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Review

Analysis of Heavy Metal Impacts on Cereal Crop Growth and Development in Contaminated Soils

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Abstract: The impact of heavy metal presence in soil on cereal crops is a growing concern, posing significant challenges to global food security and environmental sustainability. Cereal crops, vital sources of nutrition, face the risk of contamination with toxic heavy metals released into the environment through human activities. This paper explores key aspects requiring thorough investigation to foster innovation and understand intricate interactions between heavy metals and cereals. Visible symptoms and physiological changes resulting from heavy metal contamination, such as chlorosis and stunted growth, demand further research to devise targeted mitigation strategies and sustainable agricultural practices. Root barrier formation, mycorrhizal symbiosis, and metal-binding proteins emerge as critical defence mechanisms for combating heavy metal stress, offering opportunities for developing metal-tolerant cereal varieties. Research on metal bioavailability and food safety implications in cereal grains is vital to safeguard human health. This paper reveals that multidisciplinary collaboration and cutting-edge technologies are essential for promoting innovation beyond the state of the art in elucidating and mitigating the impacts of heavy metals on cereal crops. Genetic and breeding approaches show promise in developing metal-tolerant cereal varieties, while agronomic practices and soil amendments can reduce metal bioavailability and toxicity. Unravelling the complex mechanisms underlying heavy metal uptake and tolerance is essential for sustainable cereal agriculture and worldwide food sustainability. Embracing the challenges of heavy metal pollution through proactive research and collaboration can secure a resilient future for cereal crops amid evolving environmental conditions.

Keywords: cereal crops; metal toxicity; metal uptake; metal tolerance; mycorrhizal symbiosis; soil contamination

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1. Introduction

Heavy metal contamination in soil is a critical environmental issue with severe implications for crop production, food safety, and human health. The presence of these toxic elements in agricultural soils threatens crop productivity, food quality, and the overall sustainability of agriculture [1,2]. Addressing this issue requires a comprehensive approach that includes responsible waste management, sustainable agricultural practices, and regular monitoring to ensure the safety of the food supply and protect both the environment and human well-being [3,4].

The contamination of soils by heavy metals poses a substantial environmental quandary with far-reaching repercussions for the growth and development of cereal crops. These crops are indispensable for sustainable food systems as they absorb water and nutrients from the soil, potentially uptaking these toxic metals in the process [5,6]. This phenomenon, known as bioaccumulation, can lead to elevated levels of heavy metals in edible plant parts, such as grains, thereby endangering consumers when these tainted crops are consumed [7,8].

In the pursuit of understanding the complicated interplay between heavy metal contamination and cereal crop growth and development, this paper embarks on an in-depth analysis of the impacts posed by these environmental challenges. Focusing on selected cereal crops, we explore the consequences of heavy metal presence in contaminated soils, unravelling the complexities that arise as these essential crops strive to grow in such adverse conditions. Through this critical investigation based on the literature and our own knowledge, we aim to shed light on the critical implications of heavy metals in soil for world food stability and sustainable agricultural practices.

1.1. The Key Role of Cereal Crops in Ensuring World Food Resilience

Cereal crops (wheat, rice, maize, and barley), are of paramount importance for food accessibility since they serve as the cornerstone of the world's food supply, providing a substantial portion of the essential nutrients required for human sustenance [9,10]. These crops are extensively cultivated and consumed worldwide, accessible to millions of farmers and communities. Their adaptability to diverse climates and growing conditions ensures food availability across regions and demonstrates remarkable resource efficiency, producing significant grain harvests per unit of land, water, and energy invested [11–14]. This efficiency is particularly vital in regions with limited arable land and resources, as it supports sustainable food production without straining the environment.

Furthermore, cereal crops possess exceptional storage capabilities, allowing grains to be preserved for extended periods with minimal loss of nutritional value. This characteristic is crucial for regions facing erratic weather patterns, natural disasters, or disruptions, as stored grains serve as a buffer during food scarcity [15–17]. These crops are also rich in carbohydrates, proteins, fibres, vitamins, and minerals essential for human health, forming the foundation of a balanced and nutritious diet, especially in areas with limited food diversity. Additionally, cereal crops play a key role in supporting livelihoods and economic stability, contributing to income and employment opportunities for farmers, workers, and traders, thus fostering agricultural development and rural prosperity [18].

Consequently, cereal crops are irreplaceable in ensuring planetary food due to their extensive cultivation, resource efficiency, storage stability, nutritional value, and socio-economic significance. As the world's population continues to grow, the sustainable production and availability of cereal crops remain critical in addressing hunger, malnutrition, and food insufficiency on a global scale. Table 1 summarizes some of the motivations behind the significance of cereal crops in international food access.

Table 1. The starring role of cereals for worldwide food safety.

Cereals Importance	Motivation
Essential food for millions of people	- cereal crops, such as wheat, rice, maize (corn), and millet, are staple foods for billions of people around the world - these crops provide a substantial portion of the daily calorie intake for individuals in many regions, particularly in developing countries - as affordable and widely available sources of carbohydrates, proteins, and essential nutrients, cereals are indispensable for meeting basic dietary needs
Global production and consumption	- cereal crops are among the most widely cultivated and consumed crops globally - they cover vast areas of agricultural land and are grown in diverse climatic conditions, making them adaptable to various regions and climates - this wide distribution ensures a steady supply of food to different populations, regardless of geographic location

Table 1. *Cont.*

Cereals Importance	Motivation
Caloric and nutritional safety	- cereals are energy-dense crops that provide a significant portion of dietary energy for people worldwide - they are particularly important for populations with limited access to other food sources - cereals are rich in essential nutrients like iron, zinc, and B vitamins, contributing to improved nutrition and overall health
Food safety for vulnerable populations	- cereal crops are often the most affordable and accessible food options for vulnerable populations, including low-income individuals and those living in regions with limited agricultural resources - these crops play a decisive role in reducing hunger and malnutrition in poor communities.
Livelihoods and rural development	- cereal crop cultivation supports the livelihoods of millions of smallholder farmers in rural areas - farming and trading of cereals provide income opportunities for farmers and contribute to rural development and economic stability
Role in food trade	- cereal crops are key commodities in international food trade, with many countries relying on imports to meet their food demands - their global significance makes cereals vital for ensuring food safety on a broader scale, as countries can access cereals from surplus-producing regions during times of shortages or emergencies
Animal feed and livestock production	- cereal crops are critical for animal feed, supporting the livestock industry and ensuring a steady supply of animal-based protein sources for human consumption
Climate resilience	- some cereal crops, like millet and sorghum, are known for their resilience to harsh environmental conditions, such as drought and high temperatures - these crops can provide sustenance in regions with challenging climatic conditions, contributing to climate change adaptation and adequate food supply in vulnerable areas

Sources: [13,19–23].

1.2. The Challenge of Heavy Metal Contamination in Soil and Its Potential Impact on Crop Production

The contamination of soil with heavy metals stands as a significant environmental concern with wide-ranging implications for crop production and food protection. Heavy metals, naturally occurring elements like cadmium, lead, mercury, arsenic, and chromium found within the Earth's crust, have seen their levels in agricultural soils escalate substantially due to human activities, including industrial processes, mining, agricultural practices, and improper waste disposal [24–27]. The primary contributors to heavy metal contamination in soil are human activities. Emissions from industries, the utilization of fertilizers and pesticides, the application of sewage sludge, and improper waste disposal introduce heavy metals into the soil ecosystem. Mining operations further exacerbate the situation by releasing significant quantities of metals into the soil, leading to localized contamination near mining sites [28–30] (Figure 1).

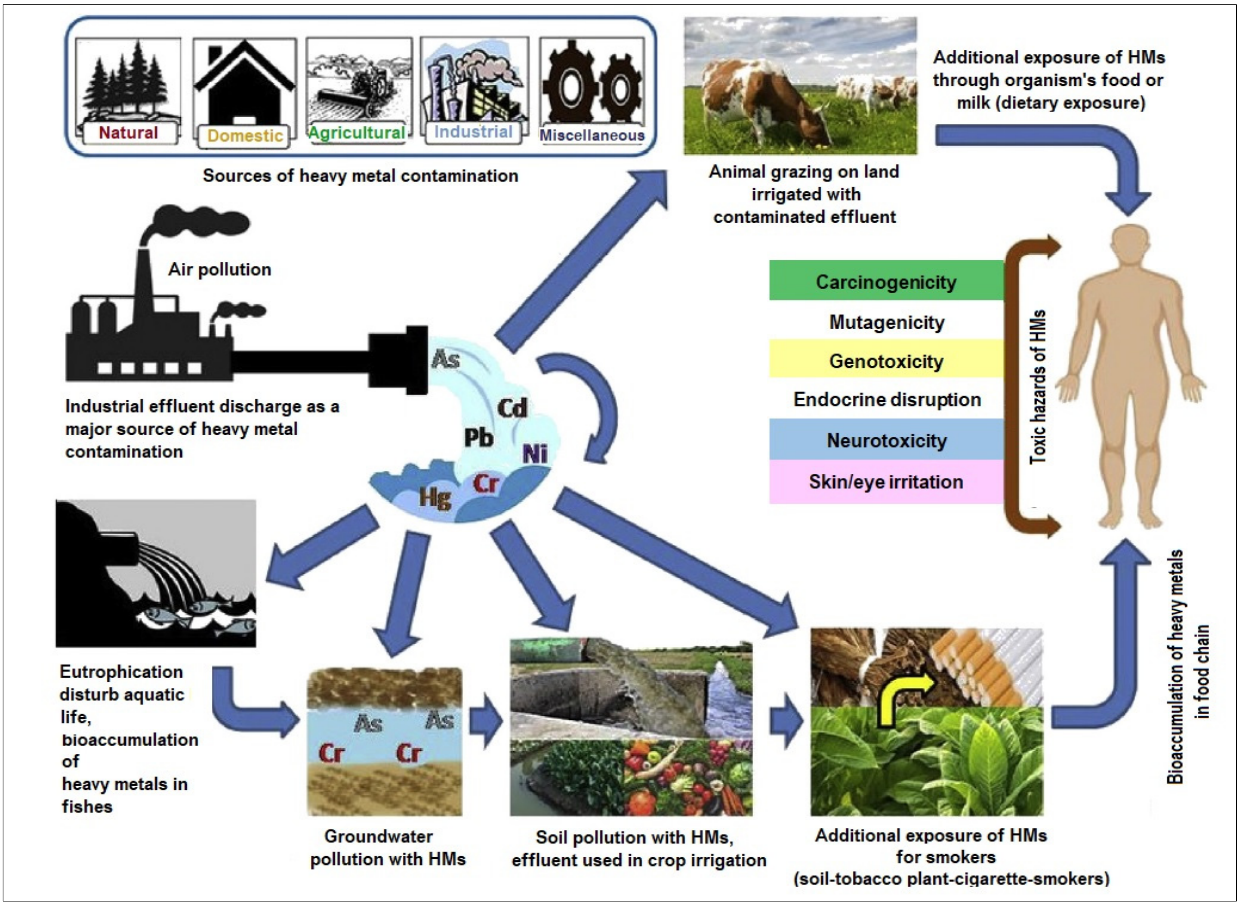

Figure 1. Sources of heavy metals contamination in food plants and trophic transfer to humans (Johnson Afonne and Chinedu Ifediba, 2020 [30], reproduced under Licence No. 5602770308955, 5 August 2023, Licenced Content Publisher Elsevier).

Heavy metals have a high degree of persistence in the environment. Once introduced into the soil, they tend to accumulate over time due to their low mobility and limited degradation. Consequently, areas subjected to prolonged exposure to heavy metals face increasing contamination levels, posing long-term threats to agricultural productivity [31]. Crops can absorb heavy metals from contaminated soils through their root systems. Some metals, like cadmium and lead, have a high affinity for root surfaces and can be readily taken up by plants, even in trace amounts [32,33]. These metals then get translocated to various plant parts, including edible portions, making them potential pathways for human exposure [34,35]. Therefore, heavy metals are toxic to both plants and humans. In plants, they can disrupt essential physiological processes, leading to reduced growth, chlorosis (yellowing of leaves), and nutrient imbalances [36,37]. Heavy metal contamination negatively impacts crop yield and quality. High levels of metals in the soil can lead to reduced plant productivity, stunted growth, and lower yields. Additionally, crops exposed to heavy metals may show a decline in nutritional quality, with decreased levels of essential nutrients like iron and zinc. Consequently, heavy metals can adversely affect soil fertility and microbial activity [38,39]. Soil microbes play a vital role in nutrient cycling and organic matter decomposition. Heavy metals can disrupt microbial populations and impair their metabolic processes, leading to imbalanced nutrient availability and degradation of soil health [40,41].

Obviously, the issue of heavy metal contamination extends beyond crop plants. Grazing animals consuming contaminated crops can experience the bioaccumulation of metals in their tissues. Humans consuming meat and dairy products from these animals also face exposure to heavy metals. Consumption of crops and food of animal origin contaminated with heavy metals can lead to a range of health issues in humans, including kidney and liver damage, neurological disorders, developmental problems in children, and an elevated risk of certain cancers [42].

In light of these considerations, heavy metal contamination poses significant food safety concerns. Regulatory bodies worldwide set maximum allowable limits for heavy metals in food products to safeguard public health [43–45]. Exceeding these limits can result in the recall of food products and substantial economic losses for farmers and the food industry.

2. Unravelling the Intricate Relationship between Heavy Metals and Cereals

The relationship between heavy metals and cereals is a complex and multifaceted one that holds significant implications for agriculture, food care, and human health. Previous research has extensively investigated the relationship between heavy metals and cereals, providing valuable insights into the uptake, translocation, and effects of these toxic elements on crop growth and development.

2.1. Uptake and Translocation of Heavy Metals in Cereals

Studies have shown that cereal crops can absorb heavy metals from contaminated soils through their root systems. The extent of metal uptake varies among different cereal species, with some crops exhibiting higher metal accumulation than others [46,47]. Several factors influence the uptake process, including soil pH, metal concentration, soil organic matter content, and the presence of other elements that can compete for absorption sites on the root surface [48–50]. For example, certain cereal crops like rice and barley are known to have a higher affinity for the uptake of heavy metals like cadmium and arsenic. In contrast, other cereals, such as wheat and corn, have been found to accumulate lower levels of these metals under similar soil conditions [51–55]. Once taken up by the roots, heavy metals can be transported within the cereal plant through the translocation process [56]. This movement of metals from the roots to other plant organs is a critical aspect of the metal's behaviour within the plant. In some cases, heavy metals may be translocated to above-ground parts of the plant, such as leaves, stems, and grains [49,50] (Figure 2). The translocation to the edible portions of the plant is of particular concern as it can lead to contamination of the human food chain. For instance, in rice, which is a staple food for nearly half of the world's population, heavy metals like cadmium and arsenic have been found to accumulate in the grains [5,57]. This accumulation can have severe health implications for consumers, as prolonged exposure to elevated levels of these toxic metals may lead to various health problems, including organ damage and increased cancer risk [58,59]. The translocation process is not uniform across all heavy metals and cereal crops. Some metals, like lead, tend to remain concentrated in the roots and are less efficiently transported to the above-ground plant parts. However, lead contamination in soils can still impact the quality of agricultural products and pose health risks to the ecosystem [60,61].

Therefore uptake and translocation of heavy metals in cereal crops are complex processes influenced by various environmental and plant-related factors. Elucidating the mechanisms of metal uptake and translocation in cereals is vital for developing strategies to minimize heavy metal accumulation in edible portions of crops and mitigate health risks associated with food consumption [7,62]. This is all the more complicated since certain cereal species show a greater propensity to accumulate heavy metals, while understanding these mechanisms and their variation is essential for safeguarding both crop productivity and human health. Implementing responsible soil management practices and exploring innovative approaches to reduce heavy metal uptake in cereals are essential steps toward ensuring food safety and promoting sustainable agriculture in a metal-contaminated world [63–65].

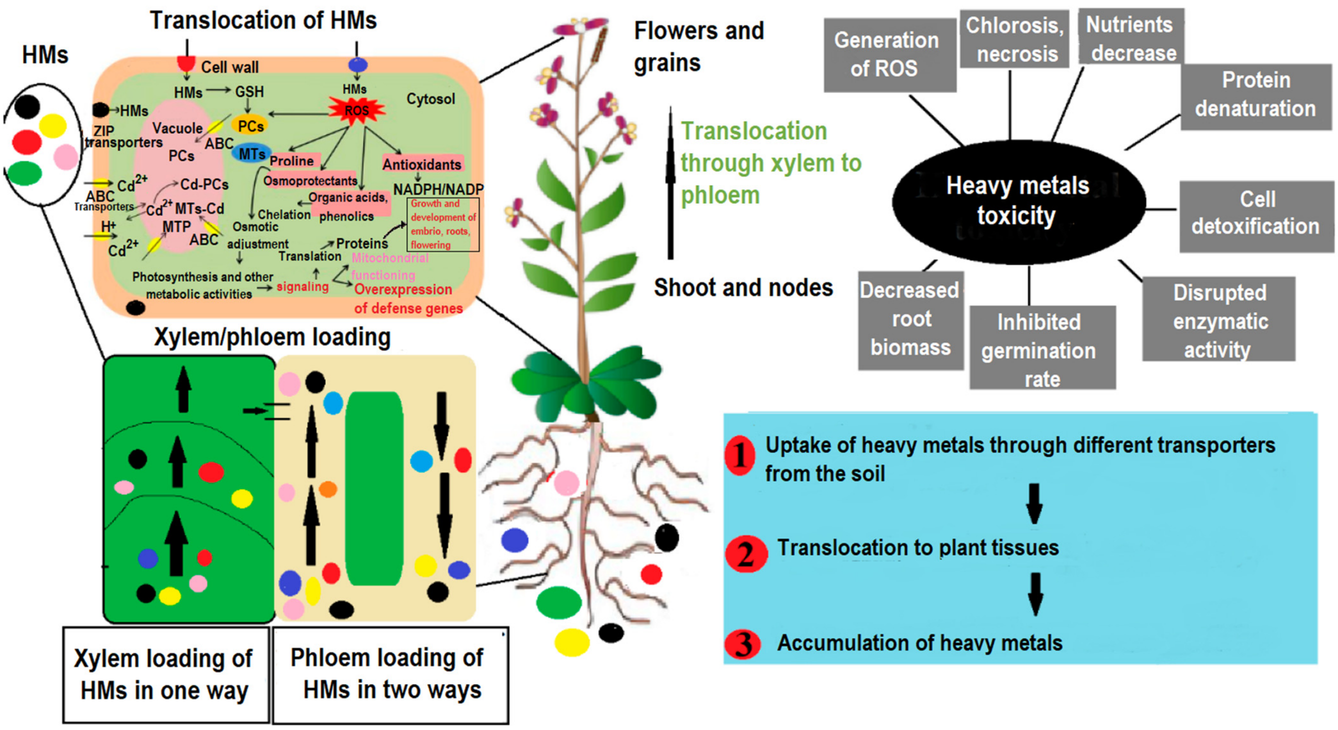

Figure 2. Schematic view of heavy metal (HM) uptake, its translocation towards aerial parts via xylem loading, and its toxicity. The uptake and transport of HMs from the roots to the leaves of plants through apoplastic and symplastic pathways. First, HMs enter the plant with the help of various transporters in the roots and are then translocated to different parts. Excessive accumulation of heavy metals (HMs) in plant tissues contributes to toxicity with associated effects such as chlorosis, protein denaturation, and decreased plant biomass (Khan et al., 2023 [50]; reproduced under the Creative Common licence CC BY), according to which any part of the article may be reused without permission, provided that the original article is clearly cited.

2.2. Metal Tolerance and Accumulation

Research has revealed that certain cereal crops exhibit varying degrees of tolerance to heavy metal stress, making them intriguing subjects for understanding plant–metal interactions and potential candidates for phytoremediation efforts. Among these tolerant cereal crops, barley and rye stand out for their remarkable ability to thrive in metal-contaminated soils without experiencing significant yield reduction. These cereal species possess natural mechanisms that enable them to withstand heavy metal stress by minimizing the toxic effects of metals within their tissues [66–68].

One notable metal-tolerant cereal crop is barley, which has been extensively studied for its ability to accumulate and sequester heavy metals, particularly cadmium and zinc, in its above-ground tissues [69,70]. Barley utilizes various strategies to cope with metal stress, including enhanced metal chelation by metal-binding compounds like phytochelatins and metallothioneins [71,72]. These compounds play an essential role in sequestering and detoxifying heavy metals, thereby protecting the plant from metal-induced oxidative damage. The metal tolerance and capacity to accumulate metals of barley make it a promising candidate for phytoremediation efforts in cadmium and zinc-contaminated soils. Similarly, rye has also exhibited exceptional metal tolerance properties, particularly in response to nickel and copper stress. Rye plants have been shown to accumulate elevated levels of these metals in their shoots without significant adverse effects on growth and yield [73,74]. This metal accumulation ability stems from the activation of various metal transporters and detoxification mechanisms that help rye plants cope with metal toxicity.

By leveraging the natural metal-accumulating abilities of barley, rye, and other tolerant cereals, it is possible to harness their potential to reduce metal levels in contaminated soils and restore ecological balance [40,75]. In addition to their applications in phytoremediation, these metal-tolerant cereal crops may also play a central role in sustainable agriculture practices. Cultivating these crops in metal-contaminated regions can not only help remediate the soil but also enable food production without compromising crop yield or quality. Utilizing metal-tolerant cereals for animal fodder or bioenergy production further expands their utility in a circular economy approach [64,76,77]. However, ensuring that the accumulated metals do not enter the food chain or pose health hazards is of utmost importance.

2.3. Impact of Heavy Metals on Plant Physiology

Heavy metal contamination can exert detrimental effects on various physiological processes within cereal crops, significantly impacting their growth and development [46,78]. Metals such as cadmium and lead are notorious for their harmful impact on plant physiology [56,79]. These toxic metals can inhibit critically enzymatic activities involved in essential plant processes, including photosynthesis and respiration. For example, cadmium interferes with the activity of Rubisco, a key enzyme responsible for carbon fixation during photosynthesis [80,81]. This disruption leads to decreased photosynthetic efficiency and a subsequent reduction in plant growth and biomass accumulation. Similarly, lead can disrupt electron transport chains in the mitochondria, impairing cellular respiration and energy production, and further compromising overall plant health [82,83].

Creating a definitive hierarchy of the toxicity of heavy metals on cereals' growth can be challenging due to variations in metal uptake, tolerance, and the specific response of different cereal species [84,85]. The information shown in Table 2, based on existing research and the literature provides a general indication of the relative toxicity of some heavy metals on cereals' growth, starting with the most toxic.

Table 2. Description of heavy metals toxicity in cereals.

Heavy Metal	Toxicity in Cereals
Cadmium (Cd)	- cadmium is known for its high toxicity to cereals, particularly rice and wheat - it can be readily taken up by cereal crops and translocated to the edible parts, posing significant health risks to consumers - the extent of cadmium toxicity depends on factors like soil pH, organic matter content, and the presence of other elements in the soil
Arsenic (As)	- arsenic is highly toxic and can accumulate in cereal grains, especially in rice - inorganic arsenic (particularly arsenite and arsenate) is the more toxic form of arsenic and is the main concern when it comes to cereal contamination, since these forms are readily absorbed by cereal plants - it is a major concern in rice-producing regions due to its potential transfer to the food chain - chronic exposure to inorganic arsenic is associated with skin lesions, cardiovascular diseases, diabetes, neurological effects, and an increased risk of various cancers, including skin, lung, and bladder cancers
Mercury (Hg)	- cereals such as rice, wheat, and barley are not considered efficient accumulators of mercury, while in a competition among heavy metals, these crops tend to absorb other elements like arsenic and cadmium more readily than mercury - although cereals generally have lower mercury uptake compared to other metals, methylmercury, a more toxic form of mercury, can form in waterlogged paddy soils and accumulate in rice
Lead (Pb)	- cereal crops, including rice, wheat, and maize, can absorb lead from the soil through their root systems, its uptake being influenced by factors like soil pH, organic matter content, and lead speciation (chemical form of lead in the soil) - lead uptake by cereals is generally lower than cadmium and arsenic - however, elevated lead levels in the soil can still lead to some accumulation in cereal crops, particularly in the roots - lead is a neurotoxic substance, and exposure to elevated levels of lead, especially in children, can lead to developmental and neurological problems. - chronic lead exposure in adults can result in cardiovascular issues, kidney damage, and other health complications

Table 2. *Cont.*

Heavy Metal	Toxicity in Cereals
Nickel (Ni)	- nickel toxicity varies among cereal species - it can interfere with essential metabolic processes, affecting plant growth - cereal crops exposed to excessive nickel may exhibit various toxic symptoms, including stunted growth, reduced biomass production, and nutrient uptake imbalances - high nickel levels can interfere with essential physiological processes in plants, affecting enzymatic activities and disrupting cellular functions - unlike some other heavy metals like cadmium and lead, nickel is generally not a major human health concern when consuming cereals, since nickel is not known to accumulate in cereals to levels that would pose direct health risks to consumers through cereal consumption
Copper (Cu)	- copper can have varying effects on cereal crops - excessive copper in the soil can lead to copper toxicity symptoms in cereal crops, which may include leaf chlorosis (yellowing), stunted growth, and reduced crop yield - high copper levels can interfere with plant metabolism, disrupt enzymatic activities, and lead to oxidative stress within plant cells - while copper toxicity in cereals can negatively affect crop growth and yield, it is generally not a significant source of human exposure or health risk through cereal consumption
Zinc (Zn)	- zinc is an essential micronutrient for plants - excessive zinc in the soil can lead to zinc toxicity symptoms in cereal crops, which may include leaf chlorosis (yellowing), reduced root growth, and impaired nutrient uptake - high zinc levels can interfere with other nutrient uptake, particularly iron and manganese, potentially leading to nutrient imbalances in plants
Chromium (Cr)	- chromium toxicity can impact cereal crops, since Cr(VI) can interfere with plant nutrient uptake and metabolic processes, affecting overall plant health, while symptoms may include reduced growth, leaf damage, and decreased crop yield - the main concern regarding chromium toxicity in cereals is associated with Cr(VI), a highly toxic and soluble form of chromium that can occur in certain soils, particularly in areas with industrial activities or polluted environments - cereal crops, such as rice, wheat, and barley, can take up Cr(VI) from the soil, and the extent of uptake depends on factors like soil pH, moisture levels, and the availability of Cr(VI) - Cr(VI) is a known carcinogen and can cause serious human health problems when consumed in contaminated cereals since chronic exposure to Cr(VI) is associated with lung cancer, respiratory issues, skin irritations, and other health effects

Sources: [46,56,78–87].

In addition to impairing enzymatic activities, heavy metals in the soil can interfere with nutrient uptake, posing another challenge to cereal crop physiology. Essential nutrients such as iron, zinc, and manganese are essential for various plant functions, and their uptake can be hindered in the presence of toxic heavy metals [86,87]. For instance, cadmium can compete with iron and zinc for uptake by plant roots, leading to nutrient imbalances and deficiencies. This interference disrupts vital cellular processes and can result in symptoms such as chlorosis (yellowing of leaves) due to reduced chlorophyll production [88].

Cereal crops often exhibit different responses to heavy metal stress, depending on the specific metal, its concentration, and the crop species, manifested by direct effects (as physiological responses) and indirect effects (as molecular and biochemical responses) (Figure 3) [89]. For example, rice plants have been found to be particularly susceptible to cadmium accumulation in the grain, which can lead to significant human health concerns when consumed [90]. In contrast, barley and certain wheat cultivars have shown better tolerance to heavy metals, enabling them to survive and produce acceptable yields in metal-contaminated soils [91,92].

Alleviating the impact of heavy metal stress on cereal crop physiology requires a multifaceted approach. Employing agronomic practices such as soil amendments, pH adjustments, and organic matter incorporation can improve soil conditions and reduce metal bioavailability to plants [55,93,94]. By identifying and selecting cereal genotypes with inherent tolerance to specific heavy metals, researchers can develop crop lines that can withstand metal-contaminated environments without compromising productivity or quality [95–97].

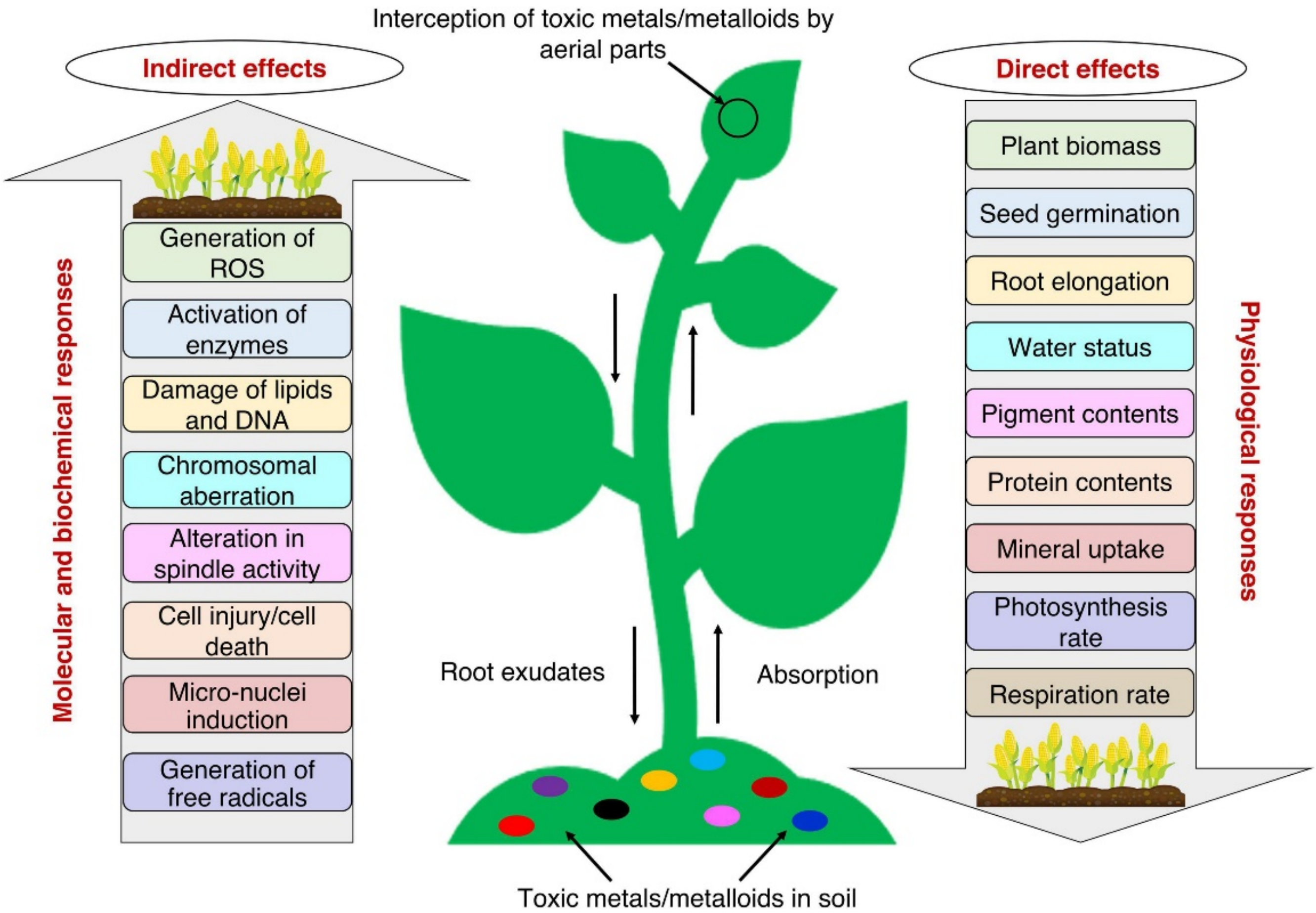

Figure 3. Plant responses to toxic metals/metalloids toxicity with possible direct and indirect effects on crop productivity. Plants interact with toxic metals/metalloids via above-ground and/or below-ground parts. The toxic effects of several toxic metals/metalloids decrease the physiological responses and increase the molecular and biochemical responses (Raza et al., 2022 [89]; reproduced under the Creative Common licence CC BY, according to which use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice).

2.4. Effects of Heavy Metals on Cereal Crop Yield and Quality

The negative impact of heavy metal exposure on cereal crop yield and quality is a significant concern for worldwide food plenty. Elevated concentrations of heavy metals in the soil can have detrimental effects on various aspects of crop production, leading to compromised yields and altered nutritional composition in harvested grains [98–100].

Heavy metals in soil can affect various growth indicators in cereal plants, with the degree of impact varying depending on factors such as the metal type, concentration, exposure duration, and the cereal species involved [101–104]. Some of the key growth indicators affected by heavy metals in soil are provided in Table 3.

Table 3. Variation in growth indicators of cereal plants exposed to heavy metal-contaminated soil.

Growth Indicators in Cereal Plants	Impact of Heavy Metals
Plant height	Stunted growth, reduced height compared to healthy plants
Root length and density	Inhibited root elongation and reduced density, affecting water and nutrient absorption
Shoot and root biomass	Decreased biomass, resulting in reduced plant size and production
Leaf area	Reduced area, limiting photosynthesis and carbohydrate production
Chlorophyll content	Decline in content, leading to chlorosis and reduced photosynthesis efficiency
Photosynthesis rate	Decreased rate due to impaired chloroplasts and enzymes
Water use efficiency	Disrupted water uptake and efficiency, causing wilting
Nutrient uptake	Interference with essential nutrient uptake, causing imbalances
Flowering and fruiting	Negative impact on flowering and fruit development, reducing crop yield
Seed germination and seedling emergence	Delayed germination and emergence, affecting early growth
Reproductive development	Disruption in reproductive development, reducing seed production and quality
Yield and grain quality	Lower crop yield and compromised grain quality, affecting economic value

Sources: [101–104].

Primary consequences of soil heavy metal contamination include reduced cereal crop yield. Metals like cadmium, lead, and mercury can disrupt crucial physiological processes in plants, leading to stunted growth, decreased photosynthesis efficiency, and impaired nutrient uptake, resulting in reduced crop productivity [105–107].

Heavy metals can also affect reproductive processes, leading to smaller seed size and reduced grain yield. For example, cadmium exposure has been linked to decreased pollen viability and lower seed production [108,109]. Moreover, heavy metal contamination can alter cereal nutritional composition, potentially leading to micronutrient deficiencies in populations reliant on cereal-based diets [110,111]. The resultant decrease in essential nutrients like iron, zinc, and manganese can impact human and animal health [112]. Food products derived from these cereals, such as bread, pasta, and breakfast cereals, may consequently have compromised nutritional value [113,114].

Addressing the impact of heavy metals on cereal crop productivity and quality demands a holistic approach that includes the remediation of heavy metals in soil, responsible soil management practices, and the cultivation of crop varieties resistant to metal exposure [69,99,115]. Ongoing soil testing and monitoring play a critical role in early intervention, and alleviating the adverse effects of heavy metal exposure on cereal yield, quality, and food safety can help reduce health risks associated with contaminated cereals [26,116].

2.5. Bioavailability and Bioaccumulation of Heavy Metals

The bioavailability of heavy metals in soil is a critical aspect of environmental science and agricultural research. It refers to the portion of heavy metals in soil that can be taken up and absorbed by plants and microorganisms, and, ultimately, enter the food chain. Cereal crops can accumulate heavy metals in grains, serving as pathways for human exposure [117,118]. The process of heavy metal bioavailability in cereals initiates at the root-soil interface. Cereals absorb water and nutrients from the soil through their root systems, and heavy metals are no exception.

The uptake of heavy metals occurs primarily through two mechanisms: (i) passive uptake, when some heavy metals, particularly those in their soluble ionic forms, can enter plant roots passively through the process of diffusion, whose intensity depends on the concentration gradient of the metal ions in the soil solution and within the root cells; and (ii) active uptake, when cereals employ specialized transport proteins, such as metal transporters, to actively pump heavy metal ions from the soil into their root cells, facilitating the uptake of specific heavy metal ions.

Bioavailability varies depending on factors like metal chemical form, nutrient interactions, and individual differences [119–121]. For example, rice efficiently takes up cadmium, a major concern in regions where rice is a dietary staple. Cadmium in its ionic form (Cd^{2+}) is highly bioavailable, while complexed or precipitated forms may be less accessible to plant roots [45,122]. Lead can be present in the outer layers of grains from lead-contaminated soils. It can be taken up by cereal crops through their root systems, primarily through active uptake processes. Lead ions can be transported into root cells by specialized transport proteins that may also transport essential minerals like calcium (Ca) and magnesium (Mg). The uptake of lead depends on the concentration of lead ions in the soil solution and the activity of these transport proteins. Once absorbed by cereal roots, lead can be translocated to above-ground plant parts, including stems, leaves, and grains. This translocation depends on the plant species, with some cereals having a greater propensity to accumulate lead in their grains. For Cr(III), which is less toxic and less mobile, it is believed that transport proteins in the root cell membranes are involved in the uptake process. These transporters likely facilitate the entry of Cr(III) ions into root cells. Cr(VI) is more soluble and poses greater toxicity. The exact mechanism of Cr(VI) uptake is not fully understood but is thought to involve the uptake of chromate ions (${CrO_4}^{2-}$) via specific anion transporters in the root cell membranes. Inside the plant, Cr(VI) can undergo chemical reduction to Cr(III). Once absorbed by the roots, both Cr(III) and Cr(VI) can be transported within the plant. This translocation occurs primarily through the plant's vascular system, involving the xylem and phloem. The movement of chromium ions to different plant tissues, including stems, leaves, and grains, is influenced by plant physiology and the chemical form of chromium [82,123,124].

Heavy metals, even at low concentrations, can have cumulative toxic effects on the human body since they can bioaccumulate in living organisms [125]. Bioaccumulation refers to the process by which organisms, such as plants and animals, accumulate and store substances, including heavy metals, at concentrations higher than those found in their surrounding environment. The chemical form or speciation of heavy metals in soil plays a critical role in their bioaccumulation. Some forms are more readily taken up by plants than others. For example, heavy metals in soluble or exchangeable forms are generally more bioavailable to cereals than those in insoluble or complexed forms. Different cereal species and cultivars exhibit variations in their ability to accumulate heavy metals. Rice is known to accumulate cadmium, particularly in its grains. This is a significant concern because cadmium can pose health risks when consumed in high concentrations. Certain rice varieties have been identified as low-cadmium rice varieties, which accumulate lower levels of cadmium in their grains. Some wheat varieties have shown the ability to accumulate cadmium and lead, especially in the grain. However, the extent of accumulation can vary among different wheat cultivars. Barley has been found to accumulate cadmium and lead to varying degrees, with certain cultivars showing a propensity for higher accumulation. Maize can accumulate cadmium and zinc in its tissues. While maize is not typically considered a hyperaccumulator, the extent of accumulation may differ among varieties and environmental conditions. Oats can accumulate cadmium in their grains, similar to rice. The accumulation potential can vary among oat cultivars. Certain millet species have demonstrated the ability to accumulate cadmium, but the extent of accumulation may differ between species and varieties. As a consequence of bioaccumulation, heavy metals can disrupt cellular functions, interfere with enzymatic activities, and induce oxidative stress, leading to various health issues over time [126–130].

Addressing bioavailability underscores comprehensive measures for heavy metal contamination in agriculture and food production, safeguarding health through awareness and regulation [131,132].

2.6. Metal Interaction and Competition

The interactions between different heavy metals and their competition for uptake within cereal crops have emerged as critical factors influencing the fate of metal contamination in agricultural ecosystems. Elucidation of these interactions is essential for predicting the behaviour of heavy metals in the soil–plant system and developing effective strategies to manage metal contamination [133,134].

Some heavy metals may exhibit synergistic effects on plant uptake and translocation. Synergism occurs when the presence of one metal enhances the uptake or accumulation of another metal in the plant. For example, zinc and cadmium have been found to exhibit a synergistic relationship in certain cereal crops. The presence of zinc in the soil can increase the uptake of cadmium by cereal plants, leading to higher cadmium concentrations in the grains [49,135]. This phenomenon can have implications for food safety, as it may result in elevated cadmium levels in cereals consumed by humans [136]. On the other hand, antagonistic effects can also occur, wherein the presence of one metal inhibits the uptake or translocation of another metal. For instance, the presence of high levels of iron or zinc in the soil has been found to reduce the uptake of cadmium and lead by cereal crops. In such cases, the iron competes with cadmium and lead for uptake sites on the root surface, limiting their entry into the plant. While this may reduce the accumulation of toxic metals in the edible parts of the crop, it can also affect the nutrient status of the plant and potentially lead to iron deficiency in the grain [137]. These interactions depend on factors like metal properties, soil characteristics, and cereal species [62,138].

Therefore, the interactions and competition among heavy metals within cereal crops are complex processes that influence metal accumulation and bioavailability in the food chain. Metal interactions and competition may require tailored approaches to mitigate the cumulative effects on cereal crops and food safety. Selecting cereal crop varieties that exhibit reduced accumulation of specific heavy metals may help lessen metal competition and reduce the potential health risks associated with metal-contaminated foods [56]. Breeding programs focused on developing metal-tolerant crop varieties can also contribute to enhancing crop resilience in metal-affected environments [135,138].

2.7. Strategies to Mitigate Heavy Metal Uptake in Cereal Crops

Efforts to mitigate heavy metal uptake in cereals are essential for ensuring safe and sustainable agricultural practices, by exploring strategies aimed at reducing heavy metal bioavailability and toxicity in cereal crops, safeguarding both crop productivity and food safety. They encompass a range of approaches, from soil management practices to genetic selection of low-accumulating crop varieties.

Soil amendments can play a vital role in mitigating heavy metal stress in cereals. Liming, for example, involves the application of lime (calcium carbonate) to acidic soils [49,139]. This practice can increase soil pH, thereby reducing the solubility and availability of certain heavy metals, such as cadmium and lead. As a result, cereal crops grown in limed soils may experience reduced metal uptake, helping to protect both crop quality and human health. Similarly, the application of organic matter, such as compost or manure, can contribute to reducing heavy metal bioavailability in the soil [140]. Organic matter binds with heavy metal ions, forming complexes that are less likely to be taken up by plant roots. Additionally, organic matter enhances soil structure and microbial activity, further influencing metal mobility and availability. Biochar, a type of charcoal produced from organic materials, can be added to soil to improve its structure and reduce heavy metal bioavailability [104,141].

Genetic approaches offer promising solutions to mitigate heavy metal stress in cereal crops. Breeding programs focused on developing metal-tolerant crop varieties can enhance a plant's ability to withstand and exclude toxic metals from entering its tissues. By identifying and selecting cereal genotypes with inherent tolerance to specific heavy metals, researchers can develop crop lines that are better suited to thrive in metal-contaminated environments [142]. For instance, through genetic screening and selection, certain wheat cultivars with reduced cadmium accumulation have been identified, showing promise for use in regions with cadmium-contaminated soils. These varieties exhibit lower cadmium uptake while maintaining high grain yields, providing a sustainable approach to minimize heavy metal entry into the food chain [52,143,144].

Agronomic practices, such as crop rotation, have been investigated to mitigate heavy metal stress in cereal crops [145,146]. Crop rotation involves alternating the cultivation of cereals with other non-cereal crops that have different metal accumulation patterns. This practice can reduce the build-up of heavy metals in the soil and provide a “break” in heavy metal exposure for cereal crops. Certain plants, known as hyperaccumulators, can be grown alongside cereal crops to absorb and accumulate heavy metals from the soil. These companion plants can then be harvested and disposed of, effectively removing heavy metals from the field. For example, leguminous crops, such as peas and beans, are known to have lower metal accumulation tendencies due to their unique root systems and symbiotic relationships with nitrogen-fixing bacteria. Introducing leguminous crops into a rotation with cereals can help mitigate heavy metal uptake by cereals, contributing to overall soil health and reducing the risk of metal transfer to the food chain [147,148].

Periodic soil testing helps farmers identify the levels of heavy metals in their fields. This information enables them to make informed decisions about appropriate soil management practices and crop selection. Continuous monitoring of heavy metal concentrations in the environment, including soil and water, is essential to assess the effectiveness of mitigation strategies and detect potential contamination sources.

Governments and regulatory agencies often set maximum allowable limits for heavy metal concentrations in food products, including cereals. Compliance with these limits is decisive in ensuring cereal crops and food quality. Regulatory bodies enforce heavy metal standards by conducting inspections and testing of food products. Non-compliant products can be removed from the market to protect public health.

3. Mechanisms of Heavy Metal-induced Growth Impairment in Plants: Favourable Conditions for Metal Toxicity

In the quest to comprehend the complex interactions between heavy metals and plants, understanding the mechanisms through which heavy metals affect plant growth is of utmost importance. These toxic elements, including cadmium, lead, mercury, and others, can exert profound effects on plant physiology, leading to growth impairment and reduced crop productivity.

3.1. Disruption of Enzymatic Activities

The detrimental effects of heavy metals on plant stems are, in part, due to their ability to interfere with the activity of essential enzymes. Heavy metals have a high affinity for enzyme-binding sites, and upon entering plant cells, they can disrupt the proper functioning of various enzymes involved in critical metabolic pathways [149,150]. One fundamental process affected by heavy metal-induced enzyme inhibition is photosynthesis, the process by which plants convert sunlight into chemical energy. This process relies on a series of enzymes facilitating the conversion of carbon dioxide and water into carbohydrates. As mentioned above, cadmium inhibits Rubisco, a key enzyme capturing carbon dioxide during photosynthesis, leading to reduced carbon fixation and overall photosynthetic efficiency [151,152]. This disruption notably impairs energy production and carbon assimilation, thereby hindering growth and biomass accumulation. Similarly, heavy metals can hinder enzymatic activities involved in cellular respiration, where stored energy (carbohydrates) transforms into usable energy (ATP) [78,153]. Lead, for instance, disrupts the electron transport chain, a critical step in cellular respiration that generates ATP. Consequently, energy production reduces, leading to lowered metabolic activity and growth constraints [82,83].

Heavy metals can also impede enzymes responsible for nutrient uptake, further compromising plant health and development. This disruption of enzymatic activities stands as a primary mechanism driving impaired growth and development in plants exposed to metal-contaminated environments. As enzymatic pathways are fundamental for essential metabolic processes, their inhibition can broadly impact plant physiology [154,155]. For instance, zinc and cadmium compete for uptake by plant roots. In zinc-deficient soils, cadmium is preferentially absorbed, leading to cadmium accumulation in plant tissues. This not only disrupts essential zinc uptake but also exposes plants to the toxic effects of excessive cadmium. Lead can replace calcium ions in calcium-dependent enzymes, inhibiting their activity. In some cases, toxic heavy metals can bind to sites on enzymes other than the active site, this being meant as non-competitive enzyme inhibition. This binding can induce conformational changes in the enzyme's structure, rendering it inactive. Non-competitive inhibition can also occur when heavy metals disrupt the enzyme's tertiary or quaternary structure, preventing proper folding or assembly. Toxic heavy metals can also affect the expression of genes encoding enzymes. They may interfere with the transcription and translation processes, leading to reduced production of specific enzymes essential for various metabolic pathways. Heavy metals can promote the degradation of enzymes by activating proteases or other protein-degrading mechanisms. This can lead to a decrease in enzyme concentration and subsequent disruption of metabolic pathways [133,155,156].

Each of these mechanisms can have different effects on specific enzymes and metabolic pathways, ultimately leading to cellular dysfunction and adverse health outcomes when toxic heavy metals are present in the body. The severity of these effects depends on factors such as the type and concentration of the heavy metal, as well as the sensitivity of the affected enzymes and biological systems. Disruption of enzymatic activities by heavy metals can generate a significant hurdle to plant growth and productivity. Through interpreting these mechanisms, progress can be made in creating resilient and sustainable agricultural systems. For instance, understanding the molecular mechanisms governing heavy metal interactions with enzymes could lead to the development of enzyme variants with enhanced metal resistance.

3.2. Reactive Oxygen Species Production

A key mechanism through which heavy metals exert toxicity in cereals is by inducing the generation of Reactive Oxygen Species (ROS), which are highly reactive molecules containing oxygen. They include superoxide radicals ($O_2^{\bullet-}$), hydrogen peroxide (H_2O_2), and hydroxyl radicals ($^{\bullet}OH$). In normal plant physiology, ROS plays critical roles in cellular signalling, growth regulation, and defence against pathogens. However, under stress conditions, including heavy metal exposure, ROS production can surpass the plant's natural antioxidant defence capacity, leading to oxidative stress [84,157,158]. Elevated levels of heavy metals can have two significant effects on plant cells. On one hand, they may lead to an increased production of ROS, while on the other hand, they might be involved in the enzymatic detoxification of ROS. Stresses such as drought, heat, and high light intensity can also result in the accumulation of ROS and damage to various cell components. These observations underline the key role of maintaining heavy metal homeostasis in plant cells.

Plants possess various forms of superoxide dismutases (SODs). SOD is an enzyme that catalyzes the dismutation reaction of the superoxide anion into oxygen and hydrogen peroxide. SODs play a critical role in protecting plants from the toxic effects of heavy metals. SODs are a group of enzymes that are part of the plant's antioxidant defence system. Their primary function is to detoxify superoxide radicals ($O_2^{\bullet-}$), which are highly reactive and toxic oxygen radicals produced during various metabolic processes, including those induced by heavy metal stress. Superoxide is produced in plants as a byproduct of oxygen metabolism, and if it is not neutralized, it can cause cellular damage. By converting superoxide radicals into hydrogen peroxide and oxygen, SODs help prevent the accumulation of superoxide radicals, which can initiate a chain reaction of oxidative damage. Cu/Zn-SODs, which exist in multiple forms, have been identified in various subcellular compartments. Meanwhile, manganese superoxide dismutase (MnSOD) isoforms have been localized within the mitochondria, and Fe-SOD is known to function as a plastidial enzyme. Notably, under drought stress conditions, there has been an observed increase in the activity of Mn-SOD. While hydrogen peroxide can also be harmful at high concentrations, it is less reactive and more easily detoxified by other antioxidant enzymes like catalase (CAT) and peroxidase (POD).

Heavy metals such as cadmium, lead, and copper can induce the accumulation of ROS in plant cells. When these metals infiltrate plant tissues, they interact with cellular components, disrupting redox homeostasis and initiating ROS formation. Cadmium exposure, for instance, generates superoxide radicals and hydrogen peroxide, triggering a chain reaction of ROS production. Excessive ROS accumulation can damage cellular structures, including lipids, proteins, and DNA [159,160]. Lipid peroxidation, the process through which ROS degrade cellular membranes, compromises membrane integrity and function. Protein oxidation can hinder enzyme activities and disrupt critical cellular processes. ROS-induced DNA damage can lead to mutations and genomic instability, affecting cell division and plant growth [160,161]. SODs contribute to the protection of essential cellular components, such as proteins, lipids, and DNA, from oxidative damage caused by heavy metal-induced ROS. By reducing the levels of superoxide radicals, SODs help maintain the integrity and function of these cellular structures.

The outcomes of ROS-induced damage are particularly evident in sensitive plant tissues, like leaves and roots, as they represent primary sites of heavy metal accumulation. Chloroplasts, the cellular organelles responsible for photosynthesis, are vulnerable to ROS due to their high metabolic activity and light exposure. Heavy metal-induced ROS production in chloroplasts leads to photo-oxidative stress, causing reduced photosynthetic efficiency and chlorophyll degradation, visible as leaf chlorosis or yellowing. Plants have evolved antioxidant defence mechanisms to counteract oxidative damage. Antioxidants like ascorbic acid (vitamin C), glutathione, and enzymes such as SODs and catalase play a vital role in neutralizing ROS and safeguarding plant cells against oxidative stress (Figure 4) [162,163].

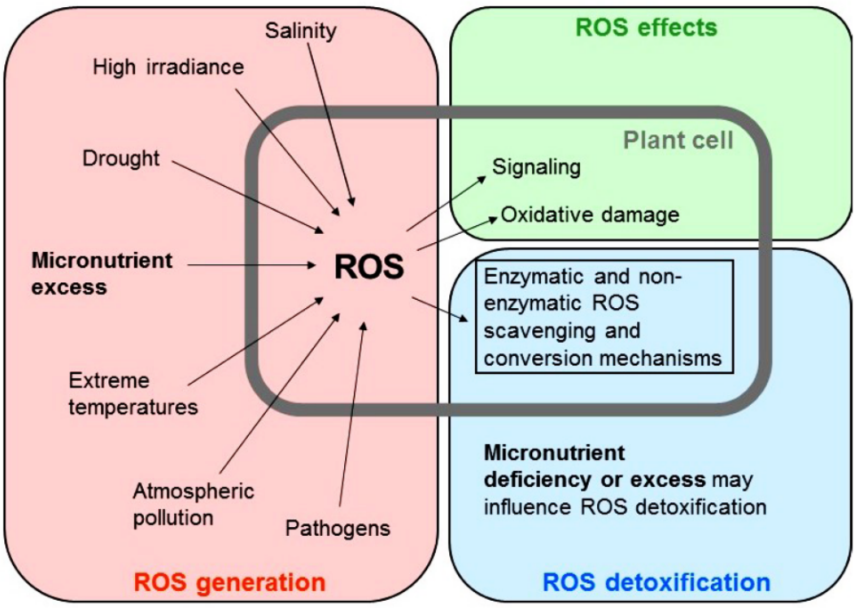

Figure 4. Involvement of micronutrients (e.g., Fe, Mn, Zn, Cu, and Ni) in the generation and detoxification of ROS in plant cells under abiotic and biotic stress. Micronutrient deficiency and excess influence ROS levels and as a consequence damages caused by them (Page and Feller, 2015 [163]; reproduced under the Creative Common licence CC BY, according to which any part of the article may be reused without permission provided that the original article is clearly cited).

When ROS generation exceeds the plant's antioxidant defence capacity, oxidative stress prevails, inflicting cellular damage and impeding growth. Young and actively growing plant tissues, like developing leaves and root tips, are particularly sensitive to oxidative stress, leading to stunted growth and reduced root elongation in metal-contaminated environments [164]. The production of ROS serves as a critical link between heavy metal stress and cellular damage in plants. ROS-induced oxidative stress disrupts cellular components and functions, leading to growth inhibition and reduced crop productivity. Mitigating the adverse effects of ROS production induced by heavy metals is a major focus of research since it can aid in developing strategies to enhance plant tolerance to heavy metal stress [165,166]. For instance, the application of exogenous antioxidants has been explored as a means to alleviate oxidative stress in plants exposed to heavy metals. Foliar sprays of antioxidants like ascorbic acid or application of natural plant extracts rich in antioxidants have shown promise in reducing ROS-induced damage and improving plant growth under metal stress. Furthermore, selecting and breeding crop varieties with enhanced antioxidant defence systems can lead to improved metal tolerance and reduced oxidative damage in metal-contaminated soils [167,168].

3.3. Nutrient Imbalances

The competition between heavy metals and essential nutrients for uptake by plant roots is a significant concern in metal-contaminated environments. Heavy metals, such as cadmium, lead, and copper, can share similar uptake pathways with essential nutrients, leading to competition for limited uptake sites. This competition disrupts the proper assimilation of essential nutrients by plants, resulting in nutrient imbalances that can have far-reaching consequences for plant health and development [82,169].

One prominent example of nutrient competition is between cadmium and zinc. As mentioned above, cadmium, being a chemical analogy of zinc, can be taken up by plant roots using the same transporters as zinc. However, cadmium is not a nutrient essential for plant growth and development. When cadmium is present in the soil, it can outcompete zinc for uptake, leading to reduced zinc uptake by the plant. Zinc is a vital micronutrient required for various physiological processes, including enzyme activation, protein synthesis, and hormone regulation. Zinc deficiency in plants can lead to stunted growth, decreased chlorophyll content, and reduced photosynthetic efficiency, adversely affecting overall plant health and crop productivity. Similarly, heavy metals like lead can compete with essential nutrients like calcium for uptake in plant roots. Lead shares chemical similarities with calcium and can be mistakenly taken up by calcium transporters. As a result, lead can inhibit the uptake of calcium by the plant, leading to calcium deficiency. Calcium is a critical nutrient involved in cell wall formation, cellular signalling, and enzyme activation. Calcium deficiency can result in weak cell walls, reduced cell division, and impaired plant growth. Nutrient imbalances caused by heavy metal competition can also impact the uptake and assimilation of other essential elements, such as iron, manganese, and magnesium [170]. Iron is essential for chlorophyll synthesis and is involved in several enzymatic reactions, while manganese plays a vital role in photosynthesis and antioxidant defence. Cadmium and zinc can interfere with the uptake of iron and manganese, leading to deficiencies of these micronutrients. Heavy metals may also disrupt the balance of anions in plant cells, affecting the uptake and transport of essential nutrients like phosphate (PO_4^{3-}) and nitrate (NO_3^-). Heavy metals can interfere with the uptake of these micronutrients, leading to deficiencies and reduced enzymatic activity [171].

In some cases, heavy metals may directly bind to root cell membranes, impairing nutrient uptake channels and reducing the overall nutrient absorption capacity of the plant. In certain instances, the presence of toxic heavy metals can induce nutrient toxicity. For example, cadmium can enhance the uptake and accumulation of other toxic elements like aluminum and arsenic by plants, exacerbating their toxic effects. Additionally, the accumulation of heavy metals in plant tissues can interfere with the plant's ability to exclude or detoxify other toxic elements, further compromising nutrient balance. Heavy metal stress can disrupt various metabolic processes in plants, including those involved in nutrient utilization. Enzymatic activities responsible for nutrient metabolism may be inhibited or altered, reducing the plant's ability to utilize absorbed nutrients effectively [169,170].

The consequences of nutrient imbalances in cereals are diverse and can negatively affect various physiological processes. Reduced nutrient uptake can weaken the plant's defence mechanisms against environmental stress, making it more susceptible to diseases and pests. Imbalances can also impair root development, leading to reduced nutrient and water uptake from the soil. Moreover, nutrient imbalances can impact grain quality and nutritional composition, compromising the nutritional value of harvested cereals. For example, zinc deficiency in cereals can lead to reduced zinc content in the grain, affecting the nutritional status of consumers who rely on cereals as a dietary staple [172,173].

Addressing nutrient imbalances in cereals under heavy metal stress demands a comprehensive approach. Selecting and breeding crop varieties with enhanced metal tolerance and nutrient uptake efficiency can help maintain balanced nutrient levels in plants facing metal-contaminated environments.

3.4. Disruption of Membrane Integrity

Heavy metals can also disrupt the integrity of cellular membranes in plants, leading to significant physiological consequences, through a combination of the actions of ROS and nutrient imbalances, at the very least. The cell membrane, also known as the plasma membrane, is essentially involved in regulating the movement of substances in and out of plant cells, maintaining cellular homeostasis, and protecting the internal cellular environment. Heavy metal exposure can compromise the structural integrity and functionality of the cell membrane, leading to various adverse effects on plant health and growth [36,107,174]. One of the primary mechanisms by which heavy metals disrupt membrane integrity is through lipid peroxidation. When heavy metals accumulate in plant tissues, they can stimulate the production of ROS, as discussed earlier. ROS can attack and degrade the lipids present in the cell membrane, leading to lipid peroxidation. As a result, the cell membrane becomes more permeable and loses its selective barrier function, allowing ions, metabolites, and other cellular contents to leak out of the cell. For example, lead-induced ROS production in plant cells can trigger lipid peroxidation, leading to the breakdown of membrane lipids. Ultimately, this damage can result in cellular death and contribute to overall tissue and plant wilting. [175,176].

Membrane integrity disruption can also affect the uptake of vital nutrients by plant roots. As the cell membrane loses its selective permeability, heavy metals can more easily access root cells, outcompeting essential nutrient ions for uptake [82,177]. Lead entry into root cells, for instance, can interfere with essential nutrient uptake, like potassium, magnesium, and calcium, leading to nutrient deficiencies [178]. Furthermore, heavy metals can impede the activity of membrane-bound transporters responsible for essential nutrient uptake. Cadmium, for instance, can inhibit potassium transporter activity, reducing potassium uptake by plant roots. Potassium is vital for maintaining turgor pressure, regulating stomatal opening, and facilitating enzymatic reactions in plant cells. Inhibiting potassium uptake disrupts these critical processes, negatively impacting plant growth and development [179,180]. Membrane integrity disruption also affects organelle function within the cell, such as chloroplasts and mitochondria. Damage to the chloroplast membrane by heavy metals can disrupt photosynthesis, reducing energy production and impairing growth [55,181]. Heavy metals can increase the permeability of cell membranes by disrupting the arrangement of membrane proteins and lipids. This increased permeability can lead to the leakage of ions and other cellular components, such as potassium (K^+) and calcium (Ca^{2+}), which are vital for maintaining cellular functions. Membrane damage caused by heavy metals can affect the plant's ability to regulate water uptake and transpiration through the roots and stomata. This disruption can result in reduced water transport, wilting, and overall water stress in the plant. Heavy metals can indirectly affect membrane-bound proteins by altering their conformations or functions. This disruption can impact the activity of transport proteins and receptors that are vital for nutrient uptake, signalling, and other cellular processes [180,181].

Hence, the disruption of membrane integrity in plants exposed to heavy metals is a critical factor contributing to growth inhibition and reduced crop productivity. The application of exogenous antioxidants or plant growth regulators can offer protection against membrane damage and improve plant tolerance to heavy metal stress.

4. Symptoms and Manifestations of Heavy Metal Toxicity on Cereal Plants

The manifestations of heavy metal toxicity on cereals are multifaceted, ranging from visible symptoms, such as chlorosis and stunted growth, to intricate physiological changes at the cellular level (Figure 5) [138,182]. These manifestations are influenced by various factors, including the specific heavy metal present, its concentration in the soil, the duration of exposure, and the inherent tolerance and susceptibility of cereal crop varieties. Some of these symptoms have been discussed in previous sections concerning the interaction between heavy metals and cereals, as well as the mechanisms behind heavy metal-induced growth impairment in plants. We will now elaborate on these symptoms in this section.

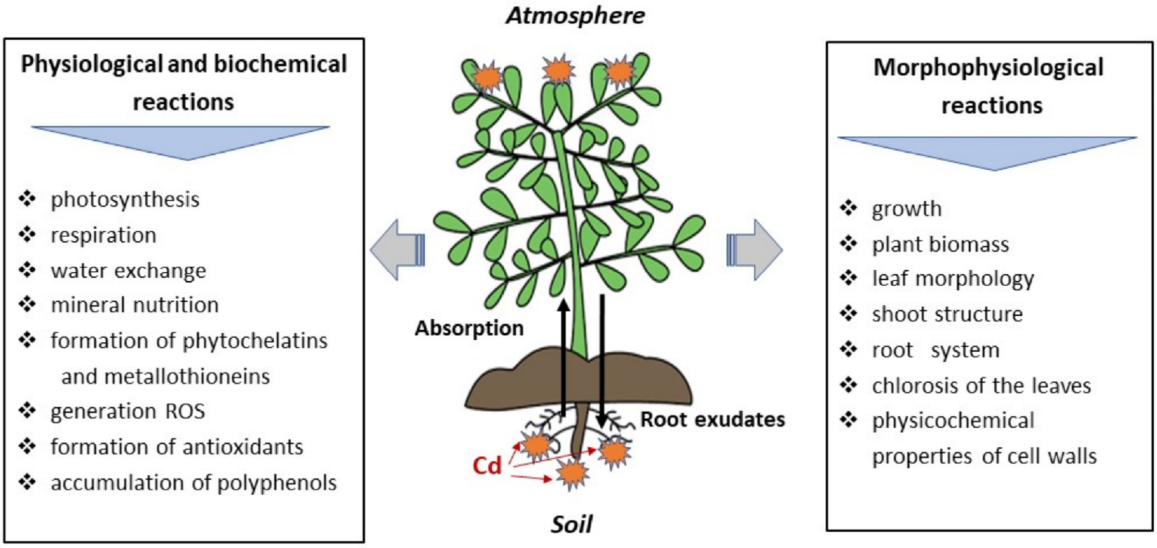

Figure 5. The penetration of cadmium into plants leads to changes in its morphology and metabolism (Goncharuk and Zagoskina, 2023 [182]; reproduced under the Creative Common licence CC BY), according to which any part of the article may be reused without permission provided that the original article is clearly cited).

4.1. Chlorosis

One of the prominent effects of heavy metal toxicity on cereals is chlorosis, a condition marked by the yellowing of leaves due to the disruption of chlorophyll synthesis. Chlorophyll, the green pigment located in chloroplasts, plays a decisive role in photosynthesis, allowing plants to capture light energy and convert it into chemical energy. [82,183]. As mentioned above, heavy metals like cadmium and lead can interfere with chlorophyll production, leading to reduced photosynthetic capacity and a characteristic yellowing of leaves. Cadmium can disrupt the biosynthesis of chlorophyll in several ways. It interferes with the activity of enzymes involved in chlorophyll synthesis, impairing the conversion of precursor molecules into functional chlorophyll molecules. As a result, chloroplasts within affected leaf cells become deficient in chlorophyll, leading to a noticeable loss of green colour [123,184]. Similarly, lead, another significant heavy metal pollutant, can inhibit various enzymes and metabolic pathways involved in chlorophyll biosynthesis. By disrupting the delicate balance of chlorophyll synthesis, lead-induced chlorosis manifests as a progressive yellowing of leaves in cereal crops. Some heavy metals can directly inhibit enzymes involved in chlorophyll biosynthesis. For example, cadmium can inhibit enzymes like δ-aminolevulinic acid dehydratase (ALAD) and protoporphyrinogen oxidase (PPO), both of which are essential for chlorophyll production. Inhibition of these enzymes disrupts the chlorophyll synthesis pathway, leading to chlorosis [185].

Chlorosis typically begins in the older leaves of cereal plants, as heavy metals are translocated from the soil to the roots and then upward to the leaves. As the heavy metal concentration in the leaves increases, the chlorophyll content decreases, leading to a gradual yellowing of the leaf tissue. In severe cases of heavy metal toxicity, chlorosis may progress to necrosis, where the yellowing leaves eventually wither and die. The consequences of chlorosis in cereals are significant [186]. Reduced chlorophyll content translates to reduced photosynthetic capacity, resulting in decreased carbohydrate production. As photosynthesis is the primary process through which plants synthesize their food, compromised photosynthetic efficiency can lead to stunted growth and reduced biomass accumulation in cereal crops. Moreover, chlorosis negatively impacts grain filling and yield in cereals. During the grain-filling stage, the plant translocates carbohydrates from leaves to developing grains. Heavy metal-induced chlorosis diminishes the availability of carbohydrates for grain filling, leading to smaller and poorly filled grains, ultimately reducing the overall yield of cereal crops [187,188]. Chlorotic plants are generally weakened and more susceptible to environmental stressors, diseases, and pests. Their overall health and vigor decline, and they may show signs of reduced growth.

Chlorosis is a noticeable manifestation of heavy metal toxicity in cereals, signifying disruptions in chlorophyll synthesis and photosynthetic capacity. The severity of chlorosis in cereals depends on several factors, including the type of heavy metal, its concentration in the soil, the duration of exposure, and the inherent tolerance of the cereal variety [165,188].

4.2. Stunted Growth

One of the most noticeable and common manifestations of heavy metal toxicity in cereals is stunted growth. Stunted growth refers to the inhibited development of cereal plants, where they fail to achieve their expected size and exhibit a reduced number of leaves and smaller stems [84,189].

Heavy metal toxicity interferes with critical physiological processes, disrupting plant growth and development at various stages of the plant's life cycle. The presence of heavy metals in the soil can directly affect root growth and function. As cereal plants take up water and essential nutrients through their root systems, heavy metals can enter the roots and cause damage. For example, cadmium exposure can lead to reduced root elongation and impaired root branching, limiting the plant's ability to explore the soil for water and nutrients. This restricted root development hinders the plant's capacity to take up essential elements and sustain normal growth. Arsenic toxicity leads to reduced plant height and tillering in cereals. It disrupts photosynthesis and interferes with nutrient uptake, particularly for phosphorus, resulting in stunted growth. Lead exposure can result in stunted growth by interfering with cell division and elongation in roots and shoots. It can also disrupt water and nutrient uptake processes, further exacerbating growth problems. [190]. Also, heavy metals can interfere with cell division and elongation in the shoot system of cereal plants. As cells in growing tissues are particularly sensitive to heavy metal stress, the elongation of stems and leaves can be hindered, leading to smaller plant size. The disrupted cell division can also result in a reduced number of leaves, further limiting the photosynthetic capacity of the plant. Furthermore, heavy metals can inhibit various enzymatic activities involved in critical metabolic processes [101,191]. For instance, lead exposure has been shown to disrupt the activity of enzymes essential for the synthesis of plant growth hormones, such as auxins and gibberellins. These hormones play key roles in regulating plant growth and development. The inhibition of growth hormones can disrupt cell elongation and division, contributing to stunted growth in cereals [192,193].

Stunted growth in cereals due to heavy metal toxicity has significant consequences for crop productivity. Smaller plants with reduced biomass have limited photosynthetic capacity, leading to reduced carbohydrate production. As a result, cereal crops exposed to heavy metal-contaminated soils may produce smaller and less-filled grains, ultimately leading to decreased yield [82,194]. Additionally, stunted growth can impact the overall health and resilience of cereal crops. Smaller plants may be more susceptible to environmental stressors, pests, and diseases, making them less resilient to adverse conditions.

4.3. Reduced Root Growth

Roots are a critical component of plant architecture and function, serving as the primary organs for nutrient and water uptake from the soil. They are particularly sensitive to heavy metal stress, as they are the first point of contact with contaminated soil. Heavy metals, such as cadmium, lead, and copper, can accumulate in the soil surrounding the roots, within the rhizosphere, leading to direct exposure and potential damage to the root system of cereal crops. High concentrations of heavy metals in the soil can directly impact root growth and function [47,195]. One of the primary effects is the inhibition of root elongation and branching. For instance, cadmium exposure can lead to the accumulation of ROS in root tissues, which in turn disrupt cell division and elongation, impairing root growth. The reduction in root elongation limits the plant's ability to explore a larger volume of soil for water and nutrients, ultimately restricting its access to essential resources [179,196].

Furthermore, heavy metals can interfere with the proper development of root hairs. Root hairs are thin, hair-like extensions of root epidermal cells that significantly increase the surface area for nutrient absorption. However, heavy metal stress can disrupt the formation and elongation of root hairs, further compromising the cereal plant's nutrient uptake capacity [197]. As the root system is responsible for water and nutrient absorption, reduced root growth has direct consequences on nutrient uptake by cereal crops. Heavy metals can inhibit the activity of root transporters responsible for taking up essential nutrients, such as potassium, calcium, and magnesium. The interference with nutrient uptake leads to deficiencies in these vital elements, adversely affecting plant health and development [198]. Additionally, heavy metals can displace essential nutrients in the soil, reducing their availability for uptake by plant roots. As mentioned above, cadmium can compete with zinc for uptake by roots, leading to reduced zinc uptake and consequent zinc deficiency in cereal crops. Zinc is essential for various enzymatic reactions and plays an important role in many physiological processes [91,194,199,200].

The reduced root growth and compromised nutrient uptake caused by heavy metal toxicity have far-reaching consequences on cereal crop productivity and health. Cereal crops with stunted root systems may exhibit poor nutrient efficiency, leading to reduced growth and overall yield.

4.4. Leaf Deformities

Leaf deformities represent another distinctive manifestation of heavy metal toxicity in cereals. Certain heavy metals, such as cadmium, mercury, and nickel, can cause physical deformities in leaves, altering their normal appearance and structure [79,201]. These deformities may include curling, twisting, irregular shapes, and abnormal growth patterns. One of the mechanisms through which heavy metals induce leaf deformities is the disruption of hormone regulation. Heavy metals can interfere with the synthesis, transport, and perception of plant growth regulators, such as auxins and gibberellins, which play critical roles in leaf development [82]. Distorted hormone signalling can lead to abnormal cell division and elongation, resulting in the misshapen and twisted leaves observed in heavy metal-exposed cereals. For example, mercury exposure has been shown to disrupt auxin signalling, leading to leaf curling and abnormal leaf development in cereal crops. Similarly, cadmium can interfere with gibberellin biosynthesis, contributing to leaf twisting and irregular leaf shapes [202,203].

Furthermore, heavy metals can cause oxidative stress in leaf tissues, leading to cellular damage and deformities. ROS generated by heavy metal exposure can attack cellular components, including proteins and lipids, disrupting cellular structure and function. This oxidative damage can manifest as irregular leaf growth, distortion of leaf margins, and abnormal leaf shapes. Additionally, heavy metals can disrupt the balance of essential nutrients in leaf tissues, leading to nutritional imbalances that contribute to leaf deformities [47,101,176]. For instance, cadmium exposure can interfere with the uptake and translocation of essential elements like calcium and magnesium, which are vital for leaf development and structure. Deficiencies in these nutrients can lead to leaf malformations and altered leaf morphology [33,155].

The consequences of leaf deformities in cereals can be detrimental to plant health and productivity [204]. Deformed leaves may have reduced surface area for photosynthesis, impairing the plant's ability to capture light and produce carbohydrates. This reduction in photosynthetic capacity can lead to reduced biomass accumulation and yield in cereal crops [205]. Likewise, leaf deformities can impact transpiration rates and water use efficiency. Altered leaf structures may affect stomatal conductance and transpiration, potentially leading to water loss and reduced drought tolerance in heavy metal-exposed cereals [206,207].

Leaf deformities are a distinct manifestation of heavy metal toxicity in cereals, reflecting disruptions in hormone regulation, oxidative stress, and nutrient imbalance. The abatement of leaf deformities caused by heavy metal toxicity requires understanding the specific mechanisms involved and implementing appropriate interventions [205,208].

4.5. Reduced Flowering and Fruit Development in Cereals

Heavy metal toxicity can have a significant impact on the reproductive processes of cereal crops, leading to reduced flowering and negatively affecting fruit development [209,210]. The reproductive stage is vital for the successful completion of the plant's life cycle, as it determines seed production and the continuation of the species. However, heavy metals can disrupt various physiological and biochemical processes involved in flowering and fruit development, affecting the reproductive success of cereal crops. One of the ways heavy metals interfere with flowering is through the disruption of hormonal signalling. Plant hormones, such as cytokinins and gibberellins, play critical roles in regulating flowering and fruiting processes [211,212]. Heavy metal exposure can alter the synthesis, transport, and perception of these hormones, leading to delayed or suppressed flowering in cereal crops [213]. For example, high levels of cadmium in the soil have been shown to disrupt cytokinin signalling, resulting in delayed flowering in cereals such as wheat and rice [214]. Similarly, lead exposure can inhibit gibberellin biosynthesis, leading to reduced elongation of flower stalks and altered flower development. Additionally, heavy metal toxicity can impact the development of floral organs, such as sepals, petals, and stamens [215]. Deformities in these floral structures can impair pollination and fertilization processes, leading to reduced fruit sets in cereal crops. Moreover, heavy metals can affect the availability and transport of essential nutrients required for flowering and fruit development. For instance, zinc deficiency caused by cadmium competition can hinder flower and fruit development in cereals like maize and barley. Zinc is an essential micronutrient involved in various metabolic processes, including those related to flowering and fruit set [49,199,200].

The negative impact of heavy metal toxicity on fruit development is also significant. Fruits are essential structures in cereal crops that contain seeds and are essential for seed dispersal and propagation. Heavy metals can interfere with the growth and development of fruits, leading to smaller and malformed structures [216]. The reduced size and altered shape of fruits can affect seed production and dispersal, ultimately impacting crop yield and quality. Furthermore, heavy metals can interfere with the development of seed embryos within the fruits. Disturbances in seed development can lead to reduced seed viability and germination rates, affecting the overall productivity of cereal crops in subsequent generations. Decreased fruit sets can directly translate into reduced seed yield and, consequently, lower crop production [217,218].

4.6. Necrosis

Necrosis is a severe manifestation of heavy metal toxicity in cereals, referring to the death of plant tissues. High levels of heavy metals in the soil can cause necrotic lesions on leaves and other plant parts, leading to tissue death and further impairing plant function. Necrosis can occur in various plant organs, including leaves, stems, and roots, and is often a result of oxidative stress and cellular damage caused by heavy metal exposure [82,219]. One of the primary mechanisms through which heavy metals induce necrosis is the generation of ROS. Heavy metals, such as cadmium and lead, can stimulate the production of ROS in plant cells (Figure 4). Excessive ROS accumulation can lead to oxidative stress, causing damage to cellular components, including proteins, lipids, and DNA. The breakdown of cellular structures and organelles results in necrotic lesions on affected tissues.

For instance, cadmium exposure has been shown to trigger ROS accumulation in the leaves of cereal crops, leading to oxidative damage and the formation of necrotic lesions. Similarly, lead-induced ROS production can result in cell death and necrosis in various plant parts [220,221]. Also, heavy metals can disrupt essential physiological processes in plants, further contributing to necrosis. For example, cadmium exposure can inhibit photosynthetic electron transport and reduce ATP synthesis in chloroplasts, leading to cellular energy deficits and impaired maintenance of cellular integrity. This disruption of essential metabolic processes weakens plant tissues and makes them more susceptible to necrosis. In some cases, heavy metals can directly interfere with the activity of enzymes involved in cellular repair and defence mechanisms. This interference hampers the plant's ability to cope with oxidative stress and repair damaged cellular structures, leading to increased tissue necrosis [221,222].

Necrosis in cereals has significant consequences for plant health and productivity. Affected tissues lose their functionality, leading to reduced photosynthetic capacity, nutrient uptake, and water transport. The death of plant tissues can also compromise the structural integrity of the plant, making it more vulnerable to physical damage and environmental stressors. Additionally, necrosis in cereal crops can lead to reduced grain filling and impaired seed development. The loss of functional photosynthetic tissues reduces carbohydrate availability for grain filling, leading to smaller and poorly developed grains, ultimately impacting crop yield. Thus, necrosis is a severe consequence of heavy metal toxicity in cereals, signifying the death of plant tissues due to oxidative stress and cellular damage. The application of antioxidants or plant growth regulators can provide protection against oxidative stress and limit the extent of tissue necrosis.

4.7. Water Stress

Heavy metal toxicity can lead to water stress in cereal crops, affecting their ability to take up and transport water within the plant [197,223]. Water is essential for plant survival and plays a crucial role in various physiological processes, including nutrient uptake, photosynthesis, and transpiration. However, heavy metals can disrupt water uptake and transport mechanisms, leading to water stress and wilting in cereal crops. One of the primary ways heavy metals induce water stress is by affecting the structure and function of root tissues. Roots are responsible for water absorption from the soil, and heavy metals can inhibit root growth and function, reducing the plant's ability to access water. For example, cadmium exposure has been shown to restrict root elongation and disrupt root cell membranes, hindering water uptake in cereal crops [224,225]. Additionally, heavy metals can interfere with the functioning of root transporters responsible for the uptake of water and essential nutrients [197,226]. The process of short-distance water transport within roots holds a pivotal position in regulating the flow of solutes and water, both entering and exiting the vascular system, through the encompassing tissues of the conducting cells. This mechanism could potentially impact the pace of long-range water transportation toward the aboveground segments of the plant (Figure 6) [223,227].

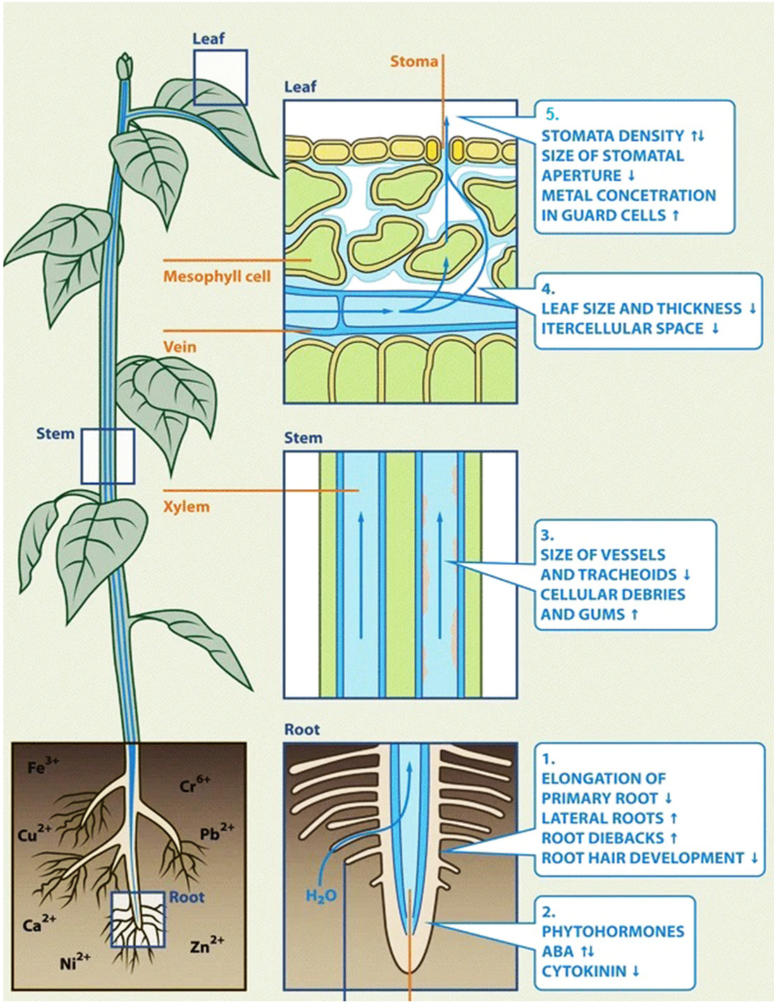

Figure 6. Long-distance water transport in plants exposed to heavy metal stress. Metal-induced disturbances in short-distance transport (via apoplastic, symplastic, and transmembrane routes) slow the movement of water into the vascular system and affect water supply to the shoot. (1) Decreased elongation of the primary root, increased root diebacks or reduced root hair exerts a deleterious effect on the root-absorbing area and water uptake. Development of lateral roots partially compensates for limited growth in the primary root. (2) Inhibited root growth affects hormone synthesis and transport, as well as stomatal movement. (3) A reduction in the size of vessels and tracheids and partial blockage of xylem elements by cellular debris or gums decrease hydraulic conductivity in the root, stem, and leaf midrib. (4) A decrease in leaf size and the lamina's thickness, intercellular spaces, density of stomata, and the sizes of the stomatal aperture reduces the rate of transpiration. Stomata closure is induced directly by heavy metals and/or is a consequence of the early effects of metal toxicity in roots and stems (Rucińska-Sobkowiak, 2016 [223]; reproduced under the terms of the Creative Commons Attribution 4.0 International Licence, http://creativecommons.org/licenses/by/4.0/, which permits unrestricted use, distribution, and reproduction in any medium, provided you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made).

The disruption of these transporters can lead to reduced water uptake and nutrient deficiencies in cereal plants. Furthermore, heavy metals can impact the transpiration process, where water is lost from the leaves as water vapour [223]. Transpiration is essential for nutrient transport and cooling of the plant, but heavy metals can affect stomatal conductance and transpiration rates. For instance, lead exposure has been shown to reduce stomatal opening, limiting water loss through transpiration and leading to water stress in cereal crops. Water stress can manifest as wilting, where the leaves of cereal plants lose their turgidity and appear droopy. Wilting is a visible symptom of water deficiency in plants and is a response to reduced water uptake and impaired water transport within the plant. The consequences of water stress in cereals are significant. Reduced water availability can impair nutrient transport and photosynthetic efficiency, leading to reduced growth and overall plant health. The lack of water can also lead to reduced cell expansion and division, further inhibiting plant growth and development [202,223].

Water stress can be particularly detrimental during critical growth stages, such as flowering and grain filling, as water deficiency can significantly impact seed development and ultimately reduce crop yield. Thus, water stress is a significant consequence of heavy metal toxicity in cereals, arising from disruptions in water uptake and transport mechanisms [177,196].

5. Factors Predisposing Cereal Crops to Heavy Metal Toxicity

In the realm of agricultural productivity and sustainability, understanding the intricate interplay between environmental factors and crop health is of utmost importance. The impact of heavy metals on cereal growth and development is influenced by an array of conditions that can predispose these vital crops to adverse effects [194,228].

Factors including soil pH, organic matter content, metal concentration, and exposure duration play pivotal roles in determining heavy metal toxicity in cereals [211,229]. Additionally, climatic conditions and water availability influence heavy metal bioavailability and uptake by cereal plants, shaping potential growth and productivity impacts.

5.1. Soil pH and Heavy Metal Bioavailability in Cereal Crops

The pH of the soil is a fundamental factor that greatly influences the bioavailability of heavy metals and subsequently impacts their toxic effects on cereal crops [229–231]. Soil pH refers to the acidity or alkalinity of the soil and is measured on a scale from 0 to 14, with 7 being neutral. Values below 7 indicate acidic soil, while values above 7 indicate alkaline soil. In acidic soils, heavy metal bioavailability tends to increase, making certain metals more soluble and accessible for plant uptake. The low pH conditions promote the dissolution of metal-containing minerals, releasing heavy metals into the soil solution. As a result, metals like cadmium, aluminium, and manganese are more readily available for uptake by cereal plants [232].

For example, in highly acidic soils with a pH below 5, the solubility of cadmium increases significantly, leading to elevated cadmium concentrations in the soil solution [233]. Cereal crops grown in such conditions are more likely to take up higher amounts of cadmium, resulting in potential toxicity [234]. Conversely, alkaline soils can reduce the bioavailability of certain heavy metals, thereby mitigating their toxic effects. In alkaline conditions, metals may form insoluble precipitates or bind to soil particles, making them less available for plant uptake [124]. For instance, in soils with a pH above 7, heavy metals like nickel, cadmium, and zinc are more likely to form less soluble compounds, reducing their potential toxicity to cereal crops [201,235].

As discussed above, the influence of soil pH on heavy metal bioavailability can have significant implications for cereal crop health and productivity [236]. Acidic soils can lead to increased uptake of toxic heavy metals by cereal crops, resulting in adverse effects on plant growth and development. This can also impact the nutritional quality of the harvested grains, as heavy metals may accumulate in edible parts of the plant. In contrast, alkaline soils may help mitigate heavy metal toxicity by limiting metal uptake and accumulation in cereal crops. However, excessive alkalinity can also lead to nutrient deficiencies and affect overall plant health, necessitating careful soil management practices. For most cereal crops, including wheat, rice, and maize, the optimal pH range for growth and nutrient uptake falls between 6 and 7. In this pH range, nutrient availability is optimized, and heavy metal bioavailability is typically moderate, reducing the risk of excessive heavy metal uptake [233,237].

5.2. Soil Organic Matter and Its Role in Mitigating Heavy Metal Toxicity in Cereal Crops

The presence of organic matter in the soil is very important in influencing the behaviour and fate of heavy metals and their subsequent effects on cereal crops. Soil organic matter comprises decomposed plant and animal residues and plays a vital role in soil fertility and structure. Its interactions with heavy metals can significantly impact metal bioavailability and reduce their toxic effects on cereal plants [232,238]. Organic matter in the soil acts as a natural chelating agent, capable of binding with heavy metal ions. Chelation is a chemical process where organic compounds form stable complexes with heavy metals, reducing their solubility and availability for plant uptake. When heavy metals are bound to organic matter, they are less likely to be leached into the soil solution or taken up by cereal crops [239]. For instance, humic and fulvic acids, which are organic compounds present in soil organic matter, have a strong affinity for heavy metal ions like lead, cadmium, and copper. These acids form stable complexes with heavy metals, reducing their mobility in the soil and minimizing their potential for toxicity to cereal crops [240].

Soils with higher organic matter content tend to exhibit lower levels of heavy metal toxicity due to the increased capacity for metal binding. Well-structured, organically rich soils act as natural filters, sequestering heavy metals and preventing their movement into the root zone of cereal plants [241]. Consequently, cereal crops grown in such soils are less likely to accumulate toxic levels of heavy metals in their tissues. Additionally, organic matter contributes to soil aggregation and enhances soil structure. Soils with good aggregation have increased pore spaces, improving water infiltration and drainage. This can be especially beneficial in reducing heavy metal toxicity as it prevents waterlogging and reduces the likelihood of heavy metal accumulation in the root zone [242,243]. Furthermore, soil organic matter fosters the growth and activity of beneficial microorganisms, such as mycorrhizal fungi and bacteria. These microorganisms play essential roles in promoting plant health and nutrient uptake [244]. Mycorrhizal fungi, in particular, can enhance the uptake of essential nutrients while simultaneously reducing the uptake of heavy metals by forming a physical barrier around the roots, as will be discussed below [245,246].

5.3. Soil Texture and Its Influence on Heavy Metal Availability in Cereal Crops

The soil texture significantly influences the fate of heavy metals in the soil and their subsequent availability to cereal crops. Soil texture refers to the relative proportions of sand, silt, and clay particles in the soil. Each soil texture type has distinct properties that influence heavy metal retention and release, directly impacting their bioavailability to plants [247,248]. Clay soils, characterized by their high proportion of fine clay particles, tend to have higher adsorption capacities for heavy metals. Heavy metal ions can bind tightly to clay particles through surface adsorption, reducing their movement and mobility in the soil. As a result, clay soils act as reservoirs, immobilizing heavy metals and limiting their bioavailability to cereal crops. For example, cadmium, a highly toxic heavy metal, has a strong affinity for clay particles. In clay soils, cadmium tends to be adsorbed to the clay surfaces, reducing its leaching potential and minimizing its uptake by cereal plants [249,250]. This natural immobilization mechanism helps protect cereal crops from excessive cadmium exposure.

In contrast, sandy soils, composed of larger sand particles, may have lower adsorption capacities for heavy metals. Heavy metals in sandy soils are less likely to bind to sand particles, making them more mobile and available for plant uptake. Sandy soils exhibit faster water movement and drainage, which can increase the leaching of heavy metals into the root zone of cereal crops. For instance, in sandy soils, metals like copper and zinc may be more mobile and have a higher likelihood of reaching the root zone of cereal plants. This enhanced mobility can increase the risk of heavy metal accumulation in cereal crops, potentially leading to adverse effects on plant growth and development [251,252]. The influence of soil texture on heavy metal availability has significant implications for cereal crop productivity and food safety. Clay soils provide a natural buffer against heavy metal toxicity, reducing the potential for metal uptake by cereal plants. On the other hand, sandy soils may require careful management practices to minimize heavy metal leaching and improve metal retention [253,254].

5.4. Plant Species and Varieties: Key Players in Heavy Metal Tolerance

In the context of heavy metal toxicity in cereal crops, plant species, and their specific varieties play a crucial role in determining the level of tolerance to these environmental stresses. The remarkable diversity among plant species and varieties translates into varying degrees of adaptability and resilience in the face of heavy metal contamination. Certain plant species have evolved unique mechanisms to cope with heavy metal stress, effectively reducing their negative impact on plant growth [9]. These mechanisms can involve the sequestration or detoxification of heavy metals, preventing their accumulation to toxic levels within plant tissues. For instance, some cereal crops, such as barley and rye, have been observed to exhibit higher levels of heavy metal tolerance. These species have developed specific biochemical pathways that facilitate metal sequestration in vacuoles or bind metals to cell walls, minimizing their translocation to vital plant organs. As a result, these cereal species can thrive even in soils with elevated heavy metal concentrations without suffering severe growth inhibition [255,256]. Moreover, distinct varieties within the same cereal species can showcase variations in their ability to withstand heavy metal stress. Through selective breeding and genetic selection, certain cereal varieties have been developed with enhanced heavy metal tolerance, making them well-suited for cultivation in contaminated environments [257]. For example, specific rice (*Oryza sativa*) varieties, known as "low cadmium rice," have been bred to accumulate lower levels of cadmium in their grains. By reducing cadmium uptake and translocation, these rice varieties safeguard the nutritional quality of the harvested grains and minimize health risks associated with cadmium consumption [258,259].

The impact of plant species and varieties on heavy metal tolerance extends beyond the biochemical level. Root characteristics, such as root exudates and root architecture, can also influence the ability of cereal crops to cope with heavy metal stress [260]. Some plant species release compounds from their roots that can chelate or immobilize heavy metals, reducing their bioavailability in the soil and protecting the plant from excessive metal uptake [261,262]. Therefore, plant species and varieties emerge as key players in influencing heavy metal tolerance in cereal crops. By harnessing the natural resilience of tolerant plant species and selecting appropriate varieties, we can foster sustainable cereal crop production and ensure the availability of safe and nutritious grains for the global population [263,264].

5.5. Metal Concentration in Soil: A Determining Factor in Heavy Metal Toxicity to Cereal Crops

The concentration of heavy metals in the soil stands as a critical determinant of their potential toxic effects on cereal crops. The level of metal contamination in the soil directly influences the extent of stress and subsequent impact on plant growth and productivity. When heavy metals are present in the soil at elevated concentrations, they are more likely to be taken up by cereal plant roots and translocated to various plant organs [265,266]. As heavy metal levels in the soil increase, so does the likelihood of exceeding the threshold at which they become harmful to plants. For example, in soils with high cadmium concentrations, cereal crops may accumulate significant amounts of cadmium in their edible parts, such as grains. Chronic consumption of these contaminated grains can lead to health risks for humans, making it crucial to manage metal concentrations in the soil. Additionally, excessive heavy metal concentrations can lead to necrosis and tissue death in affected plants, severely compromising overall plant health and productivity [267–269]. Furthermore, the interaction between different heavy metals in the soil can exacerbate their toxic effects on cereal crops. Synergistic interactions between certain heavy metals may result in a more substantial impact on plant growth and development than individual metals alone [133,134].

5.6. Influence of Environmental Factors on the Toxicity of Heavy Metals to Cereal Crops

In addition to soil-related factors, environmental conditions significantly influence how heavy metals impact the growth of cereal crops. Temperature, humidity, and water availability are critical environmental factors that can either exacerbate or ameliorate the toxicity of heavy metals in plants. Temperature is a fundamental environmental parameter that can significantly impact heavy metal toxicity. High temperatures can enhance the mobility of heavy metals in the soil, increasing their solubility and availability for plant uptake [55]. In such conditions, cereal crops may be more susceptible to absorbing elevated levels of toxic metals, leading to adverse effects on plant health. For instance, during heatwaves or periods of extreme heat, heavy metals such as lead and cadmium may become more mobile in the soil solution. These metals can then be transported to the root zone of cereal crops, increasing the risk of metal uptake and toxicity [270,271].

Humidity levels also have a significant impact on heavy metal toxicity [272]. High humidity can lead to waterlogging, reducing the oxygen availability in the soil and affecting root health. Under waterlogged conditions, heavy metal mobility may increase, causing metal ions to diffuse into the root zone more readily. This could intensify heavy metal uptake by cereal crops, leading to higher metal concentrations in plant tissues. On the other hand, low humidity conditions can exacerbate the impact of heavy metal stress on cereal crops by limiting water availability. Heavy metals can disrupt the water uptake and transport within plants, leading to water stress and wilting. In arid regions or during periods of drought, cereal crops may experience heightened susceptibility to heavy metal toxicity due to the reduced water availability exacerbating the effects of metal stress [273].

Water availability itself is a critical factor in determining heavy metal toxicity. Adequate water supply can aid in diluting and flushing heavy metals from the root zone, reducing their bioavailability and potential toxicity to cereal crops. Conversely, water scarcity can lead to increased metal concentrations in the soil solution, promoting metal uptake by cereal plants. Stressful environmental conditions can exacerbate heavy metal toxicity, highlighting the need for climate-resilient agricultural practices to safeguard crop productivity [274].

Adopting climate-resilient agricultural methods is imperative for addressing the influence of environmental factors on heavy metal toxicity. Proper irrigation and water management can help maintain optimal soil moisture levels, promoting plant health and reducing the bioavailability of heavy metals in the soil.

6. Cereal Defence Strategies against Heavy Metal Toxicity: Detoxification Mechanisms and Adaptation Strategies

When facing heavy metal toxicity, cereal crops employ a range of defence mechanisms to counteract the detrimental impact of these harmful elements. Heavy metals, such as cadmium, lead, and mercury, can pose significant threats to cereal crops, jeopardizing agricultural productivity and food safety. To thrive in metal-contaminated environments, cereal crops have developed sophisticated detoxification mechanisms and adaptation strategies [220,275].

Cereal crops employ various detoxification mechanisms to sequester or minimize the uptake of heavy metals, preventing their accumulation to toxic levels in vital plant tissues. These mechanisms include chelation, vacuolar sequestration, and metal complexation with organic compounds [187,276]. By efficiently binding heavy metal ions, cereals can reduce their bioavailability and protect themselves from potential damage. Furthermore, cereal crops showcase remarkable adaptability to metal-stressed conditions. Some varieties exhibit enhanced metal tolerance through genetic selection and selective breeding. Additionally, cereal root exudates play a pivotal role in altering the availability of heavy metals in the soil, influencing metal uptake and reducing toxicity.

Some key factors and mechanisms involved in heavy metal detoxification and adaptation strategies in cereal crops may include (Figure 7): metal transporters, chelation, metallothioneins, vacuolar sequestration, cell wall binding, rhizosphere interactions, genetic variation, regulatory proteins, and environmental factors. The key factors can act both separately and simultaneously [275,276]. These complex interactions enable plants to adjust and survive in environments with different levels of heavy metal stress. The specific response may vary depending on the particular cereal species and the conditions in the environment, as explained in the following sections.

6.1. Metal Transporters: Orchestrating Heavy Metal Transferring in Cereal Plants

In cereals and other plants, the movement of metals across cell membranes is facilitated by specific transporter proteins. We have identified some of the key transporter families involved in metal uptake and transport:

- NRAMP (Natural Resistance-associated Macrophage Protein)
    - NRAMP proteins are involved in the transport of divalent cations such as iron (Fe^{2+}), manganese (Mn^{2+}), zinc (Zn^{2+}), and cadmium (Cd^{2+});
    - They play a crucial role in metal uptake from the soil into the roots.
- ZIP (Zrt/Irt-like Proteins)
    - ZIP transporters are responsible for the uptake of essential divalent metals like zinc (Zn^{2+}), iron (Fe^{2+}), and manganese (Mn^{2+});
    - They are involved in the movement of metals from the roots to the above-ground parts of the plant.
- HMA (Heavy Metal ATPase)
    - HMA transporters are ATPases that are responsible for the transport of various heavy metals, including copper (Cu^{2+}), zinc (Zn^{2+}), and cadmium (Cd^{2+});
    - They are involved in metal compartmentalization and detoxification within plant cells.
- IRT (Iron-regulated Transporter)
    - IRT transporters are specific to iron (Fe^{2+}). They play a decisive role in iron uptake from the soil;
    - These transporters are particularly important for plants growing in iron-deficient soils.
- YSL (Yellow Stripe-like Transporters)
    - YSL transporters are involved in the uptake of metal–chelate complexes, particularly iron (Fe^{3+}) bound to phytosiderophores;
    - They play a role in iron uptake in graminaceous plants like cereals.
- Ferrous Iron Transporter (IRT1)
    - IRT1 is a specific transporter for ferrous iron (Fe^{2+}). It plays a key role in iron uptake from the soil.
- COPT (Copper Transporter)
    - COPT transporters are involved in the uptake of copper (Cu^{2+});
    - They play a role in copper homeostasis and distribution within the plant.
- MTP (Metal Tolerance Protein)
    - MTP transporters are involved in the transport of various heavy metals, including zinc (Zn^{2+}), cobalt (Co^{2+}), and cadmium (Cd^{2+});
    - They are implicated in metal detoxification and sequestration.
- MerT and MerP Proteins
    - In some bacteria, like those with the mer operon, MerT, and MerP proteins are involved in the transport of mercury (Hg^{2+});
    - These proteins work in conjunction with other components of the mer operon to facilitate mercury uptake and detoxification.
- NiCoT Transporters (Nickel and Cobalt Transporters)

- These transporters are responsible for the uptake of nickel (Ni^{2+}) in plants;
- They play a role in regulating the cellular concentration of nickel and are essential for nickel-dependent enzymes.

While the key mechanisms described above are essential, it is important to note that they are not the only ones at play. In the following subsections, we will delve into additional mechanisms involved in heavy metal detoxification and adaptation in cereal crops.

6.2. Metal Sequestration: A Key Defence Mechanism in Cereal Crops

Metal sequestration stands as a fundamental defence mechanism employed by certain cereal crops to protect themselves against the harmful effects of heavy metal toxicity. Sequestration involves the immobilization and storage of heavy metals within the root tissues, effectively preventing their translocation to the above-ground parts of the plant. By isolating heavy metals in the root zone, cereal crops can minimize their damage to essential plant organs, reducing the overall toxicity.

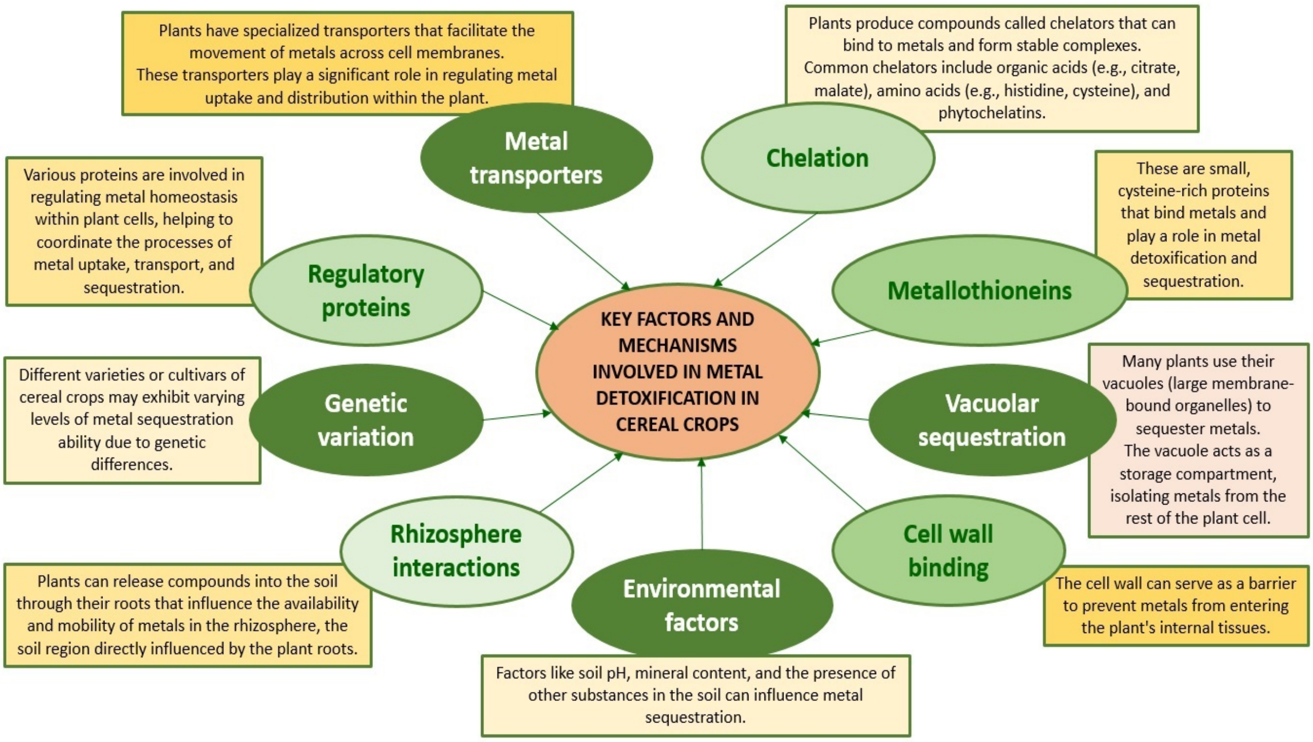

Figure 7. Key factors and mechanisms involved in heavy metals detoxification in cereal crops and short descriptions.

One example of metal sequestration in cereal crops is the binding of heavy metals to metallothioneins, which are small proteins rich in cysteine residues, which have a high affinity for heavy metal ions. When heavy metals are taken up by the roots of cereal plants, they are captured and bound by metallothioneins in the root tissues [265,277]. This sequestration of heavy metals within the roots ensures that they do not reach the shoot or grain tissues where they could exert toxic effects. Instead, the heavy metals are confined to the root zone, limiting their potential harm to essential plant organs responsible for growth and development. For instance, in rice plants, metallothioneins have been shown to play a critical role in sequestering heavy metals like cadmium [71,72]. Cadmium, a highly toxic heavy metal, can accumulate in rice grains and pose health risks to consumers.

However, certain varieties of rice that produce higher levels of metallothioneins in their roots can effectively sequester cadmium, reducing its translocation to the grains and improving the safety of the harvested rice. In addition to metallothioneins, other organic compounds present in the root tissues of cereal crops can also participate in metal sequestration. Organic acids, such as citrate, malate, and oxalate, can form complexes with heavy metals, reducing their mobility and availability for translocation to the above-ground parts of the plant [32,278].

Root cell wall modifications play a significant role in metal sequestration. Some cereal crops can alter the composition of their cell walls to trap heavy metals, preventing their passage into the plant's vascular system. These modifications can limit metal uptake and protect the shoot tissues from metal toxicity [279].

6.3. Metal Chelation in Cereal Crop Defence against Heavy Metal Toxicity

Metal chelation represents a significant defence strategy deployed by cereal crops to combat the toxic effects of heavy metals. Through the production of specialized compounds known as chelators, cereal plants can bind to heavy metal ions, creating stable complexes that immobilize the metals within the root zone. This immobilization reduces the availability of heavy metals for uptake by plant roots, mitigating their potential toxicity and safeguarding plant health [260,265].

One of the most common chelators found in cereal crops is phytochelatins, small peptides synthesized in response to heavy metal stress. When heavy metals, such as cadmium, lead, or copper, are present in the soil, cereal plants activate the production of phytochelatins in their root tissues. Phytochelatins contain sulphur-rich amino acids, such as cysteine and glutathione, which have a high affinity for heavy metal ions. Once synthesized, phytochelatins form strong bonds with the heavy metals, creating stable complexes that are less mobile and less likely to be taken up by the plant roots. For instance, in rice plants exposed to cadmium, phytochelatins have been shown to play a critical role in binding with cadmium ions, reducing their translocation to the above-ground plant parts. By forming stable complexes with cadmium, phytochelatins protect the shoot tissues, including grains, from cadmium toxicity, thereby improving the safety of rice for human consumption [277,280].

As mentioned previously, there are groups of chelators in cereal crops as organic acids, such as citrate, malate, and oxalate. These organic acids can also chelate heavy metals, immobilizing them within the root zone. Organic acids are often secreted into the rhizosphere by cereal plants, influencing the bioavailability of heavy metals in the soil. For instance, wheat plants can secrete citrate into the rhizosphere to chelate iron, rendering it more soluble and available for uptake. Similarly, some cereal crops release malate or oxalate to chelate aluminium, thereby reducing aluminium toxicity in acidic soils [281,282].

Therefore, metal chelation is a key strategy developed by cereal crops to immobilize heavy metals and reduce their bioavailability in the soil. Through the production of chelators like phytochelatins and organic acids, cereal plants can effectively protect themselves from heavy metal toxicity and maintain their productivity even in metal-stressed conditions [280,282].

By producing chelators, cereal crops can efficiently regulate the uptake of heavy metals and protect themselves from toxic metal ions. These defence mechanisms enable cereal plants to maintain optimal growth and productivity, even in metal-contaminated environments.

6.4. Enhanced Efflux: Empowering Cereal Crops against Heavy Metal Stress

Enhanced efflux is a remarkable defence mechanism employed by cereal crops to combat heavy metal stress effectively. Plants possess specialized membrane transporters that play a pivotal role in actively pumping heavy metals out of their cells. By facilitating the efflux of heavy metals, cereal crops can reduce their internal metal concentration, thereby safeguarding vital cellular processes and protecting themselves from metal toxicity [83,283].

One group of membrane transporters involved in enhanced efflux is the ATP-binding cassette (ABC) transporters. These transporters use energy derived from adenosine triphosphate (ATP) hydrolysis to pump heavy metal ions out of the cell against a concentration gradient. ABC transporters are known to be involved in the efflux of various heavy metals, including cadmium, copper, and zinc. For instance, in maize, the ABC transporter

ZmHMA3 has been shown to facilitate the efflux of cadmium and zinc from root cells. By efficiently exporting these heavy metals out of the root cells, maize can prevent their translocation to the above-ground parts, reducing the risk of metal accumulation in edible plant parts [284,285].

Another group of membrane transporters that participate in enhanced efflux is the cation diffusion facilitator (CDF) family. CDF transporters facilitate the efflux of divalent metal ions, such as cadmium, lead, and zinc, across cellular membranes. In rice plants, the CDF transporter OsHMA2 is involved in the efflux of cadmium from root cells. OsHMA2 helps prevent the entry of cadmium into the xylem vessels, thus limiting its long-distance transport to the aerial parts of the plant [286,287]. Thus, enhanced efflux is a powerful defence mechanism that allows cereal crops to actively pump heavy metals out of their cells, reducing the internal metal concentration and protecting themselves from metal toxicity. The presence and regulation of specific membrane transporters, such as ABC transporters and CDF family members, enable cereal crops to thrive in metal-contaminated environments and maintain agricultural productivity [286].

By enhancing the efflux of heavy metals, cereal crops can effectively reduce metal accumulation in vital plant organs, ensuring the continuity of essential physiological processes and promoting overall plant health and productivity. The regulation of these membrane transporters is under tight control, and their expression can be influenced by environmental factors and metal stress. Under heavy metal stress, cereal crops can upregulate the expression of specific transporters to enhance their efflux capacity, thereby adapting to the prevailing metal-contaminated conditions.

6.5. Siderophores as Nature's Metal Detoxifiers: Protecting Cereals from Heavy Metal Toxicity

Siderophores play a multifaceted role in cereal defence strategies against heavy metal toxicity. Their ability to chelate and sequester toxic metal ions, enhance metal tolerance, and foster microbial diversity highlights their importance in maintaining the health and productivity of cereal crops even in metal-contaminated environments [288]. Siderophores are small, low-molecular-weight molecules produced by microorganisms, plants, and even some animals. They have traditionally been recognized for their role in iron uptake by organisms [289]. However, recent research has revealed an intriguing connection between siderophores and heavy metal defence mechanisms in cereals. Siderophores possess a high affinity for various metal ions, including heavy metals. This characteristic allows them to form stable complexes with heavy metals in the rhizosphere, effectively chelating and sequestering these toxic ions [290].

Cereals that produce and release siderophores into the soil can benefit from enhanced metal tolerance. Siderophores aid in the detoxification process by reducing the concentration of free, bioavailable heavy metals in the root zone. This reduction minimizes the uptake of toxic ions by cereal plants, preventing their translocation to above-ground tissues. Consequently, cereals exhibit reduced symptoms of heavy metal toxicity, including stunted growth, chlorosis, and reduced yield.

Another interesting aspect of siderophores in cereal defence strategies is their role in promoting rhizosphere microbial diversity. Siderophores are not only produced by cereals but also by various beneficial microorganisms residing in the root zone [41,291]. These microbes contribute to a healthy rhizosphere environment, which can further aid in heavy metal tolerance. The microbial production of siderophores fosters competition for heavy metals in the rhizosphere, reducing the availability of toxic ions for uptake by cereals [292].

6.6. Antioxidant Production: Shielding Cereal Crops from Heavy Metal-Induced Oxidative Stress

When exposed to oxidative stress caused by heavy metals, cereal crops respond by activating the production of antioxidant enzymes [55,293]. To counteract the harmful effects of ROS, cereal crops synthesize antioxidant enzymes, such as SOD and catalase, which act as frontline guardians in neutralizing ROS and preserving cellular integrity [294]. By reducing the levels of superoxide radicals, SOD helps prevent oxidative damage to vital cellular components, including proteins, lipids, and DNA. As described before, in maize plants exposed to cadmium stress, the activity of SOD increases significantly. This enhanced SOD activity facilitates the rapid conversion of superoxide radicals, thereby minimizing oxidative damage to cellular structures and maintaining maize plant health under heavy metal stress [295,296].

Catalase is another crucial antioxidant enzyme that plays a critical role in the detoxification of hydrogen peroxide (H_2O_2). Hydrogen peroxide is a potent ROS that can cause cellular injury and disrupt metabolic processes. Catalase catalyzes the breakdown of hydrogen peroxide into water (H_2O) and oxygen (O_2), mitigating its toxic effects on cereal crops [297,298]. In wheat plants exposed to excess copper, catalase activity is induced to scavenge the accumulated hydrogen peroxide. This antioxidant defence mechanism helps shield wheat cells from oxidative damage, allowing the plants to endure copper stress without severe impairment. In addition to SOD and catalase, cereal crops also produce other antioxidant enzymes, such as peroxidases and glutathione peroxidases, which work in concert to combat ROS and preserve cellular homeostasis [299]. Furthermore, non-enzymatic antioxidants, such as ascorbate (vitamin C), tocopherols (vitamin E), and glutathione, are also synthesized in response to heavy metal stress. These antioxidants are active in neutralizing ROS directly, providing an additional layer of defence against oxidative damage.

The antioxidant protection system in cereal crops is tightly regulated, with its activation tailored to specific heavy metal stress conditions. Cereal plants can sense the presence of heavy metals and modulate their antioxidant response accordingly, allowing them to cope with a diverse range of metal stress scenarios. To enhance the antioxidant capacity of cereal crops and bolster their resilience against heavy metal-induced oxidative stress, there are investigating genetic approaches to augment the expression of antioxidant genes. By increasing the production of antioxidant enzymes and non-enzymatic antioxidants, scientists aim to fortify cereal crops against oxidative damage and improve their adaptability to metal-contaminated environments.

6.7. Mycorrhizal Symbiosis: Fungal Allies in Shielding Cereal Crops from Heavy Metal Uptake

Cereal crops establish a significant partnership with mycorrhizal fungi, creating a symbiotic relationship that extends beyond improving nutrient and water absorption. When dealing with heavy metal stress, specific mycorrhizal fungi emerge as robust protectors, assisting in lowering heavy metal uptake by cereal crops and offering additional defence against metal toxicity [300,301]. Mycorrhizal symbiosis involves a mutually beneficial interaction between cereal plant roots and specialized fungi. The two most common types of mycorrhizal associations are arbuscular mycorrhizae (AM) and ectomycorrhizae (ECM). These mycorrhizal fungi extend their hyphal networks into the surrounding soil, effectively extending the reach of cereal plant roots and increasing their access to nutrients and water [302].

Under heavy metal stress, the presence of mycorrhizal fungi can significantly impact the availability and uptake of heavy metals by cereal crops. Some mycorrhizal fungi possess unique abilities to sequester or immobilize heavy metals in the soil, acting as a protective barrier that shields plants from metal toxicity [303]. For example, certain species of AM fungi have been found to accumulate heavy metals in their hyphae, preventing these metals from reaching cereal plant roots. By sequestering heavy metals in their hyphal structures, AM fungi limit the bioavailability of metals in the rhizosphere and reduce their uptake by cereal crops. This sequestration mechanism not only protects cereal plants from metal toxicity but also contributes to heavy metal immobilization in the soil, potentially reducing the environmental impact of metal contaminants [302,304].

Additionally, mycorrhizal fungi can influence soil pH in the rhizosphere through their metabolic activities. The release of organic acids and other compounds by mycorrhizal fungi can modulate soil pH, affecting the solubility of heavy metals. Altered soil pH can promote the formation of metal precipitates, making them less available for uptake by cereal plants. By regulating soil pH, mycorrhizal fungi further contribute to heavy metal detoxification in cereal crops. Furthermore, mycorrhizal symbiosis can stimulate the production of phytochelatins and metallothioneins in cereal crops [305]. Some mycorrhizal fungi induce the expression of genes associated with heavy metal detoxification in the host plant. This enhancement of metal detoxification mechanisms in cereal crops further strengthens the plant's ability to cope with heavy metal stress and maintain cellular integrity. Mycorrhizal symbiosis serves as a strategic defence mechanism that empowers cereal crops to confront heavy metal stress. Mycorrhizal fungi act as allies, sequestering heavy metals, influencing soil pH, and stimulating metal detoxification mechanisms in cereal plants [306]. By forging this partnership, cereal crops gain an edge in mitigating heavy metal uptake and minimizing the potential toxicity of these contaminants. Expanding our knowledge of mycorrhizal symbiosis offers promising opportunities for developing metal-tolerant cereal varieties and enhancing sustainable agricultural practices in metal-affected soils.

Mycorrhizal fungi promote the growth of plants and decrease the absorption of heavy metals by plant roots through various mechanisms, such as nutrient uptake facilitation, competitive exclusion of heavy metals, improved soil structure, stimulation of plant defence mechanisms, pH modification, and enhanced tolerance (Figure 8). The specific mechanisms involved can vary depending on the type of mycorrhizal fungi, plant species, and the heavy metal in question. Additionally, the effectiveness of mycorrhizal fungi in reducing heavy metal uptake depends on factors such as the fungal species, soil conditions, and the concentration and bioavailability of heavy metals in the soil. Overall, mycorrhizal associations are an important natural strategy for improving plant health and reducing the risks associated with heavy metal contamination in the soil.

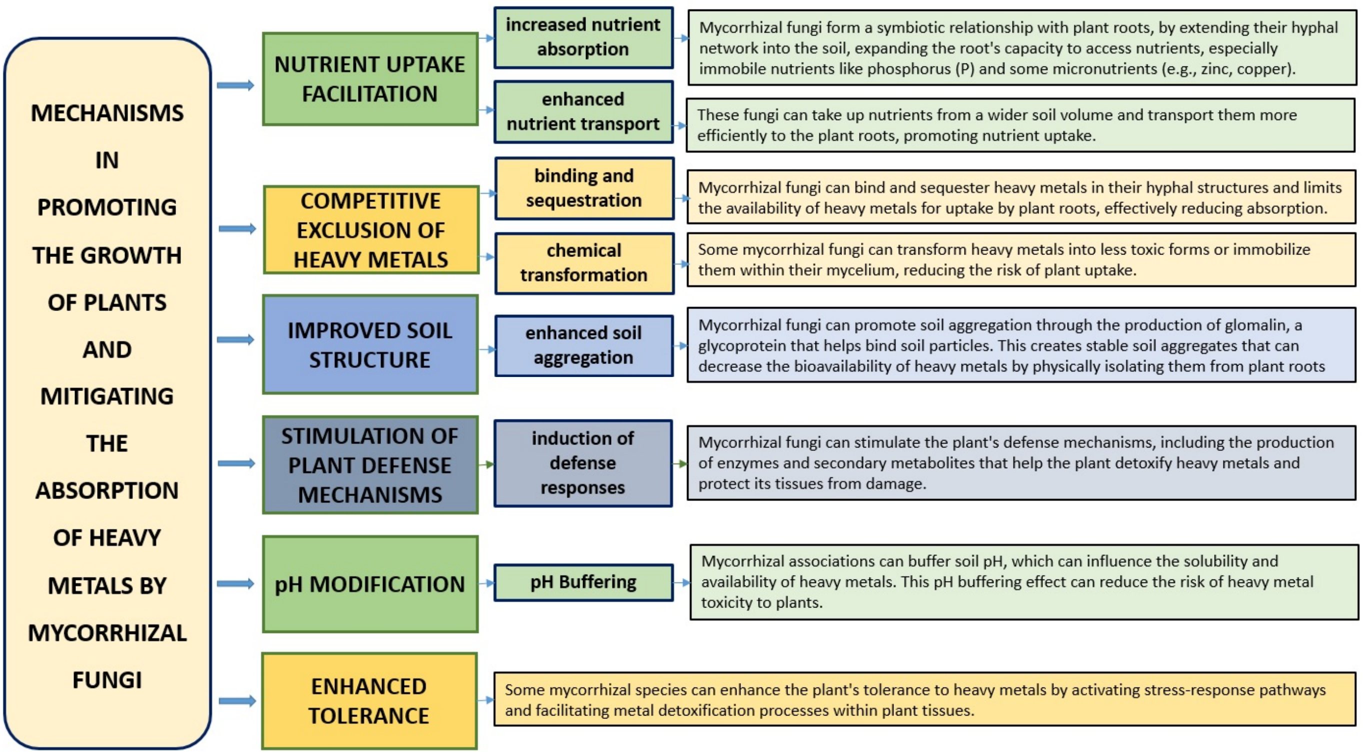

Figure 8. Illustration of mechanisms by which mycorrhizal fungi enhance plant health and reduce heavy metal uptake in roots by nutrient facilitation, heavy metal sequestration, and defence stimulation.

Not all mycorrhizal fungi provide the same level of protection against heavy metal uptake, as their effectiveness depends on various factors, including the fungal species and the type of heavy metal present in the soil [307]. However, their overall role in enhancing nutrient uptake, improving soil structure, and supporting plant health contributes to the resilience of cereal crops in metal-contaminated environments. Researchers are actively exploring the diversity of mycorrhizal fungi and their potential to enhance heavy metal tolerance in cereal crops [305,306].

6.8. Harnessing Plant Growth-Promoting Bacteria for Cereal Defence against Heavy Metal Toxicity

In response to heavy metal threats, cereal plants have developed various resistance mechanisms, and a noteworthy player in these strategies is the group of microorganisms known as plant growth-promoting bacteria (PGPB). Plant growth-promoting bacteria exert their influence on plant growth through a combination of direct and indirect mechanisms. The direct mechanisms involve enhancing resource acquisition and producing phytohormones that directly impact plant growth. On the other hand, the indirect mechanisms encompass biocontrol strategies, achieved through the production of antagonistic compounds and the initiation of systemic resistance (Figure 9). PGPB are a diverse array of bacteria that reside in the rhizosphere of plants, forming intricate relationships with their host plants [308]. These beneficial microbes are capable of alleviating heavy metal stress in cereals through a range of mechanisms, thus enhancing the plants' overall resilience to toxic metal exposure. Some PGPB possess the ability to produce siderophores, small molecules with high affinity for metal ions, including heavy metals. By sequestering heavy metals, these siderophores reduce the bioavailability of toxic ions in the rhizosphere, diminishing the likelihood of their uptake by cereal plants. This chelation and immobilization process contributes significantly to the detoxification of heavy metal-contaminated soils [309].

PGPB are known to enhance the availability of essential nutrients, such as nitrogen, phosphorus, and potassium, to plants. By improving nutrient uptake, these bacteria indirectly bolster the cereal plants' ability to tolerate heavy metal stress [310,311]. Adequate nutrient levels help in maintaining robust plant growth, which can counteract the negative effects of heavy metal toxicity. PGPB have been observed to stimulate the plants' natural defence mechanisms. This includes the activation of antioxidant pathways, which help mitigate oxidative stress induced by heavy metals. Additionally, these beneficial bacteria can induce systemic resistance, making cereals more adept at fending off heavy metal-induced damage (Figure 9) [7,312]. Some PGPB have the remarkable ability to enhance phytoremediation—the process by which plants remediate contaminated soils by accumulating and immobilizing heavy metals in their tissues. Through mechanisms such as metal ion absorption and root exudation modulation, PGPB facilitates the removal of heavy metals from the soil, contributing to its decontamination [313,314].

These beneficial microbes contribute to heavy metal detoxification, nutrient uptake enhancement, activation of defence mechanisms, and enhanced phytoremediation [261,315,316]. By partnering with these tiny allies, cereals cannot only withstand heavy metal stress but also contribute to the restoration of contaminated environments [317,318]. The presence of biosurfactant-producing microorganisms in polluted soils can significantly improve the mobility of metals. It was observed that the rhamnolipid-producing *Pseudomonas Y3-B1A* achieved an impressive 85.5% efficiency in vanadium removal [319]. The biosorption phenomenon plays a critical role in mitigating the toxicity of metals to plants.

Remarkably, *B. subtilis* was found to exhibit substantial biosorption capacity, effectively adsorbing concentrations of Cd^{2+} from soil equivalent with 10–20 mg L^{-1} [320]. Likewise, when *Mesorhizobium* sp. *RC3* cooperated with Chickpea (*Cicer arietinum*), which led to significant improvements in various growth parameters. Compared to plants without inoculation, there was a substantial increase of 71% in dry matter accumulation, an 86% boost in the number of nodules, a 36% rise in seed yield, and a 16% enhancement in grain protein content. Furthermore, nitrogen levels in both the roots and shoots experienced notable increments of 46% and 40%, respectively, reaching 136 mg Cr/kg [321].

Further research into the interplay between PGPB and cereal defence strategies holds promise for developing sustainable agricultural practices that prioritize both crop productivity and environmental health.

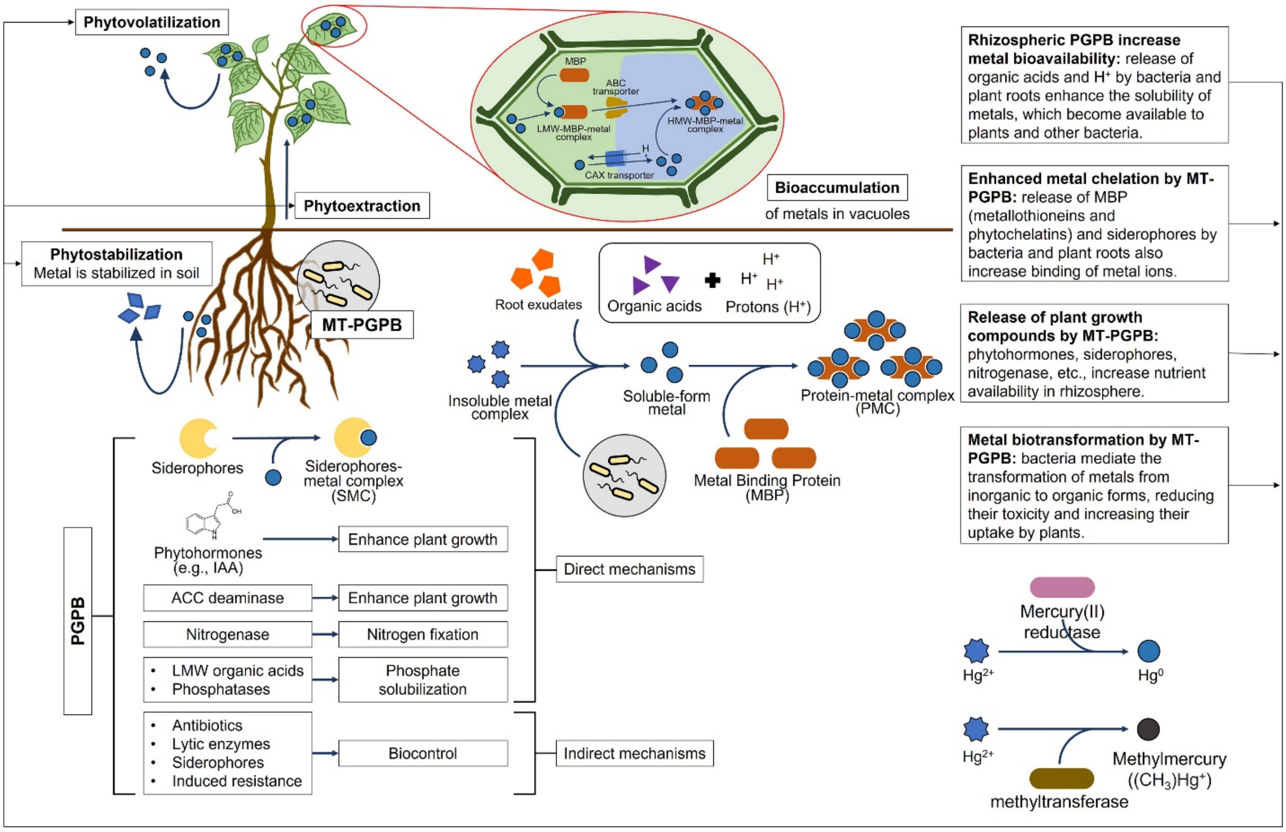

Figure 9. The role of bacteria in plant growth promotion, soil metal complexation, and phytoremediation. LMW, low molecular weight; HMW, high molecular weight; MT, metal tolerant; CAX, cation exchanger transporters; ABC, ATP-binding cassette transporters (Alves et al., 2022 [312]; reproduced under the terms of the Creative Commons CC-BY licence, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited).

7. Exploring New Frontiers: Unravelling the Impact of Heavy Metal Presence in Soil on Cereals for Promoting Innovation beyond the State of the Art

While significant research has been conducted on heavy metal contamination in soil and its impact on plants, there is a pressing need to delve deeper into the specific consequences for cereal crops. Understanding the multifaceted interactions between heavy metals and cereals is essential to devise innovative strategies that surpass the state of the art and mitigate the detrimental effects of metal pollution. Some key aspects that necessitate thorough investigation to foster innovation and deepen our understanding of the impact of heavy metal presence in soil on cereals are shown in Table 4. By exploring new frontiers and pushing the boundaries of knowledge, we can unlock novel insights that will empower us to devise sustainable solutions for safeguarding cereal crop productivity and food safety in metal-affected regions.

From exploring the molecular mechanisms of metal uptake and transport in cereal plants to interpreting the role of root exudates and mycorrhizal symbiosis in metal tolerance, there are numerous avenues for research that hold the potential for transformative breakthroughs. Moreover, investigating the synergistic or antagonistic interactions between different heavy metals and their competition for uptake within cereals can shed light on complex ecological dynamics. In addition to focusing on the physiological responses of cereals to metal stress, innovative research should also investigate the potential of genetic and breeding approaches in developing metal-tolerant cereal varieties. Furthermore, integrating advanced technologies, such as omics and remote sensing, can provide valuable insights into the spatial and temporal dynamics of heavy metal contamination in soil and its impact on cereals.

Table 4. Key aspects requiring comprehensive investigation for advancing innovation and enhancing understanding of heavy metal impact on cereals in soil.

Key Aspect to be Investigated	Focus
Metal-specific uptake and translocation	- further investigation into the metal-specific uptake and translocation mechanisms in different cereal species is essential - understanding how different heavy metals are absorbed and distributed within cereals can provide insights into metal accumulation patterns and potential risks associated with specific cereal crops
Genomic and genetic studies	- conducting genomic and genetic studies to identify genes and molecular pathways responsible for metal tolerance and accumulation in cereals is crucial - identifying key genes involved in metal transport, chelation, and detoxification can lay the foundation for targeted breeding and genetic engineering approaches to develop heavy metal-tolerant cereal varieties
Metal interactions and synergies	- investigating the interactions and synergies among various heavy metals in soil and their combined impact on cereal crops is important - some metals may exhibit synergistic effects, amplifying their toxicity, while others may compete for uptake or mitigate the effects of other metals
Soil–plant-microbe interactions	- understanding the intricate interactions between cereals, soil microorganisms, and heavy metals is vital - certain microorganisms can influence metal bioavailability, sequestration, and detoxification in the soil–plant system - exploring beneficial microbial associations that enhance metal tolerance in cereals can lead to innovative bioaugmentation or biostimulation approaches
Agronomic practices	- investigating the efficacy of different agronomic practices in reducing heavy metal uptake by cereals is critical - evaluating the impact of soil amendments, organic matter application, crop rotation, and other soil management practices on heavy metal bioavailability and crop health can inform sustainable farming methods
Phytoremediation and phytoextraction	- advancing phytoremediation and phytoextraction techniques using cereals as metal-accumulating plants can be explored - identifying suitable cereal species and optimizing growth conditions to maximize metal removal from contaminated soils will contribute to sustainable environmental remediation
Food safety assessment	- conducting comprehensive food safety assessments to evaluate the potential risks of heavy metal accumulation in cereal grains is essential - understanding the transfer of heavy metals from contaminated soils to the edible parts of cereals and evaluating the impact on human health is crucial for consumer safety
Modelling and predictive tools	- developing predictive models and innovative tools that integrate data on soil properties, metal concentrations, cereal varieties, and environmental conditions can aid in predicting heavy metal uptake and its impact on cereals - these models can help optimize agricultural practices and support decision-making for sustainable crop production.
Climate change effects	- investigating the influence of climate change on heavy metal mobility and uptake by cereals is critical - understanding how shifts in temperature, precipitation, and other climate factors may alter heavy metal behaviour in the soil–plant system can aid in climate-resilient crop management

By emphasizing multidisciplinary collaboration and leveraging emerging technologies, we can collectively work towards generating comprehensive and actionable knowledge. The findings from such research endeavours will serve as a foundation for designing targeted mitigation strategies, implementing sustainable agricultural practices, and ensuring the safety and nutritional quality of cereals in metal-contaminated environments. As we embark on this journey to promote innovation beyond the state of the art, we recognize the urgency of addressing heavy metal contamination in soil and its implications for cereal crops. Only through a concerted effort to expand our understanding and embrace innovative approaches can we pave the way toward a resilient and secure future for cereal agriculture and universal food stability.

8. Conclusions

This paper underscores the significance of unravelling the impact of heavy metal presence in soil on cereals. Thorough investigations into the molecular, physiological, and ecological aspects are indispensable for fostering innovation and developing pragmatic solutions. By advancing our understanding and embracing transformative approaches, we can pave the way for resilient cereal agriculture, ensuring adequate food supply, and ensuring the well-being of both ecosystems and humanity. Embracing the challenges posed by heavy metal contamination with proactive research and collaboration will empower us to create a sustainable and secure future for cereal crops amidst the evolving environmental landscape.

The impact of heavy metal presence in soil on cereal crops presents a complex and pressing challenge for worldwide food safety and environmental health. This paper has explored various aspects related to heavy metal contamination in soil and its effects on cereals, shedding light on crucial factors that demand thorough investigation and innovative solutions.

Understanding the intricate mechanisms of heavy metal uptake, translocation, and sequestration in cereal crops is paramount in devising effective strategies to mitigate metal toxicity. Root barrier formation, mycorrhizal symbiosis, and the synthesis of metal-binding proteins are among the key defence mechanisms employed by cereals to combat heavy metal stress. In-depth research into these mechanisms will enable us to harness their potential for developing metal-tolerant cereal varieties. Furthermore, the multifaceted effects of heavy metals on cereal growth and development, including chlorosis, stunted growth, leaf deformities, and reduced flowering, emphasize the urgent need for comprehensive studies on plant physiology under metal stress. Identifying the specific impact of different heavy metals on nutrient imbalances and impairment of photosynthesis in cereals is critical for implementing targeted management practices.

Symptoms of heavy metal toxicity, ranging from chlorosis and stunted growth to necrosis and water stress, illustrate the extensive damage incurred by cereal crops. These manifestations underscore the imperative to investigate the underlying factors that predispose cereals to heavy metal toxicity. Soil properties, pH, organic matter content, plant varieties, and environmental conditions shape the degree of impact, necessitating a comprehensive understanding of effective mitigation strategies.

Examining the bioavailability and food safety implications of heavy metal accumulation in cereal grains is essential for protecting human health. Research on metal interactions and competition in cereals will contribute to understanding the complex relationships between different heavy metals and their cumulative effects on plant health.

The resilience of cereal crops against heavy metal toxicity is both fascinating and decisive. Various strategies, such as metal sequestration, chelation, enhanced efflux, antioxidant production, and beneficial microbial associations, exemplify the plant's remarkable adaptive mechanisms. However, these strategies have limitations, urging the need for innovative research to harness genetic and breeding approaches for developing metal-tolerant cereal varieties.

The call to explore new frontiers in heavy metal impact research resonates with urgency. Investigating metal-specific uptake mechanisms, unravelling genetic pathways of metal tolerance, and understanding metal interactions in complex ecological systems hold promise for transformative breakthroughs. Additionally, predictive modelling and advanced technologies offer tools to guide sustainable agricultural practices amidst shifting climate dynamics.

Promoting innovation beyond the state of the art requires embracing emerging technologies and multidisciplinary collaboration. Integrating various interdisciplinary approaches can enhance our understanding of heavy metal dynamics in soil and its spatial distribution, facilitating precise and timely interventions. The development of metal-tolerant cereal varieties through genetic and breeding approaches holds great promise for sustainable agriculture in metal-contaminated regions. Additionally, exploring the potential of soil amendments and agronomic practices, such as liming and crop rotation, will aid in reducing heavy metal bioavailability and toxicity in soil.

This knowledge, in turn, forms the foundation for designing targeted mitigation strategies that safeguard cereals production, implement sustainable agricultural practices, and ensure the nutritional quality of cereals. As we venture beyond the current state of the art, the commitment to innovation resonates as a beacon of hope for a resilient and secure future in cereal agriculture and global nutritional safety.

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