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Deciphering lead tolerance mechanisms in maize: A thorough analysis

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Abstract
Food security and sustainable crop production are under risk due to the growing problem of lead pollution in agricultural soils. A staple crop grown all over the world, maize is especially vulnerable to lead toxicity, which reduces its yields and growth. The existence of innate tolerance mechanisms is suggested by the fact that certain maize cultivars show differing degrees of tolerance to lead stress. The goal of this review is to give a thorough summary of what is currently known about the lead tolerance strategies used by maize. We examine the physiological, biochemical, and molecular reactions of maize to lead stress, emphasizing the crucial tactics that support its growth and survival under challenging circumstances. This review provides important insights into the intricate processes behind maize's resistance to lead toxicity by highlighting recent research discoveries and outlining potential future directions. In order to improve lead tolerance in maize and provide robust and sustainable agriculture, it is imperative to comprehend these mechanisms.

Keywords: Physiological reactions, biochemical processes, molecular reactions, antioxidant defense, organic acids, phytochelatins, lead tolerance, maize, and genetic advancement

Introduction

As a staple food and a significant source of animal feed and industrial goods, maize (*Zea mays* L.), a cereal grain in the Poaceae family, is one of the most extensively grown crops in the world. In many areas, maize contributes significantly to both food security and economic stability due to its high productivity and adaptability (Shah *et al*., 2020) [6]. However, heavy metal contamination, especially lead, has become a major worry among the many abiotic stresses that frequently pose a threat to maize growth (Alloway, 2013) [1]. Both natural and man-made processes, including mining, smelting, and the use of lead-based fertilizers and pesticides, can cause lead (Pb), a hazardous and non-biodegradable heavy metal, to build up in soils (Alloway and Jackson, 2017) [2]. Toxic levels of lead prevent via the food chain, hinders maize growth, lowers yields, and endangers human health (Alloway, 2013; Shah *et al*., 2020) [1, 6].

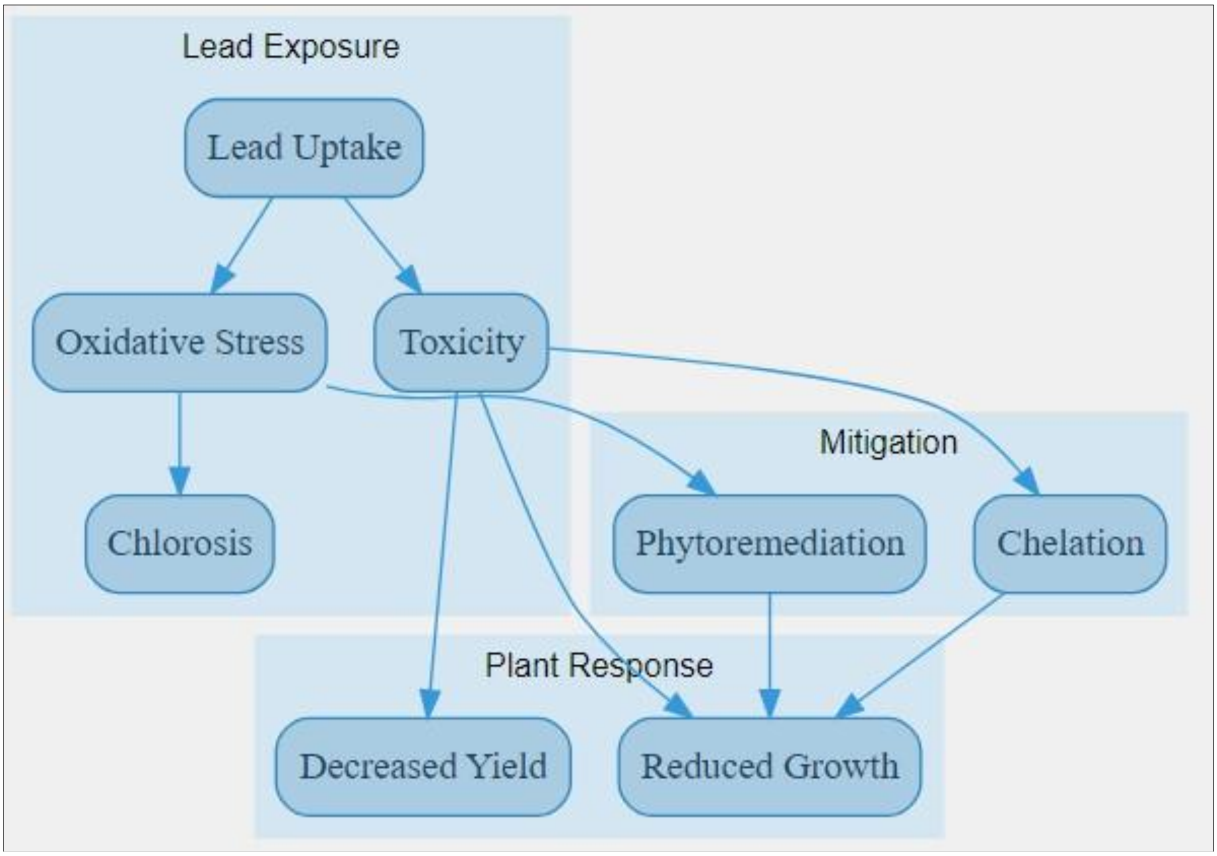
Certain maize cultivars exhibit variable resistance despite the negative effects of lead stress, indicating the existence of innate systems that allow them to deal with lead toxicity (Gallego *et al*., 2012) [3]. In order to improve maize resilience and guarantee sustainable crop production in lead-contaminated areas, it is crucial to unravel these tolerance mechanisms. The goal of this review is to present a thorough summary of the state of the art regarding lead tolerance strategies in maize, including physiological, biochemical, and molecular reactions, as well as their implications for further study and farming methods.

Physiological Reactions in Maize to Lead Stress

A variety of physiological alterations brought on by lead stress in maize are a part of the plant's adaptive mechanisms for surviving hazardous environments. To combat the harmful effects of reactive oxygen species (ROS) produced by lead toxicity, one of the main reactions is the activation of the plant's antioxidant defense system (Shah *et al*., 2020) [6]. In response to lead stress, maize plants increase the activity of antioxidant enzymes such as glutathione reductase (GR), peroxidases (POX), catalase (CAT), and superoxide dismutase (SOD) (Gallego *et al*., 2012; Shah *et al*., 2020) [3, 6].

In order to minimize oxidative damage to proteins, lipids, and nucleic acids, these enzymes are essential for scavenging excess ROS, such as superoxide anions (O2^-) and hydrogen peroxide (H2O2), and preserving cellular redox equilibrium (Shah *et al.*, 2020) [6].

Lead stress causes alterations in root morphology and architecture in addition to the antioxidant response. In comparison to susceptible cultivars, maize cultivars that can withstand lead stress have been found to have longer and denser root systems, indicating improved root growth (Gallego *et al.*, 2012) [3]. Better soil exploration is made possible by the increased root growth, which also makes it easier for the plant to absorb nutrients and water and may help prevent lead poisoning (Gallego *et al.*, 2012) [3]. Additionally, tolerant cultivars frequently exhibit altered root hair development, with longer and denser root hairs that can improve nutrient and water absorption as well as aid in the immobilization and exclusion of lead (Gallego *et al.*, 2012; Shah *et al.*, 2020) [3, 6].

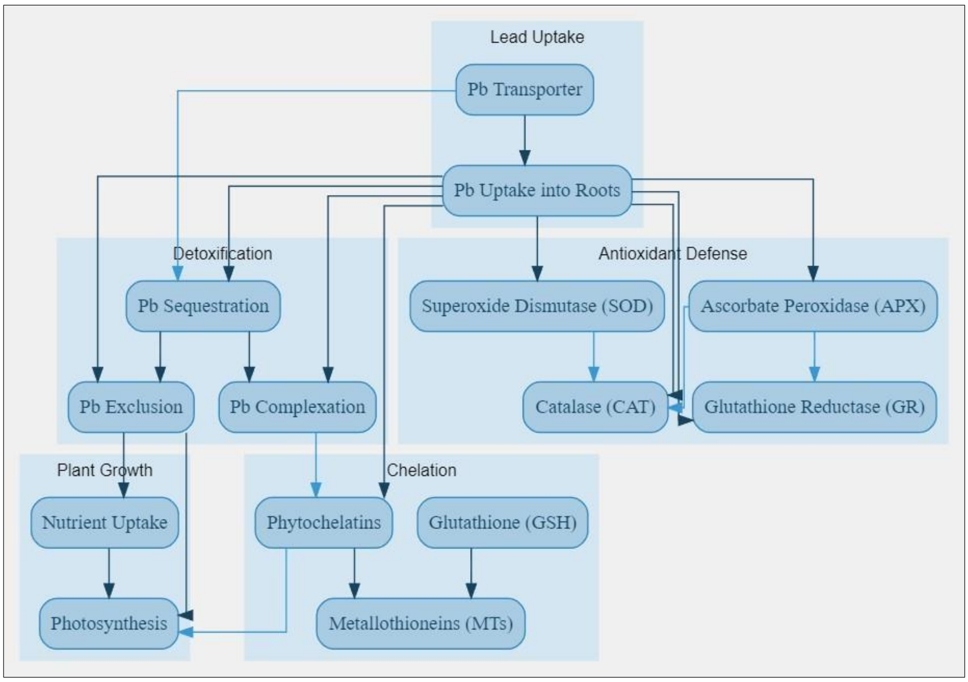


Mechanisms of Lead Tolerance in Maize Through Biochemistry

In order to tolerate and detoxify lead in the rhizosphere and inside plant tissues, maize uses a variety of biochemical processes. The production and exudation of organic acids, especially citric and malic acids, constitute one important mechanism (Shah *et al.*, 2020) [6]. Exuded from the roots, these organic acids have the ability to chelate lead ions in the soil, lowering their bioavailability and consequent root uptake (Alloway and Jackson, 2017) [2]. Organic acids reduce lead toxicity in plants by preventing lead ions from entering the root symplast by the formation of stable complexes with them (Shah *et al.*, 2020) [6].

The buildup and sequestration of lead in root vacuoles is a significant biochemical mechanism of lead tolerance in maize (Gallego *et al.*, 2012) [3]. It has been demonstrated that tolerable cultivars have effective vacuolar sequestration systems that stop lead from moving to aboveground areas (Gallego *et al.*, 2012) [3]. Phytochelatins are short, cysteine-rich peptides that bind to lead ions, making them less poisonous and making it easier for them to be sequestered in vacuoles (Shah *et al.*, 2020) [6]. Lead stress triggers the manufacture of phytochelatins, which is controlled by genes encoding phytochelatin synthases (PCS) (Gallego *et al.*, 2012) [3].

Furthermore, by producing lead-binding proteins such metallothioneins (MTs), some maize cultivars have improved lead tolerance (Alloway and Jackson, 2017) [2]. MTs are proteins with a low molecular weight that have a strong affinity for lead and other heavy metals. By attaching to lead ions and blocking their interaction with essential cellular components, they serve a critical role in detoxifying lead ions (Alloway and Jackson, 2017) [2]. Lead stress frequently triggers the production of MTs, and their presence helps plants resist and tolerate lead toxicity (Alloway, 2013) [1].

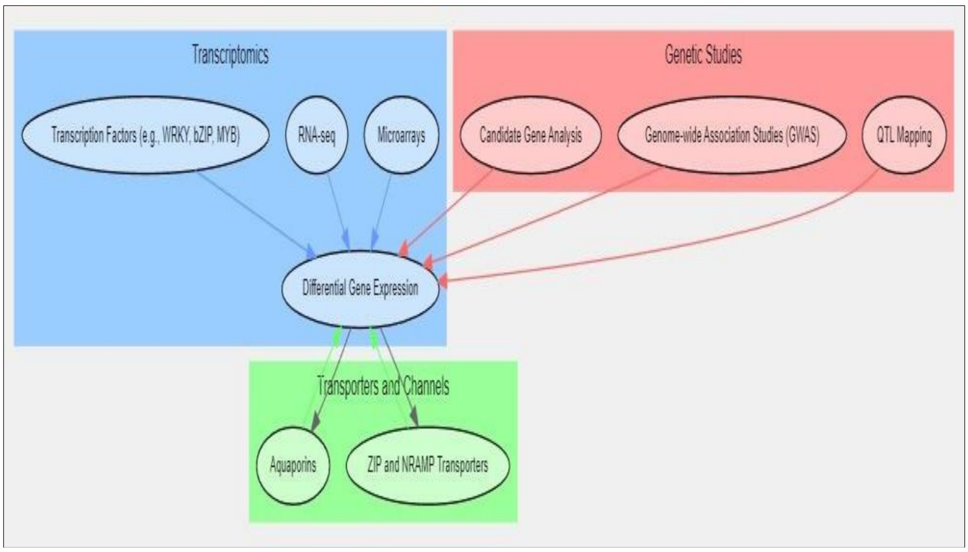


The Genetic Foundation and Molecular Reactions of Lead Tolerance in Maize

Recent developments in transcriptomics and genomes have shed important light on the molecular reactions of maize to lead stress. Differential gene expression patterns in response to lead toxicity have been identified by transcriptomic analyses employing microarrays and RNA-seq (Gallego *et al*., 2012; Shah *et al*., 2020) [3, 6]. Among the most highly regulated genes are those related to detoxification, metal ion homeostasis, antioxidant defense, and stress response (Shah *et al*., 2020) [6]. Important transcription factors have been linked to controlling gene networks that support lead tolerance, including WRKY, bZIP, and MYB (Gallego *et al*., 2012) [3]. For instance, ZmWRKY17 overexpression in maize improved lead tolerance by altering the expression of genes related to metal ion transport and ROS scavenging (Li *et al*., 2019) [5].

Additionally, transporters and channels are essential for the absorption, translocation, and detoxification of lead in maize. Lead uptake and translocation in plants have been demonstrated to be mediated by metal ion transporters, including Zn/Fe-regulated transporter-like proteins (ZIP) and natural resistance-associated macrophage proteins (NRAMP) (Shah *et al*., 2020) [6]. These transporters' participation in lead tolerance pathways is suggested by their differential expression under lead stress (Gallego *et al*., 2012) [3]. Furthermore, lead transport and exclusion in maize have been linked to aquaporins, which help move water and tiny molecules (Shah *et al*., 2020) [6].

Quantitative trait loci (QTL) linked to lead tolerance features in maize have been found through genetic research. Genome-wide association studies (GWAS) and QTL mapping have identified loci associated with antioxidant enzyme activities, lead buildup, and root growth (Gallego *et al*., 2012; Shah *et al*., 2020) [3, 6]. For example, chromosome 7 was found to harbor a substantial QTL for lead accumulation, qPB-7, which accounts for a considerable amount of the variance in phenotype (Gallego *et al*., 2012) [3]. ZmMTP7, a putative cation diffusion facilitator (CDF) gene implicated in vacuolar sequestration of lead, was discovered using fine mapping and candidate gene analysis inside this QTL region (Gallego *et al*., 2015) [4].



Breeding Maize for Increased Lead Tolerance

Significant progress has been made by breeding programs in creating maize cultivars with increased resistance to lead. Cultivars with improved lead tolerance qualities have been created by combining traditional breeding methods with marker-assisted selection (MAS) employing QTL and candidate gene markers (Shah *et al*., 2020) [6]. According to Gallego *et al*. (2012) [3], these cultivars have better root architecture and growth, stronger antioxidant defenses, and effective lead exclusion or sequestration mechanisms. For instance, in breeding projects, the lead-tolerant maize cultivar 'B73' has been employed as a donor parent, bringing tolerance qualities to new hybrids (Gallego *et al*., 2012) [3].

To increase maize's resistance to lead, genetic engineering techniques have also been investigated. Transgenic maize plants with enhanced lead tolerance have been produced by overexpressing important lead tolerance genes, including ZmWRKY17, ZmMTP7, and ZmPCS (Li *et al*., 2019; Gallego *et al*., 2015; Shah *et al*., 2020) [5, 4, 6]. The potential of genetic engineering to confer lead tolerance was demonstrated by these transgenic plants, which showed greater root growth, higher phytochelatin production, and decreased lead accumulation in shoots (Li *et al*., 2019; Shah *et al*., 2020) [5, 6].

Conclusion and Prospects

In order to improve lead tolerance and guarantee sustainable maize production in polluted soils, it is essential to comprehend the physiological, biochemical, and molecular mechanisms underlying lead tolerance in maize. In order to thoroughly discover and characterize the important genes, proteins, and metabolites involved in lead tolerance, future research should concentrate on combining omics methods, such as genomics, transcriptomics, proteomics, and metabolomics (Shah *et al*., 2020) [6]. A more comprehensive knowledge of the many networks and mechanisms underpinning lead tolerance in maize will be possible thanks to this systems biology approach.

Furthermore, marker-assisted selection and breeding for improved lead tolerance will be made easier by increased research on the genetic basis of lead tolerance, including the discovery of new QTL and candidate genes (Gallego *et al*., 2012) [3]. More effective and accurate breeding programs will be made possible by the creation of molecular markers associated with lead tolerance traits, which will speed up the integration of tolerance traits into elite cultivars (Shah *et al*., 2020) [6]. To sum up, maize responds to lead stress in a variety of adaptive ways, such as molecular modifications, biochemical processes, and physiological alterations. The creation of organic acids and phytochelatins, alteration of root architecture, activation of antioxidant defense systems, and variable expression of genes and transporters all help maize withstand and adapt to lead toxicity. By dissecting these tolerance techniques, scientists can use the information to create practical plans for improving lead tolerance in maize through genetic engineering and breeding. In regions impacted by heavy metal pollution, ensuring maize's resistance to lead-contaminated soils is essential for preserving food security and sustainable agriculture.

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