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Review article

Review: Strategies for limiting dietary cadmium in cereals

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ABSTRACT

Cadmium (Cd) is a toxic metal, which in some production areas reaches levels above allowed limits in cereals. Thus, reducing its concentration in cereals is crucial for mitigating health risks and complying with food safety regulations. This review evaluates strategies to reduce Cd accumulation in cereal grains by mitigating soil Cd contamination and its bioavailability to plants. It covers methods for Cd estimation in soil and explores biological, chemical, and genetic approaches to limit Cd uptake by crops. The effectiveness of these strategies depends on genetic factors, soil properties, and crop type. Key approaches include traditional breeding, genome editing, digital and predictive soil mapping, and silicon (Si) and selenium (Se) supplementation. Traditional breeding, enhanced by modern genetic tools, enables the development of high-yielding, low-Cd cultivars but is time-consuming. Genome editing, particularly CRISPR-Cas9, offers precise gene modifications to reduce Cd uptake but faces regulatory constraints. Digital and predictive soil mapping provide high-resolution maps for targeted interventions but require extensive calibration. Silicon supplementation is a promising approach, as it competes with Cd for uptake sites, and limits Cd translocation to edible plant parts. Additionally, Si enhances plant tolerance to abiotic stresses, making it a multifunctional solution. Selenium supplementation can also reduce Cd accumulation while offering health benefits. However, the effectiveness of both Si and Se vary with dosage and crop type. An integrated approach combining these strategies is essential for effective Cd reduction in cereals. Continued research, technological advancements, and supportive policies are crucial for ensuring safe and sustainable cereal production.

1. Introduction

Cadmium (Cd) is a highly toxic heavy metal to many living organisms, including humans (Nordberg et al., 2022; Åkesson et al., 2014). In non-smoking populations, diet is the primary source of exposure. Among crops, cereals such as rice and wheat contribute considerably to Cd in the human diet following their importance as staple crops. Although Cd is slowly eliminated from the body via urine, Cd body burden increases with age due to half-life of 10–40 years in the body (Akerstrom et al., 2013; Nordberg et al., 2022). Dietary Cd exposure can cause a number of adverse health effects. Cd can damage the kidneys (Elinder and Barregard, 2022; Friberg, 1950) and decrease bone density (Åkesson et al., 2014; Wallin et al., 2021), both constituents of the itai-itai disease observed in rural Japanese communities growing rice on Cd polluted soils (Kido et al., 1990). Furthermore, Cd is carcinogenic (IARC, 2012) having been associated with hormone-related cancers in women (Åkesson et al., 2008; Julin et al., 2012a; Julin et al., 2012b) including breast cancer (Andersson et al., 2021; Larsson et al., 2015; Lin et al., 2016). Cadmium is also a risk factor for cardiovascular disease (Chowdhury et al., 2018; Fagerberg and Barregard, 2021; Tinkov et al., 2018). Finally, prenatal exposure to Cd is linked with developmental impairments in children (Chatzi et al., 2019; Gustin et al., 2020; Khoshhali et al., 2020), affecting growth and cognition adversely (Gustin et al., 2018; Malin Igra et al., 2021; Sanders et al., 2015).

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Among heavy metals, Cd is especially detrimental to plants. Even low concentrations (1.2–6 mg/kg in soil) result in a range of physiological damages leading to inhibited germination and growth, lower yields and even plant death (El Rasafi et al., 2022; Haider et al., 2021). Depending on soil parent material, Cd is naturally present in concentrations between 0.01 and 1 mg/kg in unpolluted soils, with a global mean of 0.36 mg/kg (Kubier et al., 2019). Hence, even limited increases in Cd concentration can cause toxicity in crops on specific soil types. Soil Cd content can increase naturally through weathering of rock, airborne soil particles, sea spray, biogenic material, forest fires, and volcanic activity (Kubier et al. 2019) (Fig. 1). However, since the beginning of the twentieth century, anthropogenic sources of Cd are the most notable source of Cd pollution. Cd is released into the air during high-temperature natural and industrial processes (Genchi et al., 2020). Airborne Cd is highly reactive, forming many water-soluble inorganic compounds, thus rapidly becoming a soil and water pollutant (IPCS, 1992). Furthermore, Cd is introduced into arable soil by using contaminated water for irrigation, phosphorus fertilizers, sewage sludge or manure (Ballabio et al., 2024).

Estimated 3 000 tonnes of anthropogenic Cd was emitted in mid-1990 worldwide (Pacyna and Pacyna, 2001), with Chinese researchers reporting emissions of about 750 tons for China alone in 2014 (Cheng et al., 2014). Although the EU has seen a 40 % drop in Cd emissions over the past two decades (2002–2022) (EEA, 2024), such reductions cannot necessarily be extrapolated to the entire world, as Cd contamination is often a highly localized issue. A recent review of soil Cd levels across the EU found that most countries have low contaminations, with Ireland and Poland exhibiting the highest levels (0.51–2.24 mg/kg soil), largely due to the use of Cd-contaminated fertilizers such as sewage sludge (Ballabio et al., 2024). However, studies have shown that certain localized areas can have significantly higher Cd levels (2.5–64 mg/kg soil), often linked to current or historical mining and industrial activities. Notable examples include the Goslar region in Germany (Ballabio et al., 2024) or the Hunan region in China (Liu et al., 2016), the latter being an important rice production province.

Awareness of the health risks associated with dietary Cd exposure has increased, prompting regulatory measures to limit intake. Various national (ATSDR, 2012; US EPA, 1989) and international (EFSA, 2012; World Health Organization et al., 2011) organisations have defined tolerable daily intake levels for dietary Cd in the range of 0.1–1 μg Cd/kg body weight. However, certain population groups such as children and vegetarians (EFSA, 2012) often exceed these limits. In Europe the average dietary Cd intake is estimated at 10–20 μg/day (EFSA, 2009; World Health Organization et al., 2011). The EU has also set maximum permissible Cd levels in various food products, including cereals (0.05–0.18 mg/kg) (European Commission Regulation (EC) No.2023/915, European Commission, 2023). As research continues to reveal health effects of Cd exposure, these limits are expected to highlight the urgent need for effective strategies to reduce Cd accumulation in crops.

Various tools and strategies have been developed to reduce dietary Cd exposure, including characterization and remediation, as well as development of crop cultivars with low Cd accumulation. While these approaches are supported by theoretical foundations, not all are

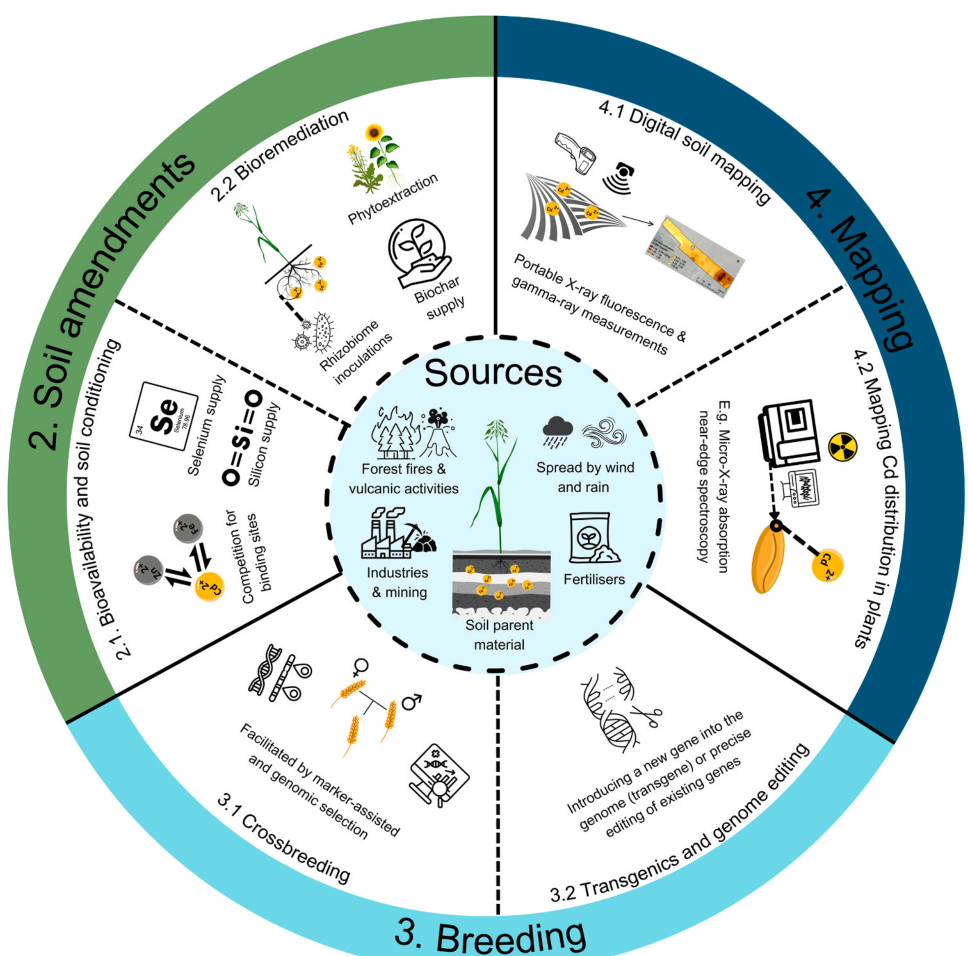


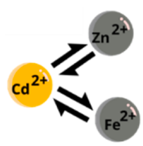
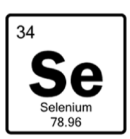
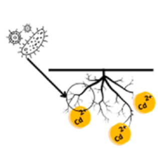
Fig. 1. An overview of the sources of cadmium (Cd) contamination and corresponding strategies for mitigating Cd accumulation in cereals. The inner circle highlights the various sources of soil Cd contamination and the outer circle the strategies reviewed in chapters 2–4. Image created using Canva (www.canva.com).

currently practically applicable. In this review, we critically evaluate the existing tools and strategies (Fig. 1) for reducing Cd levels in soils and cereals, highlighting their practical applicability and providing recommendations for the most effective approaches.

2. Strategies for lowering soil cadmium and its bioavailability

Plant roots grow in a complex soil matrix with variable abiotic conditions competing for space, water and nutrients with a plethora of organisms. Microbial activities are most intense in the zone surrounding the roots (the rhizosphere), a place where numerous processes important for the bioavailability and distribution of nutrients and their

Table 1
Strategies for lowering soil cadmium (Cd) and its bioavailability, their underlying mechanisms, and potential for practical application, as reviewed in Chapter 2. Images are created using Canva (www.canva.com).

Section	Strategy		Mechanism	Potential
2.1.1	**Alkaline additives and soil pH adjustment**		High pH levels lead to a decreased Cd bioavailability, resulting in a reduced Cd uptake by the plant.	The optimal pH level for reducing Cd uptake aligns with crop cultivation pH recommendations but varies by species and impacts essential micronutrients. Further research is needed to develop species-specific responses to pH management strategies.
2.1.2	**Applying divalent cations**		Cd competes with divalent cations for binding sites on soil particles and for uptake by the divalent cation transporters in the plant.	Studies indicate that Zn supplementation, particularly in Zn-deficient or Cd-contaminated soils, can significantly reduce Cd levels in wheat grains. Foliar Zn applications, however, have yielded mixed results. Similarly, Fe supplementation has been effective in reducing Cd accumulation in rice grains. The impact of these micronutrients is context-dependent, highlighting the need for further research to optimize their application strategies.
2.1.3	**Silicon (Si) supply**	O=Si=O	Si reduces Cd uptake by inhibiting Cd transporter gene expression, limiting entry through root cell wall complexation, and promoting Cd release into the rhizosphere via phenolic or organic acid exudation, alleviating Cd phytotoxicity.	Si supplementation shows promise for reducing Cd uptake, but further field research across various soil and crop types is needed to evaluate its effectiveness under standard practices. The optimal form, dosage, and frequency of application also require clarification for sustainable use in different regions.
2.1.4	**Selenium (Se) supply**		Se may reduce Cd uptake by forming Cd-Se complexes, thickening plant cell walls, promoting Cd precipitation, limiting root surface area, enhancing metal sequestration, thus reducing Cd mobility.	Se supplementation shows promise in reducing Cd uptake by 10–50 %, depending on its form and dosage. However, most studies have been conducted under controlled conditions, and further research is needed to assess its effectiveness, optimal formulation, dosage, and application under practical farming conditions.
2.1.5	**Fertilisers**		NH_{4+} addition lowers soil pH, which increases Cd bioavailability. Additionally, the chloride (Cl^-) ions form soluble Cd-Cl complexes, facilitating uptake by plants.	For NH_{4++}, the effect is most pronounced at supra-optimal application rates, with Cd uptake likely increasing due to pH reduction. The impact of Cl^- remains unclear, as results vary across studies. Given these uncertainties, further research is needed before making definite recommendations regarding the use of Cl- containing fertilizers.
2.2.1	**Phytoextraction and intercropping**		Cd is removed from the soil through the growth of hyperaccumulating plant species, such as rapeseed, sunflower and Salix, which accumulate Cd in their aboveground parts.	While effective, phytoextraction can make fields unproductive during hyperaccumulator growth, and compatibility with industrial farming is challenging. Therefore, innovations in disposal methods, harvesting, and separation technologies are crucial for making these strategies viable.
2.2.2	**Organic matter additives**		Biochar forms insoluble complexes with Cd, preventing its adsorption by plant roots.	Using biochar to reduce Cd uptake is not recommended, as it requires large quantities for effectiveness, and its impact remains uncertain.
2.2.3	**Rhizobiome inoculations**		Not fully understood, but different bacterial inoculations have been shown to affect Cd bioavailability and uptake.	Certain strains, like *Bacillus altitudinis* and *Pseudomonas* spp., have demonstrated effectiveness in reducing Cd accumulation in crops, while others may increase bioavailability for bioremediation purposes. The complexity of rhizosphere-plant interactions and possible unintended effects requires further research.

subsequent uptake into the plant take place. Here, factors of importance are concentration gradients due to depletion generated by active root uptake, active root growth and altered water potential gradients (Marschner, 2011).

Cadmium is one of the abiotic variables within the soil matrix. However, the amount of Cd present in the soil does not always directly translate into increased Cd in the plant. Various factors present in the soil matrix affect the overall bioavailability of Cd as well as the accessibility of Cd to the crop plant. Adjustment of these factors constitutes the first group of strategies that can be used to limit Cd uptake in crops. Hence, a thorough understanding of the local soil conditions can not only guide the choice of suitable crops for specific fields but also inform the necessary amendments for the best outcomes for the field. In this chapter, we present strategies for quantifying Cd in the soil and amending the conditions within, either through biotic or abiotic means (Table 1).

2.1. Bioavailability and soil conditioning

2.1.1. Alkaline additives and soil pH adjustment

Soil pH levels below 6.5 increase Cd bioavailability and uptake as Cd is adsorbed to metal binding sites in plant roots (Adams et al., 2004; Iretskaya and Chien, 1999; Wei et al., 2023). Alkaline additives, such as biochar and calcium carbonate (lime), are known to lower Cd bioavailability by increasing soil pH, but the effect varies depending on the crop (He et al., 2021, Wei et al., 2023). Recent meta-analyses have indicated that liming reduces Cd levels in both shoots (45.2 %) and grains (51.4 %) in rice and other crops (He et al., 2021). Several studies have explored the effects of multi–year liming and found conflicting results on the effects of repeated years of liming. These discrepancies may be due to differences in lime application rates used and soil types, with sandy soils receiving lower lime applications showing no accumulative effects (Liu et al., 2020a, 2020b; Zhang et al., 2023). This was further supported by the meta-analysis, which highlighted significant variations in liming effects on pH depending on soil properties such as clay content (He et al., 2021). Furthermore, increases in pH levels are known to reduce the availability of essential micronutrients such as zinc (Zn), manganese (Mn) and iron (Fe) (Yang et al., 2021a, 2021b).

2.1.2. Applying divalent cations

Root uptake of Cd from the soil occurs through the same divalent cation transporters as root uptake of essential micronutrients such as Fe, Zn, Mn, magnesium (Mg) and copper (Cu) (Abedi and Mojiri, 2020; Huang et al., 2019; Song et al., 2017). The non-specificity of these transporters poses challenges towards the reduction of Cd uptake. The plant uptake is inversely affected by the availability of these nutrients to the plant, due to the fact that Cd competes with mentioned micronutrients both for binding sites on soil particles and for plant uptake, the plant uptake is inversely affected by the availability of these nutrients to the plant. Deficiency for one of these essential micronutrients can lead to increased uptake of Cd, as has been reported for Fe (Nakanishi et al., 2006) and Zn (Honma and Hirata, 1978) deficient rice.

A few studies have demonstrated the possibility of reaching a significant reduction of Cd in grains of cereals when supplementing the plants with these micronutrients, reaching a 19–43 % decrease in grain and shoot Cd concentration in wheat and rice (Wang et al., 2022; Zhao et al., 2023). A meta-analysis in rice showed that Fe supplementation contributed the largest average decrease in grain Cd levels with a 43 % decrease, while Mn supplementation showed the smallest average effect with a 22 % decrease with the largest variation in results across studies (Zhao et al., 2023). Bread wheat and durum wheat showed the best results if Zn soil supplementation was conducted on soils with low Zn levels or on highly Cd contaminated soils (Choudhary et al., 1994; Oliver et al., 1994; Wu and Zhang, 2002). Likewise, Fe supplementation has shown the potential to decrease Cd accumulation in rice grains (Watanabe et al., 2009). However, Zn supplied as foliar spray has shown conflicting results and seems to have the largest potential on soils with low Zn levels (Hussain et al., 2018; Jiao et al., 2004; Saifullah et al., 2014). One benefit that micronutrient supplementation has over many of the other supplementation methods is that it does not affect soil pH, making it a good option for controlling Cd uptake on alkaline soil types (Wang et al., 2022).

2.1.3. Silicon supply

Silicon (Si) can reduce Cd uptake in crops by inhibiting the expression of Cd transporter genes and limiting entry through complexation in the root cell wall (Liu et al., 2023; Riaz et al., 2021). Si can also stimulate the exudation of phenolic or organic acids, which may help alleviate Cd phytotoxicity by promoting Cd release into the rhizosphere (Vaculík et al., 2020). Additionally, Si supplementation in Cd-contaminated soils has been shown to enhance photosynthesis, respiration, antioxidant capacity and biomass resulting in increased crop yields by 10–20 % (Liu et al., 2024a, 2024b; Huang et al., 2024). Furthermore, Si can improve soil quality by increasing soil pH, organic matter, and available phosphorus content, which can further contribute to Cd immobilization in the rhizosphere (Ma et al., 2021a, 2021b; Song et al., 2021).

A recent meta-analysis of 105 studies, spanning from 2000 to 2023, which included many studies from China and India, evaluated the effects of four exogenous Si application modes—Si-based fertilizers, nano-Si, Si-based materials, and silicates—on Cd accumulation in the grains of wheat, maize, and rice (Liu et al., 2024a, 2024b). The meta-analysis showed a significant reduction by the treatments in Cd accumulation, not only in grains (43 %) but also in roots (23 %), shoots (40 %), and leaves (26 %). Among the treatments, nano-Si resulted in the highest reduction in grain Cd (75 %), followed by Si-based materials (54 %) and silicates (51 %). Based on these findings, Liu et al. (2024a, 2024b) recommend using nano-Si or silicates at ≤ 250 mg/kg, particularly through root applications, to reduce Cd accumulation and enhance yield.

However, 62 % of the studies in Liu et al. (2024a, 2024b) were conducted under controlled conditions, and 43 % involved artificially contaminated soils. As a result, the findings may not be directly applicable to natural soils and agricultural settings, where Cd contamination levels and climatic factors significantly influence Cd uptake and accumulation. Future research should address these limitations by conducting long-term field experiments across different soil types, crops and growth stages as well as to find the optimal dosage and frequency of the application to assess the sustainability and feasibility of Si supplementation in agricultural systems. The form of application might also need to be tailored to different regions, where e.g. water-soluble Si forms are more effective in arid or semi-arid areas, whereas stable Si forms are necessary in humid regions with high precipitation (Huang et al., 2024). Moreover, there is a need for better understanding of the long-term effect of Si application on soil structure and soil health, as Si can form stable aggregates with soil particles, affecting soil porosity (Huang et al., 2024), and interact with microorganisms (Yuan et al., 2024).

2.1.4. Selenium supply

The interaction between selenium (Se) and Cd is not fully understood. One proposed mechanism is the formation of a poorly soluble CdSe complex in the soil. However, such a reaction requires an anaerobic environment, like a rice paddy, to occur (Gustafsson, 2013; Husson, 2013). Another hypothesis suggests that Se reduces Cd uptake by forming poorly soluble compounds of Cd-Se compounds within the plant or by inducing thicker plant cell walls, thereby limiting Cd absorption (Cui et al., 2018; Gómez Ojeda et al., 2013).

Additional mechanisms have been proposed, including the ability of Se to influence Cd accumulation by promoting Cd precipitation and adsorption to soil humus, reducing root surface area and fine root development, and enhancing metal sequestration in cell walls, vacuoles and root iron plaques, thereby limiting Cd mobility (Feng et al., 2021). A meta-analysis by Affholder et al. (2019), which reviewed 33 studies conducted between 2008 and 2019 across 16 different crops, found that Se supplementation reduced Cd uptake by 10–50 %, depending on the applied amount and the specific form of Se, with selenite proving more effective than selenate.

Since Se is an essential mineral for both humans and animals, its supply could also have beneficial health implications. A recent study of 31 diseased human lungs found that a lower Cd-to-Se ratio was associated with non-diseased lungs (Smith et al., 2023). Moreover, metabolic pathways, particularly those involved in inflammatory signalling, showed opposing associations with Cd and Se, suggesting a potential antagonistic relationship between the two. However, further validation in healthy living humans is needed. These findings highlight the potential benefits of Se supplementation in mitigating the harmful effects of Cd exposure.

While current research supports the promise of Se supply, most studies on its role in Cd mitigation, like those on Si, have been conducted under controlled conditions or in artificially contaminated soils. Consequently, additional research is needed to assess its effectiveness and to determine the optimal Se formulation, dosage, frequency and mode of action under practical farming conditions.

2.1.5. Fertilisers

Nitrogen (N) fertilization is known to significantly influence Cd uptake in crops, depending on various factors, including the N form, pH, soil buffering capacity, and initial Cd levels in the soil. N application in agriculture is a complex and multifaceted factor affecting Cd dynamics in soil-plant systems (Yang et al., 2020). Proposed mechanisms include N-driven changes in soil electrochemical potential, upregulation of NO-induced divalent cation transporters, influencing cell wall components and chelation, and influencing antioxidative systems (Yang et al., 2020). Understanding these interactions is essential for sustainable crop production and minimizing Cd contamination in food crops. In field conditions or pot experiments with arable soil, Cd uptake is often increased when ammonium-based (NH_4^+) fertilisers are used (Eriksson, 1990; Florijn et al., 1992; Gao et al., 2011). This is likely due to the pH reduction caused by NH_4^+ addition, which boosts Cd availability. In some cases, nitrate fertilisers can increase Cd uptake more than NH_4^+ fertilisers do, potentially due to the simultaneous introduction of Ca, displacing Cd ions and increasing their availability, particularly in higher pH soils (Grant and Bailey, 1998; Yang et al., 2020).

The chloride (Cl^-) content in soil and fertilisers influences Cd uptake in crops, but the impact varies depending on soil conditions, the timing of fertilisation, and crop type. Cl^- ions form soluble complexes with Cd, which are then taken up by plants similarly as Cd^{2+}. Studies have shown that Cl^- addition from soil-improving residual products as well as from fertilisation with NH_4Cl at sowing results in higher Cd levels in wheat kernels (Dahlin et al., 2016; Ishikawa et al., 2015). However, whether Cd uptake is lower or the same when fertilising with ammonium sulfate ($(NH_4)_2SO_4$) as with NH_4Cl remains unclear (Söderström and Eriksson, 2018).

The serious health and environmental risks posed by Cd metal and Cd oxide in phosphorus (P) fertilisers have been recognised by the EU. Regulation (EU) 2019/1009 has established a limit of 60 mg/kg P_2O_5 in P fertilizers, with a planned gradual reduction to 20 mg/kg P_2O_5 over 12 years. While inorganic P fertilization is a source of Cd contamination, P itself is shown to have a negative effect on Cd uptake and accumulation in rice with a 20–40 % decrease depending on the plant part (Zhao et al., 2023). As such, though beneficial, the source of the used P should be carefully considered.

2.2. Bioremediation

2.2.1. Phytoextraction and intercropping

Phytoextraction is one of the few methods of extracting Cd from polluted soils, outside of large-scale soil washing and replacement (which fall outside the scope of this review). Phytoextraction relies on species with high soil Cd uptake and accumulation into easily harvestable aboveground parts of the plant, the so-called hyperaccumulators. Many species, including *Brassica* species (Rizwan et al., 2018), *Salix* species (Dickinson and Pulford, 2005), and rice (Takahashi et al., 2021), have shown potential to be used for Cd phytoextraction. Phytoextraction with non-crop species, such as *Salix*, does not produce immediate value for the farmer and requires multiple years to achieve noticeable effects, making phytoextraction often economically unfeasible. Crop species, especially oilseed crops, such as oilseed rape (*Brassica napus*) and sunflower (*Helianthus annuus*) show potential as “producing” phytoextractors as Cd levels are usually low in the extracted oil (Rosca et al., 2021; Yang et al., 2017). In certain varieties of rice, such as YaHui2816, translocation of Cd from the leaf to the grain is limited (Guo et al., 2019). Cultivars with this kind of division of Cd content could be useful for production on Cd-polluted soils, producing clean grain while storing Cd in the straw, thereby removing bioavailable Cd from the paddy soil (Guo et al., 2019). However, the disposal of the Cd-contaminated biomass remains an issue, which requires the use of expensive and specialized methods (reviewed in Liu and Tran, 2021).

Intercropping various hyperaccumulator species with crops has shown promising results for reducing Cd accumulation in cereals. Wheat intercropped with the hyperaccumulator *Sedum plumbizincicola* resulted in a significant decrease in Cd content in the wheat with only minor losses in biomass (Zou et al., 2021). Intercropping rice with water spinach promoted growth and yield while lowering grain Cd content in rice (Kang et al., 2020). Intercropping with black nightshade (*Solanum nigrum*) decreased Cd uptake and accumulation with no negative effects on yield or biomass in maize (Huo et al., 2018) and rice (Yang et al., 2021a, 2021b). However, the presence of black nightshade increased Cd accumulation in wheat (Wang et al., 2020). Similar results with significant reductions in crop quality have been seen in other hyperaccumulator intercropping systems (Wu et al., 2020; Zou et al., 2021). Outside of potential effects on crop quality, intercropping is not directly compatible with industrialized farming. Furthermore, some of the most promising hyperaccumulators such as black nightshade are toxic. Hence, intercropping systems require innovations in harvesting and separation technologies to be a feasible strategy for lowering Cd accumulation in crops, and similarly for phytoextraction, since contaminated material requires specialised disposal methods.

2.2.2. Organic matter additives

A high amount of soluble organic matter resulting from e.g. fertilizing with sewage sludge or manure increases Cd bioavailability through the formation of organo-metallic complexes and, which in turn promotes Cd adsorption through co-adsorption with dissolved organic carbon (Adams et al., 2004; Almås and Singh, 2001). However, insoluble organic matter, such as biochar, decreases bioavailability mainly through the formation of insoluble complexes not available for root adsorption (Almås and Singh, 2001) and through increasing soil pH (Wei et al., 2023). The impact of increasing organic matter on Cd uptake by plants remains uncertain and should be assessed in future research.

A review of 21 studies using different types of biochar, soils, and crops, demonstrated an average 40 % decrease in Cd uptake following the addition of biochar to the soil (Natasha et al., 2022). However, the effect varied considerably among the different studies, with some even indicating a negative effect of biochar application (Lahori et al., 2017; Sigua et al., 2019). The achieved effect depends largely on the type of biochar applied as well as on the soil texture and initial Cd level in the soil. Effectiveness of biochar application has also been found to be dependent on the initial pH of the soil with application on acidic soils yielding better results than alkaline soils (Wei et al., 2023). In some cases, application of biochar on alkaline soils (pH > 7.5) has led to increases in bioavailable Cd (Meng et al., 2022). Aging biochar also loses its adsorption effectiveness over the years, slowly releasing Cd back into the soil. However, since biochar also increases soil pH, the Cd released during biochar degradation may remain biologically unavailable due to this pH increase (Meng et al., 2022; Cui et al., 2021). Therefore, the potential benefits of biochar application are still unclear, and further research is needed on various soil types and biochar formulations, as well as on other possible effects, such as impact on yield. Current reports suggest that achieving the desired effect may require around 20 tons of biochar per hectare. Given the high cost of biochar (Söderkvist et al., 2021), this method may be less attractive.

2.2.3. Rhizobiome inoculations

The composition and structure of the microbial communities of the rhizosphere affect the bioavailability and the efficiency of the uptake of specific nutrients and non-nutrients, including Cd (Li et al., 2019; Sheng and Xia, 2006; Zheng et al., 2022). Rhizobacterial inoculations have the potential to adjust Cd bioavailability and uptake and have been an expanding field of study in recent years (summarized in Shahid et al., 2018; Shi et al., 2024). Alkalizing bacterial strains (*Bacillus altitudinis*) reduced Cd accumulation in the edible parts of *Brassica rapa* (Zhang et al., 2021a, 2021b), while *Pseudomonas* TCd-1 strain inoculation led to similar results through increases in pH and various enzyme activities (Wang et al., 2021). The genus *Pseudomonas* has been the subject of many studies (Al-Dhabi et al., 2019; Cheng et al., 2021; Wu et al., 2020) for its bioremediation potential. Increasing bioavailability via bacterial inoculation is also possible, e.g. *Bacillus megaterium, Rhizobium radiobacter* and *Enterobacter sp.* have all been found to increase Cd uptake up to two-fold (Jeong et al., 2012; Shi et al., 2024). The understanding of the rhizosphere-plant interactions is currently limited, and introducing soil microbes to systems where they have not been previously present might result in unexpected effects not only on the crops themselves but also on the native plant, animal and microbe species. Hence, further research into rhizobiome-plant interactions is needed before extensive practical applications can be formulated, but the utilization of microbial inoculations shows significant promise.

3. Genetic strategies for lowering cadmium uptake and translocation to cereal grains

Root uptake and subsequent translocation of various important ions, such as Ca^{2+}, Mg^{2+}, Fe^{2+}, Zn^{2+}, Mn^{2+} and Cu^{2+}, is facilitated by low-specificity divalent cation transporters or channels in the plasma membrane and transporters into the vacuole (Ismael et al., 2019; Lux et al., 2011; Song et al., 2017). Plants take up Cd^{2+} using these pathways and are hence tangled with the uptake of necessary ions (Clemens, 2006). Once taken up in the root, Cd^{2+} ions are transported in the xylem to the shoot. The cation diffusion transporter gene family mediates the ion loading to the xylem, whereas phloem loading is channelled via low-affinity calcium transporters (Uraguchi et al., 2014). Studies of the Cd^{2+} transport from soils to grains, particularly in cereals, have been intense during the last ten years (Clemens and Ma, 2016; Ma et al., 2021a, 2012b).

As the plant facilitates Cd^{2+} uptake and transport itself, breeding for lower Cd accumulation is a feasible strategy. However, this may impose negative effects of essential metal ions needed in feed and food products, leading to complexity in utilizing traditional breeding methods, i.e. crossbreeding, to achieve this. Analysis of zinc-regulated, iron-regulated transporter-like proteins (ZIPs), a metal transport family involved in the uptake and allocation of metals like Zn^{2+}, Cu^{2+}, Cd^{2+}, Fe^{2+} and Mn^{2+} have demonstrated those limitations (Grotz et al., 1998; Milner et al., 2013; Vatansever et al., 2017). However, extensive research has produced numerous potential target genes for adjusting Cd distribution patterns in crops. Not all these target genes are as intimately entangled with the transport of other ions. Furthermore, novel breeding tools, such as genomic selection and gene editing, are opening new avenues of approach to these problems, allowing far more fine-tuned adjustment of crop genomes to limit grain Cd accumulation. In this chapter, we will present these strategies and discuss many of the breeding targets for lowering Cd uptake and grain accumulation in cereals (Table 2).

Table 2
Genetic strategies for lowering cadmium (Cd) uptake and translocation to cereal grains, their underlying mechanisms, and potential for practical application, as reviewed in Chapter 3. Images are created using Canva (www.canva.com).

Section	Strategy		Mechanism	Potential
3.1	**Crossbreeding**		Traditional crossbreeding leverages natural genetic variation by selecting and combining low-Cd-accumulating parent lines to create offspring with reduced Cd uptake and translocation through recombination and selection over multiple generations.	The potential is large since the trait is highly heritable. Crossbreeding can be significantly accelerated with molecular markers and genomic selection, enabling more efficient identification and selection of low-Cd-accumulating genotypes while maintaining agronomic performance.
3.2	**Transgenics and genome editing**		These approaches directly modify or introduce genes regulating Cd transport, uptake, or sequestration, enabling precise control over Cd accumulation pathways in the plant.	Genome editing and transgenics offer precise and efficient methods to reduce Cd accumulation in cereals by directly modifying key genes involved in uptake and translocation. While transgenic approaches remain strictly regulated worldwide, genome editing is increasingly accepted and has a great potential for rapid trait improvement.

3.1. Crossbreeding

Understanding the genetic differences underlying Cd uptake and translocation mechanisms is important for plant breeding. Genetically determined variation in Cd accumulation has been reported in various crops, including wheat (Hussain et al., 2012; Lan et al., 2024). This variation enables the utilization of plant breeding methods such as genome-wide association studies (GWAS), which can be used to uncover markers associated with Cd-related traits. Functional studies of the marker-linked genes and the proteins they encode can then be used to identify and confirm candidate genes for selection or genome editing. Molecular markers identified through GWAS can also be directly utilized for parental selection, genetic diversity analysis, linkage drag reduction and genomics-assisted breeding. Additionally, marker-assisted selection (Collard and Mackill, 2007) and genomic selection (Meuwissen et al., 2001) are important selection support systems in plant breeding, providing a faster and more efficient approach to estimate Cd accumulation phenotypes of an individual compared to traditional laboratory-based biochemical evaluation of cereals (Kondic-Spika et al., 2023).

The availability of whole-genome reference sequences and pan-genome sequencing data has the potential to accelerate gene discovery and facilitate marker-assisted selection. Molecular tools such as Kompetitive Allele Specific PCR (KASP) markers contribute to genotype identification and marker-assisted selection as well as marker-assisted backcrossing for selecting genotypes with low Cd accumulation in edible plant parts. Several studies have identified quantitative trait loci (QTL) associated with low grain Cd accumulation in cereals, for which KASP markers could be developed (Table 3). Furthermore, research in wheat, barley, maize, and durum wheat shows a high broad-sense heritability (H^2) of Cd accumulation (Table 3), suggesting strong genetic control and excellent breeding prospects for developing low-Cd cultivars.

The number of publications concerning genomic prediction of Cd accumulation in cereals is still limited but has been reported in maize (Yan et al., 2023), wheat (El-Soda and Aljabri, 2022) and rice (Muvunyi et al., 2022). Since Cd accumulation in plants is influenced by environmental factors such as soil Cd levels, cultivation practices, and abiotic conditions, the development of robust molecular tools and genomic prediction models require multi-location and multi-year trials under diverse regimes to account for the many factors affecting Cd uptake. New soil mapping technologies, discussed in chapter 4, enable precise control of within- and between- field variations, such as soil Cd levels, pH, and soil texture, down to the plot level. At the same time, it is crucial to monitor micronutrient levels to avoid unintentional selection of genotypes with both low Cd and reduced micronutrient levels.

3.2. Transgenics and genome editing

Transgene technologies and genome editing allow for novel strategies for lowering Cd accumulation in edible parts. However, these strategies are currently difficult to implement due to regulatory challenges and low public acceptance of genetically modified organisms

Table 3
Regions associated with cadmium (Cd) accumulation in cereals.

Species	Population	Marker system	QTL/Gene	Chromosome	H^2	Plant part	Reference
Hordeum vulgare	AM	Barley oligonucleotide pooled assay 1	15 QTL	2 H, 3 H, 4 H, 5 H, 7 H	0.7	Grain	(Wu et al., 2015)
	BP	Barley oligonucleotide pooled assay 1	2 QTL (Sukkula-like TE)	5 H	NA	Grain	(Lei et al., 2020)
	DH	SNP	*HvPAA1*	7 H	NA	Shoot	(Wang et al., 2019)
Triticum aestivum	AM	90 K iSelect	5 SNPs	5AL	0.8	Grain	(Guttieri et al., 2015)
	AM	90 K iSelect	2 QTLs	2 A and 2B	NA	Grain	(Hussain et al., 2020)
	AM	90 K iSelect	5 SNPs	1 A and 1D	NA	Grain	(Safdar et al., 2020)
	DH	90 K iSelect	10 QTL	2 A, 2D, 4B, 4D, 5B, 5D, 6 A, 7B, 7D	0.7	Grain	(Qiao et al., 2021)
	DH / Cultivars	SNP, SSR	2 QTL	4B, 6B	NA	Grain	(Ban et al., 2020)
	RIL	SSR, EST-SSR, ISSR, SRAP, TRAP, Glu	2 QTL	4 A, 5D	NA	Root	(Ci et al., 2011)
Triticum durum	BP	Microsatellite, SSR, DArT®	*Cdu1*	5BL	NA	Grain	(Knox et al., 2009)
	DH	Expressed sequence markers	2 QTL (including *Cdu1*)	5BL	NA	Grain	(Wiebe et al., 2010)
	RIL	9 K iSelect, SSR	2 QTL, 7 SNPs	2B, 5BL	NA	Grain	(AbuHammad et al., 2016)
	RIL	90 K iSelect, KASP	1 QTL	5BL	0.8	Grain	(Oladzad-Abbasabadi et al., 2018)
Zea mays	AM	SNP	191 SNPs	2	0.8	Grain	(Baseggio et al., 2021)
	AM	Maize SNP50, RNA seq	73, 67, 55, 95, 117, 87, 103 QTL in different trials	1, 2 (major QTL), 3, 4, 5, 6, 7, 9, 10	0.7	Grain	(Tang et al., 2021)
	AM	Maize SNP50	63 SNPs	1, 2, 4, 5, 7, 8, 9	0.6–0.8	Leaf	(Zhao et al., 2018)
	AM	GBS-SNP	65 SNPs	1, 2 (major QTL), 3, 4, 5, 6, 7, 8, 9, 10	0.9–1.0	Grain	(Zhao et al., 2022)
	DH, AM	Composite interval mapping	5 QTL	2, 5, 7, 8, 9	0.6–0.8	Leaf	(Zhao et al., 2018)
	RIL	RFLP, SSR	1 QTL	2	0.8	Grain, leaf	(Zdunić et al., 2014)
Avena sativa	BP	RAPD, REMAP, SRAP	2 RAPDs, 1 REMAP, 1 SRAP / 1 QTL	-	NA	Grain	(Tanhuanpää et al., 2007)
Oryza sativa	AM	SSR	3 QTL	3, 5	NA	Grain	(Huang et al., 2015)
	AM / NIL	SNP, SSR	12 QTL	2, 3, 4, 6, 10	NA		(Yan et al., 2019)
	BIL	SSR	1 QTL	7	NA	Various above-ground parts	(Abe et al., 2011)
	BIL	RFLP, SSR	2 QTL	2, 7	0.8	Grain	(Ishikawa et al., 2010)
	BIL / NIL	RFLP	3 QTL	4, 11	NA	Various above-ground parts	(Kashiwagi et al., 2009)
	CSSL	RFLP	3 QTL	3, 6, 8	NA	Grain	(Ishikawa et al., 2005)
	DH	RFLP, SSR	3 QTL	3, 4, 6	NA	Grain and straw	(Zhang et al., 2011)
	RIL	CAPS, SSR	2 QTL	3, 11	NA	Grain	(Sato et al., 2011)
	RIL	SSR	5 QTL	3, 5, 9, 10, 11	NA	Grain	(Yan et al., 2013)
	RIL / CSSL	SNP, InDel	3 QTL	3, 5, 7	NA	Grain	(Liu et al., 2020a, 2020b)
Synthetic wheat	AM	SNP	5 SNPs	1 A, 2 A, 2D, 3 A, and 6D	0.3	Grain	(Bhatta et al., 2018)

Abbreviations: AM, association mapping panel; BP, Bi-parental lines; CSSL, chromosome segment substitution lines; DH, Doubled haploid lines; RIL, recombinant inbred lines; NIL, near isogenic lines; BIL, Backcross inbred lines, H^2, broad-sense heritability.

Table 4
Altered transcription levels of genes associated with cadmium (Cd) transport in cereals and their close relatives.

Plant species	Locus/gene	Approach	Observation	Reference
Aegilops markgrafii /Triticum aestivum	*AemNAC2, AemNAC3*	OE	Decreased Cd concentration in the root, shoot and grain	(Du et al., 2020)
Aegilops tauschii	*AetSRG1*	OE	OE reduced Cd accumulation	(Wei et al., 2022)
Oryza sativa	*OsPCS1, OsABCC1, OsHMA3*	Co-overexpression	Low-As and low-Cd lines were obtained	(Gui *et al.*, 2024)
	OsLCD	KO	Reduced Cd accumulation	(Chen et al., 2023)
	OsMYB45	KO	Decreased Cd tolerance	(Hu et al., 2017)
	OsHMA2	KO	Decreased translocation of Cd and Zn	(Satoh-Nagasawa et al., 2012)
	OsPCS1	KO	Reduced Cd accumulation	(Uraguchi et al., 2017)
	DEP1	OE	Increased Cd tolerance and accumulation	(Kunihiro et al., 2013)
	OsCDT1	OE	Increased Cd tolerance, decreased Cd accumulation	(Kuramata et al., 2009)
	OsIRT	OE	Increased Cd accumulation in shoots and roots	(Lee and An, 2009)
	OsHIR1	OE	Decreased Cd accumulation in shoots and roots, increased Cd tolerance	(Lim et al., 2014)
	OsHMA2	OE	Decreased Cd concentrations in leaves and grain	(Takahashi et al., 2012)
	OsHIPP16	OE, KO	OE decreased Cd accumulation, KO increased Cd accumulation	(Cao et al. 2022)
	TaHsfA4a/OsHsfA4a	OE, KO	OE increased Cd tolerance KO decreased Cd tolerance	(Shim et al., 2009)
	OsZIP1	OE, RNAi	*OsZIP1* is required for detoxification of Cd	(Liu et al., 2019)
	OsGSTZ4	OE, RNAi	OE improved plant growth, attenuated Cd-induced toxicity, and accumulated more Cd in roots. RNAi led to only minor negative changes in growth.	(Liu et al., 2024a, 2024b)
	OsMT1e	OE, RNAi	OE increased root and shoot Cd accumulation, decreased Cd sensitivity RNAi decreased Cd accumulation and increased Cd sensitivity	(Rono et al., 2021)
	OsHMA3	Promoter swap	Reduced grain Cd	(Shao et al., 2018)
	OsPDR20	RNAi	RNAi, led to Cd accumulation in tissues, decreased Cd tolerance.	(Li et al., 2024)
	OsMTP1	RNAi	Decreased Cd accumulation levels in leaves, stems and grain. Increased levels of Cd in roots. Decreased heavy metal tolerance.	(Yuan et al., 2012)
	OsNRAMP1	sgRNA	Decreased root uptake of Cd, and Cd accumulation in rice shoots and grains	(Chang et al., 2020)
	FC19 /OsLRX10	sgRNA	Altered Cd metabolism and cell wall synthesis led to reduced Cd accumulation	(Dang et al., 2023)
	OsABCG36	sgRNA	Decreased Cd tolerance, increased Cd concentration in root cell sap	(Fu et al., 2019)
	OsCCX2	sgRNA	Reduced grain Cd	(Hao et al., 2018)
	OsNramp5 *OsLsi2*	sgRNA	Hybrid breeding using novel alleles of *OsNramp5* and *OsLsi2* resulting in ultra-low heavy metal accumulation	(Hu et al., 2024)
	CF1/allelic to OsYSL2	sgRNA	*CF1* down regulation reduces grain Cd accumulation, and increases grain-Fe, the latter via suppressed *OsNRAMP5*	(Li et al., 2022)
	OsPMEI12	sgRNA	Increased Cd accumulation	(Li et al., 2022)
	OsLCT1, OsNRAMP5	sgRNAs	Reduced grain Cd, *OsLCT1* mutation led to normal growth and reduced grain Cd	(Songmei et al., 2019)
	OsZIP7	sgRNA	Retention of Zn and Cd in roots and nodes decreased upward mobility	(Tan et al., 2019)
	OsNRAMP5	sgRNA	Reduced grain Cd	(L. Tang et al., 2017)
	OsCd1	sgRNA	Decreased Cd accumulation in root, shoot, and grain	(Yan et al., 2019)
Triticum aestivum	*WRKY74*	KO	Decreased Cd tolerance, increased Cd accumulation	(Li et al., 2022)
	OsHMA3	OE	Decreased root-to-shoot Cd translocation in wheat, deceased grain Cd	(Zhang et al., 2020)
	TaPUB1	OE, RNAi	OE reduced Cd uptake and accumulation and increased tolerance RNAi increased Cd accumulation	(Zhang et al., 2021)
Triticum polonicum	*TpNRAMP5*	OE	Increased Cd concentration in roots, shoots, and whole plants	(Peng et al., 2018)
Zea mays	*ZmWRKY4*	RNAi, OE	Expression of antioxidant enzymes downregulated in RNAi Expression and activity of antioxidant enzymes upregulated by overexpression	(Hong et al., 2017)

Abbreviations: As, arsenic; OE, overexpression; KO, knockout; sgRNA, single guide RNA; RNAi, RNA interference; TF, transcription factor.

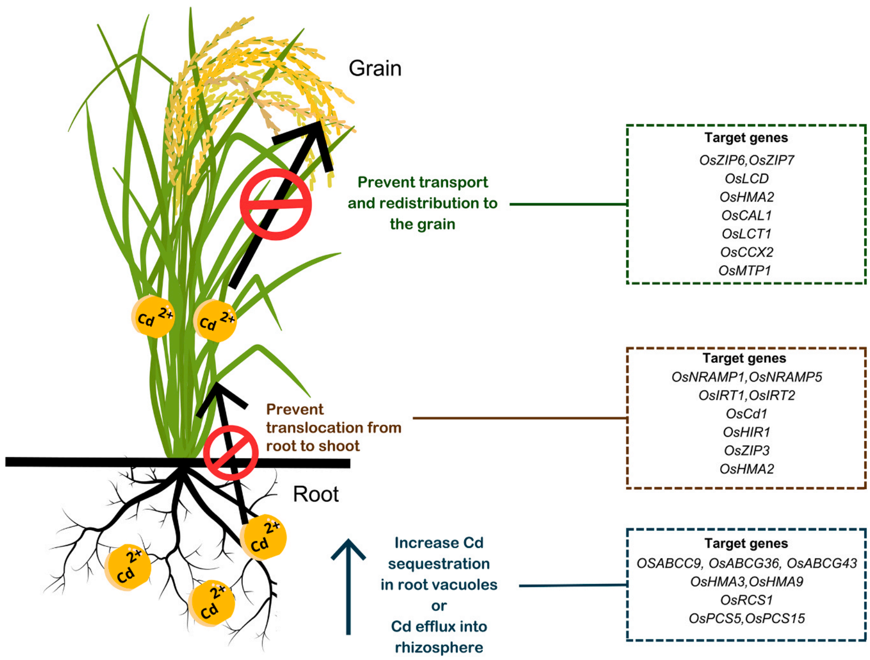


Fig. 2. Schematic representation of a rice plant and genes involved in cadmium (Cd) root uptake, sequestration in the roots, translocation from root to shoot and from shoot to grain, respectively. These genes represent potential targets for breeding or genome editing strategies aimed at minimizing Cd accumulation in cereal grains and are discussed in chapter 3.3. Image created using Canva (www.canva.com).

(GMOs) in parts of the world. Europe has some of the strictest regulations on genomic editing and GMOs, along with some of the lowest public acceptance levels globally (Ewa et al., 2022; Kato-Nitta et al., 2023; Sprink et al., 2022). However, a recent scientific opinion requested by the European Parliament concluded that easing regulations on certain crops is scientifically justified (EFSA Panel on Genetically Modified Organisms 2024). Genome editing technologies have recently unlocked new opportunities for precise gene modification (Debernardi et al., 2020; Molla et al., 2021; Wada et al., 2020). At their core, these technologies mimic spontaneous or induced mutations in a targeted manner. Advances in genome editing allow for precise control over genetic modifications, including changes in gene expression levels, protein properties and substrate specificities (Anzalone et al., 2020). Modifications of Cd-associated genes, transcription factors and their effects are summarized in Table 4.

Rice is highly amenable to tissue culture techniques, explaining the high number of publications on genome editing, including down-regulation of Cd-related genes (Li et al., 2022; Lin et al., 2020). Other important cereals have larger and more complex genomes, and transgenic-related methods are slowly gaining momentum, including gene editing technologies. With a growing understanding of gene regulation and continuous advancements in genome editing technologies, further breakthroughs are expected soon (Buchholzer and Frommer, 2023).

3.3. Candidate target genes for selection or editing in cereals

Much of the current knowledge on Cd uptake, translocation and accumulation derives from rice research but is likely applicable to other crops. The main root Cd transporters in rice are *OsNRAMP5*, *OsNRAMP1*, *OsCd1*, *OsZIP3*, *OsHIR1*, *OsIRT1* and *OsIRT2*, whereas *OsZIP6*, *OsZIP7*, *OsLCD*, *OsHMA2*, *OsCAL1*, *OsCCX2*, *OsLCT1* and *OsMTP1* mediate the long-distance transport (Zhang et al., 2022). Orthologues of these genes present promising targets in other species (Table 4, Fig. 2).

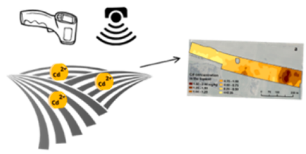
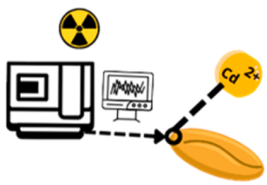
Until now, most interest has been directed towards *OsNRAMP5* and *OsLCT1* orthologues as target genes for breeding. Both are transporters of other divalent cations, but are associated with Cd transport due to low transport specificity. *NRAMP5* has been downregulated or knocked out using RNA interference (RNAi) and CRISPR-Cas9 with conflicting effects on Cd uptake and plant growth (Ishimaru et al., 2012; Sasaki et al., 2012). The RNAi results showed a decrease as well as an increase in Cd uptake, and both studies reported a decrease in Mn levels. *OsLCT1* has been targeted in rice with CRISPR-Cas9 mutagenesis in parallel with *OsNRAMP5* mutations (Songmei et al., 2019). Mutations in *OsNRAMP5* resulted in lower grain Cd levels than mutations in *OsLCT1*. In another combinatorial study, CRISPR-Cas9 mutation of *OsLCD* was found to have benefits compared to *OsNRAMP5* loss of function in that *OsLCD* did not affect the uptake of essential elements as did *OsNRAMP5* (Table 4) (Chen et al., 2023). Another overexpression target could be *OsCF1*, where specific naturally occurring alleles have been found to decrease Cd uptake while improving Fe uptake (Li et al., 2022). The plasma membrane transporter *OsNRAMP1*, upon mutagenesis with CRISPR-Cas9, yielded a smaller effect on Cd uptake than *OsNRAMP5*, with additive effects if both were knocked out (Chang et al., 2020). *OsCF1* is a Fe transporter with no affinity for Cd. However, increased expression of *OsCF1* induced by Fe concentration suppresses *OsNRAMP5* expression, resulting in reduced Cd accumulation. *OsHMA3* facilitates the translocation of Cd into the root vacuoles. Utilizing regular transgene technology, *OsHMA3* was overexpressed in rice, resulting in increased root vacuole levels of Cd with a decrease in grain levels (Shao et al., 2018).

4. Strategies to improve understanding of the spatial cadmium distribution in soil and cereals

Understanding the spatial distribution of Cd in agricultural soils is critical for managing and decreasing its accumulation in cereal grains. Since Cd levels remain relatively stable over time, mapping a field’s Cd profile can be one of the strategies, which could provide long-term value for farmers, guiding crop selection and management practices. Current advances in geospatial analysis, digital soil mapping and predictive modelling offer powerful tools to estimate and visualize Cd concentrations at varying scales.

Equally important is understanding how Cd moves within plants, particularly into cereal grains. Emerging imaging and spectroscopy

Table 5
Strategies to understand the spatial cadmium (Cd) distribution in soil and plant, their underlying mechanisms, and potential for practical application, as reviewed in Chapter 4. Images are created using Canva (www.canva.com).

Section	Strategy		Mechanism	Potential
4.1	**Digital soil mapping**		Combines geostatistical models, machine learning, and multiple covariates (e.g., gamma-ray data, elevation, soil texture) to estimate and visualize Cd concentrations in agricultural soils.	Provides high-resolution maps for guiding crop selection and management; cost-effective alternative to traditional soil analysis; useful for large-scale assessments.
4.2	**Mapping Cd distribution in plants**		Uses advanced imaging (e.g., synchrotron micro-X-ray fluorescence, neutron-computed tomography, LA-ICP-MS) to track Cd uptake, translocation, and accumulation in plant tissues, e.g., cereal grains.	Provides insights into Cd distribution at the tissue and cellular level; helps identify mechanisms of Cd sequestration and transport. Can support breeding for reduced Cd accumulation in edible plant parts.

techniques have revealed key insights into the mechanisms of Cd uptake, translocation, and compartmentalization in grain tissues. This knowledge is essential for breeding future cereal cultivars with reduced Cd accumulation, ensuring safer food production. By integrating soil mapping with physiological studies, targeted breeding strategies and agronomic solutions can be developed to mitigate Cd contamination in cereals. Strategies to understand the spatial cadmium distribution in soil and plants are presented here (Table 5).

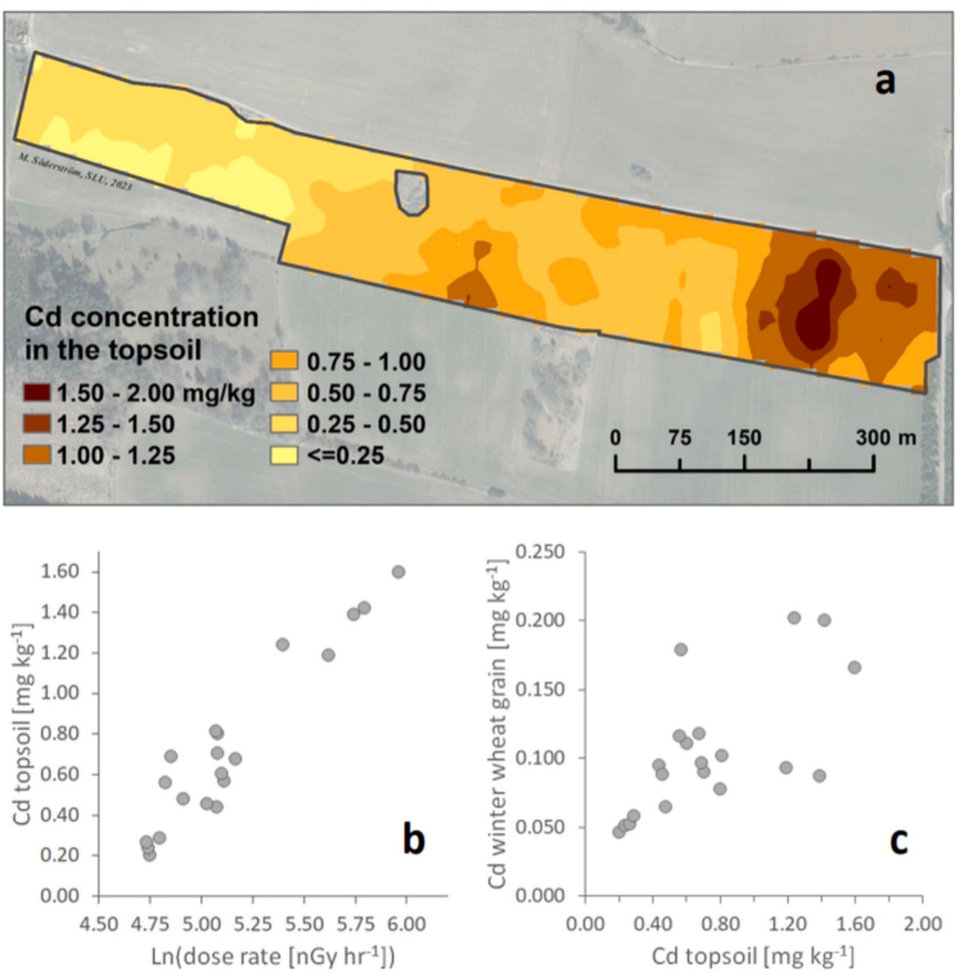


Fig. 3. Example of spatial variation of Cd in the topsoil in a 15-ha agricultural field (a). In this case, the variation and the relatively high Cd concentration are mainly caused by fragments of Cd-rich black shale from the soil parent material. The mapping was done by scanning with a gamma-ray spectrometer. Locally, there is a strong relationship (R^2=0.90) between the total gamma-ray counts (dose rate) and Cd measured in the topsoil (b). Nevertheless, topsoil Cd does only partly explain (R^2=0.45) the Cd concentration in wheat grown in this field (c). Data from Söderström & Eriksson (2018).

4.1. Digital soil mapping

There are several ways of estimating the Cd concentration in soil using either data from sensors or information from soil samples, often in combination with statistical modelling. Estimating Cd concentration spatially in soil has been done using geostatistical methods, *e.g.* different types of kriging (Birke et al., 2017; Cao et al., 2017; Lado et al., 2008), and using machine learning methods (Adler et al., 2023; Qiu et al., 2016). The preferred method can vary depending on the data available and the reasons behind the spatial variation (Agyeman et al., 2021). The best approach for mapping Cd concentration in the soil may differ depending on whether the concentration is mainly due to geogenic factors or anthropogenic activities, such as industrial pollution or the application of Cd-rich sewage sludge or fertilisers (Söderström and Eriksson, 2013).

Estimation of Cd concentrations can be done locally at a point location or on the go on the field scale. For example, research has shown that portable X-ray fluorescence measurements of other elements, such as iron (Fe), calcium (Ca), and zinc (Zn), can also be used to estimate Cd concentrations. This approach works most efficiently on sieved, homogenized, and dried soil samples (Adler et al., 2020), but in principle, measurements can also be done *in situ*. Cd concentrations in soil are normally too low to be measured directly with currently available portable X-ray fluorescence instruments. However, recently reported improvements in the level of detection of such instruments suggest that direct measurements may be possible (Dekeyrel et al., 2024).

Gamma-ray measurements of the naturally occurring radionuclides uranium-238 (^{238}U), thorium-232 (^{232}Th) and potassium-40 (^{40}K) provide, in addition to measurements of radioactive pollution, also information on the parent material of the soil and its texture (IAEA, 2003). Soil clay content is often positively correlated with total Cd concentrations in soil (Zhao et al., 2007), and it has been shown that data from gamma-ray measurements often are very well correlated to soil clay content (Piikki et al., 2015). Thereby, radioelement mapping can be useful as a co-variable for soil Cd predictions, but since there are several different properties that may influence concentrations of the different isotopes, local calibrations are recommended (Adler et al., 2023; van der Graaf et al., 2007). Cd concentrations are generally higher in sedimentary rocks, and in turn, in soils influenced by these rocks (Kubier et al., 2019). For example, in certain conditions, black shales have high Cd concentrations and similarly high U content (Alloway, 1990; Rosenbaum and Söderström, 1996), the latter being measurable using gamma-ray spectrometry. Hence, gamma-ray measurements of ^{238}U have been useful for locating areas of high Cd concentration in the topsoil in arable land in Sweden, both on a field level and a larger scale (Fig. 3) (Adler et al., 2023; Söderström and Eriksson, 2013).

Digital soil mapping (McBratney et al., 2003) and predictive soil mapping (Scull et al., 2003) combine multiple covariate map layers with soil property data from soil samples. Covariates such as gamma radiation data, elevation and soil texture classes have been used to map total soil Cd concentration using machine-learning models (Adler et al., 2023; Ballabio et al., 2024). It has been shown that true and estimated soil Cd concentrations were highly correlated with Cd concentrations in winter wheat grain (Adler et al., 2023; Strawn et al., 2022). Additionally, a range of environmental and soil conditions affect Cd uptake (Eriksson and Söderström, 1996; Smolders and Mertens, 2013). To develop digital soil mapping methods that could be used to predict Cd accumulation with high precision would require a larger calibration data set than earlier reported as well as multi-year and multi-location trials and data on relevant soil variables. It would also be important to include several cultivars in such an attempt since it is known that the heritable effect is a significant factor influencing Cd accumulation in plants. Nevertheless, digital soil mapping can provide high-resolution maps faster and to a much lower cost compared to traditional chemical mineral analysis. Such maps would offer great value for both advisors and farmers, guiding them on whether a field is suitable e.g. for growing wheat intended for baby food production.

4.2. Mapping cadmium distribution in plants

Latest advances in imaging techniques, such as synchrotron micro-X-ray fluorescence and non-invasive neutron computed tomography (NTC), are important tools that have the potential to provide information on the distribution of Cd and other elements such as arsenic (As), Fe, Cu, Mn, lead (Pb), nickel (Ni) and Zn in plant parts. However, the studies that have been performed on Cd distribution in cereals, mainly in roots and grains of bread wheat and maize, are still quite few (Clemens and Ma, 2016; Van Malderen et al., 2017; Imran et al., 2017). Interestingly, micro-X-ray fluorescence revealed no differences in Cd uptake between a high and a low Cd cultivar (Tefera et al., 2020). However, different Cd retaining mechanisms were found in the high vs. low Cd cultivar, providing more clarity on the uptake. The observed mechanism was related to the inability to sequester Cd into roots which further resulted in inefficient transport to the shoots and overall lower Cd in the grain, a transport mechanism related to genes *OsHMA3* and *OsHMA2* (Tefera et al., 2020).

Laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) may also be used to identify and quantify microelements in various seeds (Van Malderen et al., 2017). However, this is more difficult to do with Cd (Yan *et al.*, 2017) as Cd is often present in low concentrations across the plant, which limits its detection and quantification. A combined approach of micro-X-ray absorption near-edge spectroscopy (Yan et al., 2020), combining dissection and quantitative assessment of the distribution of Cd among grain tissues could be explored and used to obtain phenotypic data. With this approach, it was possible to highlight specific areas with high accumulation of Cd (alone and with other elements like molybdenum (Mo) and Cu, like the crease and endosperm in wheat (Yan et al., 2020). Since Cd is accumulated mostly in the pigment strand and forms associations with sulphur (S) ligands, it was possible to obtain high-resolution maps, which can be further used to identify QTL. However, a thorough identification screening is needed to determine Cd loading in the grain, which seems to be rather restricted (Liu et al., 2003; Liu et al., 2017; Yan et al., 2020).

5. Limitations and future directions

While many of the methods presented in this review are theoretically feasible, not all are currently suitable for practical application in modern farming. Different farming systems have their own requirements. For example, post-green revolution agriculture relies on large fields, monocultures, and specialized equipment – hereafter referred to as industrial farming. Furthermore, farmers, including those using industrial farming methods, often lack the financial capacity to absorb excessive additional costs or revenue losses, particularly in less developed regions of the world.

Given the realities of modern agriculture, the most effective and widely applicable strategies for reducing Cd in crops must meet three main criteria:

1. Compatibility with most common farming systems
2. Low cost of application
3. No negative impact on field productivity

Below section evaluates the practical applicability of the previously discussed methods, assessing their feasibility and suggesting future directions for improvement.

5.1. Bioavailability and soil conditioning

Most abiotic soil additives, regardless of type, generally align with the first and third criteria but often fail to meet the second criteria, as their application can incur costs with often limited or inconsistent benefits. The long-term effectiveness of many of these additives remains poorly understood, and the potential need for repeated applications could rapidly escalate costs and benefits for field productivity in contaminated soils. Among the abiotic soil amendment strategies examined, Si application appears to be the most reliable, offering application costs and benefits for field productivity in contaminated soils. Additionally, Se application shows considerable promise, not only for its potential role in reducing Cd accumulation but also for its additional health benefits. However, due to the incomplete understanding of its mechanisms in reducing Cd accumulation, further research is needed to validate its feasibility.

5.2. Bioremediation

The use of hyperaccumulators, whether in monoculture or intercropping systems, generally does not meet any of the three criteria. However, intercropping may hold potential in alternative cropping systems, such as agroforestry. Hyperaccumulators like the rice variety YaHui2816, combined with biochar production, offer a promising strategy to reduce soil Cd levels. Straw from such cultivars could be converted into biochar and returned to the soil to further limit Cd bioavailability. While challenges remain, including high costs, regulations and potential toxicity of the biochar, advances in pyrolysis or Cd extraction could enhance the feasibility of this approach in the future.

Inoculations of crops with bacterial strains known to alter bioavailability and uptake of Cd appear to meet all three key criteria for effective Cd reduction. Moreover, different bacterial strains can have varying effects on Cd uptake and accumulation, offering flexibility for reducing crop uptake as well as enhancing bioremediation in hyperaccumulators. However, our understanding of the broader ecological effects of bacterial inoculations is limited. Research is needed to assess their impact on native microbial communities in agricultural soils, as well as in surrounding ecosystems, including adjacent lands and water bodies. Additionally, identifying and utilizing locally adapted bacterial strains could mitigate potential ecological disruptions caused by introducing non-native microbes. Further studies are also necessary to investigate the effects of bacterial inoculations on the uptake of other contaminants and essential nutrients.

5.3. Crossbreeding

Breeding approaches represent the most traditional, straightforward and widely applicable strategy, meeting all three criteria with ease. Farmers already purchase new cultivars regularly, meaning the adoption of Cd-efficient cultivars would not require systematic changes to farming practices or additional financial investment. However, a critical aspect is to ensure that a low grain Cd cultivar still maintains a high nutritional quality.

5.4. Transgenics and genome editing

Genome editing and GMOs offer promising avenues for accelerating breeding efforts, though strict regulatory frameworks currently restrict their application in some countries. As these technologies integrate with conventional breeding programs, there is no impact on farming systems. As these technologies bypass the need for multiple generations of crossing and selection, they have the potential to reduce both the cost and time required for cultivar development. These savings could ultimately translate into lower seed prices for farmers. Given these advantages, the regulatory restrictions on genome editing and GMOs should be critically evaluated, a process that is already underway in several countries and organisations.

5.5. Digital soil mapping

Soil mapping for Cd requires specialized equipment and expert knowledge, limiting its accessibility to individual farmers. In addition to the technical requirements of soil sampling, adjustments to predictive models are needed to improve accuracy, further emphasising the need for professional services. However, it is conceivable that companies already offering soil analysis services could expand their portfolios to include Cd-specific assessments. If widely available, soil Cd mapping could serve as a highly complementary tool to all other mitigation strategies discussed in this review. It would enable farmers to assess Cd levels in their fields more precisely, optimize crop rotations, and make informed decisions about the end use of their harvests. Moreover, it could significantly reduce the cost of soil amendments by allowing targeted application to localized problem areas rather than entire fields. Hence, soil Cd mapping holds substantial potential for improving Cd management in agriculture.

5.6. Mapping cadmium distribution in plants

In contrast, knowledge about the physical distribution of Cd within plants is of limited direct use to farmers but is critically important for advancing research on Cd uptake and accumulation. Understanding how Cd is distributed within plants, particularly in response to soil amendments, genetic modifications, or microbial treatments, could enhance our understanding of the underlying mechanisms governing Cd uptake, transport and accumulation. These insights could, in turn, facilitate the identification of novel regulators of Cd metabolism and improve breeding strategies. Additionally, high-resolution phenotypic data from such distribution studies could be leveraged in breeding programs, particularly for the development of hyperaccumulating cultivars akin to the rice cultivar YaHui2816, which could be utilized for bioremediation. Currently, this type of research remains underexplored, presenting opportunities for new discovery.

Based on the criteria we set and present knowledge, we consider breeding for low grain Cd cultivars using traditional techniques and the new gene technologies like genome editing as the most powerful approach available. Furthermore, we believe using digital and predictive soil Cd mapping will provide important information about the soil Cd distribution at farm level. Information that together with knowledge regarding present cultivars grain Cd levels can further inform the farmer regarding the choice of cultivar, field or e.g. soil amendments to use. Among the methods for soil conditioning reviewed here, and considering the criteria set, the most promising soil additives are silicon and selenium. In conclusion, lowering grain Cd levels in cereals will require an integrated approach that combines the strengths of various strategies and where ongoing research, technological advancements, and policy support will be essential to fully realize their potential and ensure safe, sustainable food production.

CRediT authorship contribution statement

Söderström Mats: Writing – review & editing, Writing – original draft, Visualization. **Lan Yuzhou:** Writing – review & editing, Writing – original draft. **Lilja Tua:** Writing – review & editing, Writing – original draft. **Johansson Eva:** Writing – review & editing, Writing – original draft. **Kuktaite Ramune:** Writing – review & editing, Writing – original draft. **Harari Florencia:** Writing – review & editing, Writing – original draft. **Hofvander Per:** Writing – review & editing, Writing – original draft. **Bengtsson Therése:** Writing – review & editing, Writing – original draft, Funding acquisition, Conceptualization. **Barregård Lars:**

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Declaration of Competing Interest

The authors declare no conflict of interest.

Data availability

Data sharing not applicable – no new data were generated.

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Glossary

ATSDR: Agency for Toxic Substances and Disease Registry
Body burden: The amount of a harmful substance in a person's body
CCX: Cation/Ca2+ exchanger
EFSA: European Food Safety Authority
EPA: Environmental Protection Agency
HMA: Heavy metal transporting ATPase
IRT: Iron-regulated Transporter
KASP: Kompetitive Allele Specific PCR
MTP: Metal tolerance protein
NRAMP: Natural resistance-associated macrophage protein
QTL: Quantitative trait locus
RNAi: RNA interference
ZIP: Zinc-regulated, iron-regulated transporter-like protein