The Mechanism of Plant Resistance to Heavy Metal

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Abstract: Heavy metal pollution in the soil results in the accumulation of heavy metals in plants. While heavy metals are toxic to plants, plants also resist the toxicity of heavy metals through the mechanism of avoidance and tolerance. In this paper the research progress on the mechanism of plant resistance to heavy metal stress is reviewed in order to provide scientific reference for further research in this area.

1. Introduction
The overuse of fertilizers, pesticides combined with sewage irrigation, solid waste and gas deposition often lead to heavy metal pollution[1-2]. Some heavy metals are non-essential elements of plant growth, such as cadmium, lead, chromium, arsenic, mercury, etc. Product safety quality declines even at lower metal concentrations. When the metal concentration is higher, it will have a toxic effect on plants[3-4]. The other heavy metals are essential elements for plant growth. When the concentration is too high, it will also have toxic effects on plants, including iron, manganese, zinc, copper, nickel, etc.

Most plants have gradually formed an avoidance mechanism and tolerance mechanism in the heavy metal stress environment. Avoidance mechanisms include plants affecting mobility of heavy metals and microbial activity through root exudates, fine isolation and regionalization of cell walls, cell membranes and vacuoles[5-6]. Avoidance mechanisms are to reduce the amount of heavy metals into the plants. The tolerance mechanism is that the plant itself has mechanisms to reduce the toxicity of heavy metals in the body, including chelation, osmotic adjustment and antioxidant systems[7]. This paper discussed the latest research progress of the plant mechanisms of heavy metal avoidance and tolerance, in order to provide reference for further research in this aspect.

2. The mechanisms of plant resistance to heavy metal

2.1. Root exudates

2.1.1. Organic acids
Under heavy metal stress, the secretion of organic acids such as oxalic acid, citric acid, malic acid, tartaric acid and succinic acid increase. Organic acids normally have one or more carboxyl groups that can chelate with heavy metals to form non-toxic compounds that prevent them from entering the plant. Chen et al. showed that organic acids secreted by roots of Phyllostachys pubescens can increase soil phosphorus content[8]. Phosphate ions can form precipitates with lead, and the lead is fixed in the soil to avoid root absorption. Under cadmium stress, the total amount of organic acid secretion in roots of cadmium-tolerant rice was 1.76-2.43 times that of cadmium-sensitive varieties[9]. The secretion of
tartaric acid, oxalic acid and acetic acid in the roots of cadmium-tolerant varieties of pepper was significantly higher than that of cadmium-sensitive varieties\textsuperscript{[10]}. In addition, the organic acids secreted by the roots can also provide carbon sources for microorganisms.

2.1.2. Amino acid
Under heavy metal stress, the secretion of amino acids in plant roots increase significantly \textsuperscript{[9]}. For example, the secretion of methionine, lysine and histidine in rice roots increase significantly with the increase of Cd concentration\textsuperscript{[11]}. Root amino acid secretions can provide nutrient sources for rhizosphere microorganisms such as bacteria, fungi, yeasts and sulfur bacteria\textsuperscript{[11]}. Bacteria and fungi use their secretions and metabolites to inhibit the absorption of heavy metals by plant roots. Sulfur bacteria can also react with heavy metals to form sulfide precipitates, preventing heavy metals from entering the plant\textsuperscript{[12]}. Root amino acid secretions can also directly chelate with heavy metals, alleviating the toxic effects of heavy metals\textsuperscript{[13]}.

2.1.3. Soluble sugar and soluble protein
Plant cells will actively accumulate some soluble solutes, such as soluble proteins and soluble sugars, which aims to reduce intracellular osmotic potential to ensure the normal supply of water under heavy metal stress conditions and maintain the normal physiological functions of cells\textsuperscript{[14]}. The content of soluble sugar and soluble protein in ryegrass and Timothy grass increased first and then decreased with the increase of cobalt (Co) concentration\textsuperscript{[15]}. In order to cope with the heavy metal stress, the soluble sugar and soluble protein content increased. A research showed that soluble sugar secreted by roots can also form non-toxic compounds directly with lead\textsuperscript{[16]}.

2.2. subcellular structure

2.2.1. Cytoderm
The cell wall is composed of cellulose, hemicellulose, pectin and protein. Its surface has functional groups such as carboxyl group, hydroxyl group, amino group and aldehyde group, which can be combined with metal ions to restrict the transmembrane transport of heavy metals. Under lead stress, the lead content in the lateral root cell of radish accounted for 71.08% ~ 80.40% of the total lead in the lateral root\textsuperscript{[6]}. After removal of hemicellulose from the root wall of common cabbage, leaf lettuce, pepper, tomato and rice, the accumulation of zinc in the root cytoderm decreased significantly and the accumulation in the shoot increased\textsuperscript{[17]}. In addition, cysteine-rich proteins are present in the rice root cytoderm to fix lead\textsuperscript{[18]}. Exogenous application of nitrogen oxides enhances the tolerance of rice and Kandelia to cadmium by increasing the content of hemicellulose and pectin in the root cytoderm\textsuperscript{[19]}.

2.2.2. Cytomembrane
There are many transport proteins on the plant cytomembrane. Some of the proteins are related to heavy metal transportation processes, such as heavy metal ATPase (P-ATPase), ATP-binding cassette transporter (ABC) and cation diffusion facilitator (CDF). A study by Sasaki et al. showed that the overexpression of OsHMA3 (a subclass of HMA family members of P-ATPase) enhanced the tolerance of rice roots to cadmium\textsuperscript{[20]}. But the overexpression of NtHMA3a and NtHMA3b did not increase tobacco tolerance to mercury, while ABC transporters play an important role in tobacco response to mercury toxicity\textsuperscript{[21]}. Studies by Sun et al. showed that overexpression of PtABCC1 enhanced the tolerance of Arabidopsis and poplar to mercury\textsuperscript{[22]}. The overexpression of AtMRP and AtPDR in the ABC family is directly regulated by cadmium and lead. AtMRP3 acted as a cadmium transporter on the cytomembrane to transport cadmium to vacuole, and AtPDR12 acts as an efflux pump for lead\textsuperscript{[23]}.  

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2.3. Chelation

2.3.1. Metallothionein
Metallothionein (MT) is a widely occurring low molecular weight, cysteine-rich and metal-binding protein. MT is directly synthesized by mRNA transcription induced by heavy metal stress [24]. The MT gene can be expressed at different stages of plant growth, responding to the stress of different heavy metal ions. The MT gene has been cloned in peas [25], mustard, tobacco [26] and Arabidopsis. It was found that the MT2 gene in Arabidopsis was expressed under the induction of Zn$^{2+}$, which increased the tolerance to Zn$^{2+}$ [25]. Transferring the SaMT3 gene into the escherichia coli enhanced the resistance of cells to copper and lead [27].

2.3.2. Phytochelatins
Phytochelatins (PC) have large sulfhydryl groups and strong affinity for heavy metals. Cadmium, copper, mercury, lead, zinc, silver, strontium, gold, tin, nickel, arsenic and selenium can all induce the production of PC in corn and wheat. Different heavy metals have different binding abilities to PC, among which cadmium has the strongest binding ability, followed by lead, zinc, antimony, silver, mercury, arsenic, copper, tin, gold and strontium [28]. Metal ions which enter the plant can form a stable chelate with PC to isolate the vacuole medium, thereby reducing the concentration of free metal ions in the plant cells.

2.3.3. Reduced glutathione
Reduced glutathione (GSH) is an amino acid derivative composed of glutamic acid, cysteine and glycine. It can act as a ligand to chelate with heavy metals and reduce the toxicity of heavy metals [29]. Exogenous application of GSH promoted the formation of phytochelatins in seedlings of Dianthus chinensis and poplars, and formed non-toxic chelate with cadmium to alleviate toxicity to the plants [30].

3. Conclusion
The plants resistance to heavy metals reflects their ability to reduce the toxicity of heavy metals. Plants that are resistant to heavy metals mainly use methods such as blocking the absorption of heavy metals, extracellular complexation, cytoplasmic complexation and chelation. To do this, plants must be able to activate their defense responses, such as activating the expression of antioxidant enzymes, preventing or repairing oxidative stress damage caused by oxidative stress. With the development of molecular biology, molecular biology is more widely used in studying the plant tolerance to heavy metals. However, due to the different types of heavy metals that plants face, the resistance mechanism of plants to heavy metals is also very complicated. Further research is therefore required to help us better understand the resistance mechanism of plants to heavy metals.

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