS inhibits photosynthesis [16]. This contributes to apoptosis or defense system activation through gene expression, i.e., antioxidant defense system activation [12][17].

2.1. Classification and Occurrence of Hyperaccumulators

Metallophytes, found in heavy-metal-contaminated areas, occur in 34 unrelated flowering plant families. Most metallophytes belong to the Brassicaceae (25%), Asteraceae, Cayrophyllaceae, Plumbaginaceae, Cyperaceae, Violaceae, Poaceae, Fabaceae, and Euphorbiaceae [2][4][18]. About 450 flowering plant species are known hyperaccumulators, which represents about 0.2% of all known species, although this number is still growing. However, some species may be removed from the hyperaccumulator list, which happens when they are classified only based on field samples, and where the trait has not been experimentally confirmed under controlled conditions [8]. To avoid such situations, it is necessary to thoroughly analyze and evaluate a plant as a hyperaccumulator.

A plant may accumulate one (most frequently) or several metals [8]. Most hyperaccumulators are flowering dicotyledonous and herbaceous plants. Most hyperaccumulators (90%), such as *Alyssum discolour*, *Alyssum inflatum*, *Minuartia baldaccii*, and *Viola dukadjinica*, are endemic plants found on serpentine soils (rich in Ni, Co, Cr, and Mn) [19][20]. However, hyperaccumulators can also be found on calamine soils (rich in Pb, Zn, and Cd). For example, *Armeria elongata*, *Silene vulgaris*, *Biscutella laevigata*, *Viola lutea*, *Festuca rubra*, and *Agrostis stolonifera* can be found on copper-bearing soils [21]. Another interesting example is the island of New Caledonia, where Ni hyperaccumulators are found in every taxonomic group, since most of the islands' surface is covered by magma rocks rich in Mn, Ni, and Fe [20]. Europe is home to hyperaccumulator species such as *Thlaspi caerulescens* [22] and *Arabidopsis halleri* [23], which accumulate Zn and Cd, and *Agrostis capillaris* L., *Holcus lanatus*, *Calamagrostis epigejos* L., which accumulates As [24].

2.2. Parameters for Assessing Heavy Metal Resistance

For a plant to be classed as a hyperaccumulator, its heavy metal resistance must be assessed based on parameters such as bioaccumulation, tolerance, and contamination indices, as well as the translocation factor [25]. The bioaccumulation index indicates how efficiently plants accumulate metals and is expressed as the ratio of metal concentration in the plant relative to its surrounding soil content. The tolerance index indicates the extent to which the plant stops growing under culture conditions in contaminated soil. The contamination index is expressed as the ratio of the amount of plant dry matter in the contaminated soil relative to the amount of plant dry matter in the control medium. The translocation factor determines whether heavy metals are efficiently moved by the plant and is expressed as the ratio of metal content in the above-ground sections relative to the root metal content [26].

Using these indicators, a suitable plant can be selected, for example, in phytoremediation processes. Hyperaccumulators enable the rehabilitation of heavy-metal-contaminated soils which threaten human health [27]. Studying hyperaccumulators and remediation processes is therefore crucial.

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