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Review

Addressing Cadmium in Cacao Farmland: A Path to Safer, Sustainable Chocolate

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Abstract: Cacao cultivation is an important economic and social activity for tropical regions worldwide. Elevated cadmium (Cd) concentrations in soil and cacao beans have become a serious concern for producers and consumers, particularly following the implementation of stricter Cd limits for cacao products in the European Union since 2019. Cadmium is a potentially toxic element that can bioaccumulate in different plant tissues, raising concerns about the future of cacao exports and posing a significant threat to the food chain through consuming products with high Cd concentrations. Therefore, understanding the origins of Cd in cacao-producing countries' agricultural soils is essential. Equally important is the need to investigate the factors influencing its availability, uptake, translocation, and distribution within the cacao plant, in addition to strategies for mitigating its effects or reducing its concentration in agriculturally relevant tissues. This review aims to contextualize the sources of Cd in the cacao agroecosystems while highlighting recent advances and perspectives in applying essential and beneficial elements, selecting low-accumulator genotypes, and utilizing associated microbiota. These strategies seek to mitigate Cd bioaccumulation and minimize its negative impacts on the cocoa value chain.

Keywords: food safety; *Theobroma cacao*; trace element; cadmium bioavailability; mitigation strategies

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1. Introduction

Cadmium (Cd) is a potentially toxic element with well-documented harmful effects on plants, animals, and humans. This element has no known biological function in living systems [1] and poses a significant risk to human health due to its low excretion rate through metabolism, which leads to its accumulation in tissues. Cadmium contamination can impair the immune system, reduce sperm motility, cause organ degeneration, and trigger hormonal changes in the ovaries [1,2].

An emblematic case was recorded in 1968, with Itai-Itai disease (osteomalacia or bone disease) caused by the prolonged ingestion of Cd-contaminated rice in Japan. Later studies also identified high Cd levels in the blood of workers exposed to battery manufacturing environments [3]. To mitigate risks, the FAO/WHO established a tolerable monthly intake of Cd at 25 μg kg^{-1} of body weight, along with maximum allowable limits for Cd in foods [4].

Cadmium enters agroecosystems through natural sources such as forest fires, wastewater, volcanic eruptions, and the weathering of rocks—particularly sedimentary rocks with high Cd concentrations [5]. Anthropogenic activities, including industrial processes, metallurgy, mining, combustion emissions, excessive pesticide use, and phosphate fertilization, also contribute significantly to Cd contamination [6–8]. In many cases, Cd concentrations in soil are closely related to the composition of the parent material [9]. For example, cacao plantations in Latin America have reported Cd levels up to seven times more than those in other regions, suggesting that some soils may naturally contain high Cd levels. However, the interaction between anthropogenic inputs and interactions between natural and human-driven sources cannot be ruled out [10].

Cacao *(Theobroma cacao* L.) is of great economic and social importance for millions of farmers in tropical regions and consumers worldwide [11]. A member of the Malvaceae family, cacao is a cauliflorous tree that produces large pods containing 20 to 60 seeds embedded in a dense pulp [12]. Cacao trees are commonly found in tropical forests with their center of origin in the upper Amazon region of northwestern South America. There is remarkable genetic diversity in Peru, Ecuador, Brazil, and Colombia [13–15].

Cacao-producing regions in Latin America face significant challenges related to high levels of potentially toxic elements, such as cadmium and lead in soils and, consequently, in cacao beans [16]. Cadmium enters the food chain when it accumulates in cacao beans, with reported concentrations ranging from 0.02 mg kg^{-1} DW in Ghana to above 10 mg kg^{-1} DW in Colombia [17–19]. Although there are no official limits for Cd in cacao beans, unofficially, industry guidelines often consider a range of 0.50 and 1.10 mg kg^{-1} DW [10,20]. For peeled cacao beans, maximum safe levels of 0.6 and 0.8 mg kg^{-1} FW have been suggested. However, some buyers impose stricter limits, rejecting beans exceeding 0.1 or 0.3 mg kg^{-1} due to concerns about the total Cd concentration in the final product [17,20].

This issue poses a significant threat to small-scale producers, as high Cd concentrations in beans can affect exports [10,21]. For instance, in Peru, elevated Cd levels led to a 30% reduction in exports to Europe [22], and this can open the opportunity to expand the cacao export market for other countries, like Asia. While chocolate is often considered a luxury product, according to the European Food Safety Authority (EFSA), cocoa-based products contribute to 4.3% of the Cd entering the human food chain from plant-based sources [23]. Annual chocolate consumption ranges from 100 g $year^{-1}$ per capita in China to 8.8 kg $year^{-1}$ per capita in Switzerland [24].

To address this risk associated with Cd, the European Commission implemented Regulation (EU) No. 488/2014 in 2019, setting Cd limits in chocolate and cocoa powder at 0.10 and 0.80 mg Cd kg^{-1} dry matter, depending on the cacao content of the product [25]. While these regulations are essential for protecting consumer health, they raise concerns about the future of cacao production and exports in South America, where soils naturally contain higher Cd levels [26]. For example, a study by Barraza et al. [27] found that 53% of cacao bean samples from six provinces in Ecuador exceeded the threshold of 0.80 mg kg^{-1} DW. Similarly, Gramlich et al. [28] reported an average Cd concentration of 1.1 mg kg^{-1} DW in cacao beans from 55 farms in Honduras.

These regulations place additional pressure on small-scale farmers, who often rely on cacao as their primary source of income. Therefore, it is critical to identify the factors influencing Cd accumulation in cacao beans and implement effective mitigation strategies [29,30]. Although previous studies have addressed Cd contamination in cacao, surveys conducted in recent years have provided new data on Cd concentrations in cacao-producing regions of Latin America, including Honduras, Ecuador, Colombia, Peru, and Costa Rica [10,28,31–36].

Understanding the dynamics of Cd-rich soils is essential to guiding future investigations into potential mitigation strategies. Recent findings highlight promising approaches, such as the use of manganese and zinc, to reduce Cd uptake, exploring the role of calcium oxalate crystals, examining the relationship between Cd and other abiotic stress, and evaluating the potential of specific rootstock genotype combinations. This review does not aim to cover all aspects of Cd in cacao exhaustively but instead aims to consolidate recent data and discuss key advancements in mitigating Cd contamination in cacao products.

2. Cadmium Sources in Cacao Agroecosystems

Cacao thrives in humid tropical climates, requiring specific soil and climate conditions for optimal growth. These include fertile soils, with a minimum depth of 0.80 m, medium to clayey textures, and an average annual rainfall of 1500 mm [37]. The cacao tree tolerates a wide pH range, growing in soils with pH values between 4.50 and 7.49 in Costa Rica and 5.5 to 6.0 in Brazil, among other regions [36,37]. In Latin America, soils in certain cacao-producing regions contain naturally high cadmium (Cd) levels (Table 1). These soils are predominantly young and volcanic, with Cd concentrations reaching up to 27 mg Cd kg^{-1} in areas such as Santander, Colombia [32,38]. Contrastingly, uncontaminated soils generally contain Cd levels between 0.1 and 1.0 mg Cd kg^{-1}, with average concentrations estimated within the 0.1 and 0.3 mg Cd kg^{-1} range [39].

Cacao beans from Latin America often exhibit Cd concentrations up to seven times higher than beans from other regions [10]. For instance, South and Central America report average concentrations of 1.39 mg kg^{-1} and 0.54 mg kg^{-1}, respectively. In contrast, East and West Africa present averages of 0.51 mg kg^{-1} and 0.09 mg kg^{-1}, while Asia averages 0.33 mg kg^{-1} [16,17]. The elevated Cd levels in Latin American soils result from geogenic sources, such as the weathering of bedrock, alluvial sediment deposition, and volcanic activity, as well as from anthropogenic activities like fertilizer use, mining, and irrigation with Cd-contaminated water [10,31–33,38] (Figure 1).

Some researchers argue that geogenic sources predominantly explain the Cd presence in cacao soils, while others highlight the role of anthropogenic inputs [17,28]. In Peru, a study of 2051 data points from 1047 farms identified geology as the primary predictor of Cd in soils, with minimal contributions from fertilizers due to their limited use [33]. Argüello et al. [31] suggested a low geogenic influence on Cd content in cacao farms in Ecuador but noted that this input cannot be overlooked. Another Ecuadorian study investigated Cd concentrations in different soil layers and linked higher concentrations in topsoil to anthropogenic activities [40].

The cycling of Cd through litter decomposition also influences soil Cd dynamics. Cacao farms typically maintain a permanent litter layer composed of fallen leaves and pods, releasing Cd into the topsoil during decomposition [40–42]. Fine roots can reabsorb this Cd, creating a secondary source of contamination [30]. In Colombia, researchers found the highest Cd concentrations in litter compared to the leaves and beans [43,44].

In regions where geogenic sources contribute minimally, anthropogenic activities, particularly the use of phosphate fertilizers, often dominate Cd inputs [10,27,40]. Studies in the cacao-producing areas of Colombia and Peru identified fertilizers as a significant source of Cd in soils and plants [34,38]. This occurs because cacao is frequently cultivated in acidic, low-fertility soils and highly weathered soils that require regular fertilization [45].

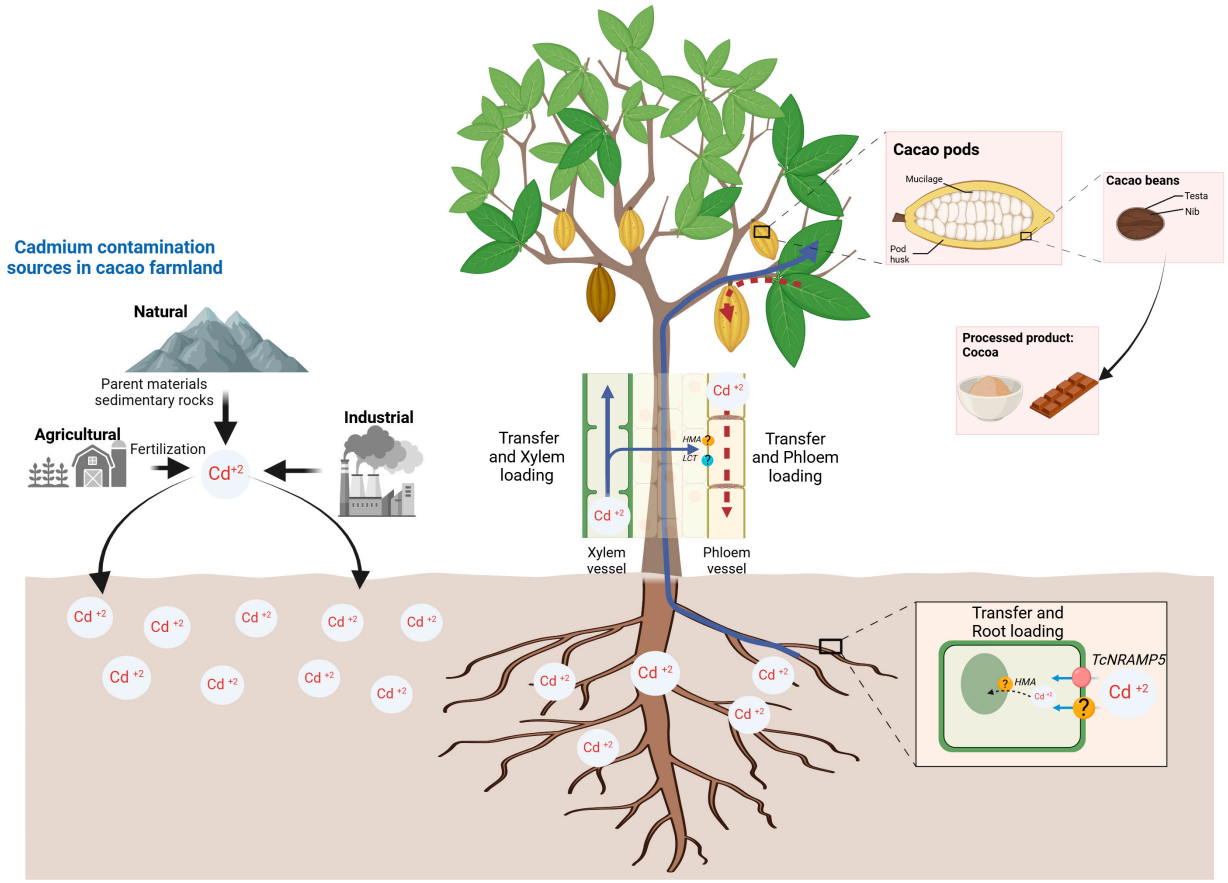


Figure 1. The schematic diagram for Cd uptake, transport, distribution, and remobilization in the cacao tree. Cadmium is taken up by the root cells from the soil, a process mediated by TcNRAMP5, among other transporters. After entering the root cells, Cd can be transported to the vacuole through unspecified proteins of the HMA family. The transpiration drives Cd through the xylem to the leaves or directly to the beans via HMA or metal/cation transporters such as ZIP. The Cd stored in the leaves is remobilized through the phloem. Created in BioRender. Garcia, G. (2025) https://BioRender.com/b08p409.

Some phosphate fertilizers originate from phosphate rocks containing abnormal levels of toxic metals, including Cd. Sedimentary phosphate rocks generally have higher Cd concentrations than igneous ones [46,47]. The weathering of these parent materials and sediment transport further contribute to Cd deposition in alluvial soils, enhancing geogenic Cd accumulation in cultivated lands [28]. Although Latin American soils are known for their higher Cd concentrations, the presence of this metal is not omnipresent, i.e., cadmium content is not elevated in all cacao cultivated areas. Similarly, the predominance of geogenic or anthropogenic sources may differ among regions and countries and is affected by several factors.

Considering the high Cd uptake potential of cacao trees, which are often grown in acidic, Cd-rich soils with years of fertilizer application, prioritizing low-Cd phosphate fertilizers becomes critical. In addition, a pioneering study on the cacao genotype IMC-67 (a low-Cd) demonstrated a positive correlation between Cd accumulation in plant tissues and water deficit (a massive problem for cacao non-irrigated areas), highlighting the need to investigate the combined effects of Cd and other stresses [48].

Table 1. Cadmium concentrations in some cacao-cultivated areas in Latin American countries.

Country	Soil Cd (mg kg^{-1})	Quantification	Soil pH	Bean Cd	Reference
Colombia	<0.20 to >1.12	ICP-MS Monochromatic X-ray fluorescence	5.5–6.0	0.78 mg kg^{-1}	[19]
Colombia	0.01 to 27	ICP-OES			[32]
Costa Rica	<0.1 to 1.05 0.22 (average)	ICP-OES	4.50–7.49	0.41 and 0.56 mg kg^{-1}	[36]
Colombia	8 to 90	X-ray fluorescence (XRF)			[38]
Costa Rica	0 to 4.0 0.38 (average)	ICP-OES	4.8–6.3	0 and 8.70 mg kg^{-1}	[49]
Ecuador	0.44	ICP-OES	<5.5	0.55 and 0.90 mg kg^{-1}	[31]
Peru		GFAAS		0.17 ± 0.41 μg g^{-1} and 1.78 ± 0.35 μg g^{-1}	[21]
Ecuador	0.88 to 2.45 (surface) 0.06 to 2.59 (subsurface)	ICP-OES	4.92–7.97	0.02 to 3.0 mg kg^{-1}	[40]
Peru		GFAAS		0.2–12.56 mg kg^{-1} 2.46 mg kg^{-1} (average)	[35]
Honduras	0.25 ± 0.02 (0–10 cm) 0.16 ± 0.01 (10–25 cm)	GFAAS	4.6–7.8	1.1 ± 0.1 mg kg^{-1}	[28]

The origin and total concentration of Cd in agricultural soils are key indicators for assessing contamination levels and associated ecological risks. Mapping Cd distribution in cacao-cultivated areas is crucial in guiding mitigation efforts and evaluating the impact of regulatory decisions. Identifying variables that influence Cd concentration in cacao farms is equally important. Cadmium availability in soils arises from a complex interplay of factors, including soil pH, organic matter (OM), soil texture, mineralogy, cation exchange capacity (CEC), electrical conductivity, microbial activity, Fe and Al oxides, and nutrient availability. These factors collectively influence Cd adsorption, mobility, and soil bioavailability [31,33,40,50–53].

A meta-analysis of 785 paired soil–plant data points from seven studies revealed a significant trend: Cd concentration in cacao beans increases with total soil Cd, lower pH, and reduced soil organic carbon [17]. The multivariate analyses provided a predictive equation for bean Cd concentrations based on these factors. In South American cacao plantations, researchers have consistently observed strong correlations between Cd levels in beans and total soil Cd, with lower soil pH enhancing Cd availability for plant uptake [31,40].

In Peru, rainfall patterns also affect soil Cd levels. Higher rainfall correlates with lower soil Cd concentrations due to increased leaching at local and regional scales [33]. This finding explains the observed trend that alkaline soils in Peru contain more Cd than acidic soils. Reduced leaching in alkaline soils, combined with their higher CEC (dominated by Mg and Na) and the presence of 2:1 clay mineral, contributes to greater Cd adsorption.

The influence of soil texture on Cd bioavailability in cacao remains unclear, but OM negatively correlates with Cd availability [28,31]. Generally, higher CEC and pH reduce Cd bioavailability by promoting its adsorption into soil particles. Conversely, as CEC and pH decrease, competition between H^+ and Cd^{2+} for binding sites increases, driving Cd release into the soil solution [10]. In cacao plantations, negative correlations between bioavailable Cd and pH have been widely reported [27,28,31,32]. However, pH variations

in the rhizosphere add complexity to this relationship. The root exudation of organic acids can locally acidify the rhizosphere, potentially altering Cd bioavailability. These dynamic interactions may explain variations in Cd uptake across different studies and cultivation conditions.

3. Cadmium in Cacao: Uptake, Transport, Accumulation, and Remobilization

Cacao trees exhibit a remarkable ability to extract substantial amounts of cadmium (Cd) from soils compared to other plant species without significantly impacting their growth and development [30]. Studies have shown that most Cd absorbed by cacao is translocated to aerial tissues [54,55], with neighboring crops in Ecuador exhibiting 70-fold lower Cd concentrations in their fruits than cacao pods [27]. The transfer factor (TF) for cacao exceeds 1, reaching values up to 6, which identifies cacao as a moderate Cd accumulator despite not meeting other criteria, such as >100 mg kg^{-1} accumulation and efficient detoxification [17]. However, the mechanisms underlying Cd tolerance and toxicity in cacao remain largely unexplored.

Cadmium uptake by cacao plants does not solely depend on total soil Cd concentrations. Even soils with low Cd levels can lead to significant uptake by cacao [56]. Consequently, total soil Cd is not a reliable predictor of Cd availability for crops. Instead, soil pH emerges as the primary factor influencing Cd uptake, followed by soil Cd bioavailability, genotype, geographical location, phosphate fertilizers, and interactions with minerals such as Zn and Mn [29].

Besides these variables, the cacao root system, comprising a deep taproot (up to 2 m) and extensive surface roots, influences Cd absorption [57]. However, the impact of root distribution on Cd uptake remains unclear. A pioneering study using a ^{108}Cd isotope demonstrated that Cd uptake shifts within the soil profile when liming is applied to the surface layer, likely due to pH changes in the rhizosphere or compensatory mechanisms [56]. Fine roots, primarily located in the upper 20 cm of soil (especially in the first 10 cm), play a crucial role in water and nutrient absorption. These roots exhibit rapid turnover (1–10 days) and respond dynamically to environmental factors such as rainfall, fertilization, and shading management [57]. Seasonal photoassimilate production and pod development changes further influence the fine root growth [58].

In soil, Cd predominantly exists as Cd^{2+}, with its bioavailability governed by complexation with other elements, such as $CdCO_3$ (at high pH) and CdS (at low pH). These forms can be readily converted into plant-accessible species [59]. Despite being a non-essential element, cadmium in soil solution is highly mobile and is transported to roots through diffusion, advection, and nutrient transporters [60,61]. Five families of proton/metal transporter proteins were identified to facilitate Cd uptake in various plant species: NRAMP (Natural Resistance-Associated Macrophage Protein), HMA (Heavy Metal ATPase), ZIP (Zinc–Iron Regulated Transporters), ABC (ATP-Binding Cassette), and YSL (Yellow Stripe-Like) [62]. However, the identification of these genes in cacao plants is still incipient.

The NRAMP genes have been identified in cacao, with TcNRAMP5 demonstrating Cd transport capabilities in functional yeast studies [63]. The plant NRAMP gene family is highly conserved to uptake divalent cationic nutrients like Fe^{2+}, Mn^{2+}, Zn^{2+}, and Cd^{2+}. A study investigating the induction of Cd isotopes fractionation by NRAMP5 and HMA evidenced that NRAMP5 plays a vital role in Cd uptake in cacao roots and suggested the HMA family as responsible for Cd complexation in thiol groups and Cd sequestration ("hiding" Cd into vacuoles to protect plant cells by reducing metal mobility) as reported for rice [64]. However, the extent of these mechanisms in cacao is still unclear.

After entering roots, Cd can follow several pathways: sequestration in vacuoles, translocation to shoots, or transport via xylem and phloem to aerial tissues, with this last

pathway being the most common for Cd [65,66]. According to a summary by Vanderschueren et al. [17], Cd dynamics in cacao follow these general steps: (i) uptake by root cells, mediated primarily by the TcNRAMP5 membrane transporter, although other transporters also contribute [64]; (ii) root storage or transport, i.e., Cd may be sequestered in vacuoles via HMA transporters or transported through the xylem to aerial parts of the plant [67]; (iii) remobilization from leaves, i.e., Cd stored in leaves is redistributed via the phloem to the pods [55]; and, (iv) cadmium cycling, i.e., Cd enters the food chain through the pod or returns to the soil via leaf decomposition [54] (Figure 1).

Blommaert et al. [55] observed minimal and non-specialized Cd retention in cacao roots of the NA-312 genotype, a high-Cd accumulator from the International Cocoa Genebank, Trinidad (ICGT), with most Cd loaded into the xylem. This highlights low vacuolar sequestration and suggests efficient translocation to aerial parts. The lack of understanding regarding Cd transport in cacao and the regulatory mechanisms is evident. Identifying and characterizing involved genes is crucial to facilitating future investigations and guiding agronomic and breeding solutions for obtaining low-Cd cacao plants.

Cacao plants have a great potential to accumulate Cd in different tissues, including roots, stems, leaves, pods, and beans [10]. However, Cd accumulation varies across cacao tissues, typically in the order of root > stems > leaves > pod husks > beans [68]. Even though the origin and accumulation of Cd in the beans might come from direct transport from the stems and branches, cadmium is translocated from the pods to the developing seeds (cacao beans) [54]. During seed development, Cd initially accumulates in the seed coat (up to 1.8 times higher than the seed) [17]. However, as the seeds develop, a remobilization process transfers most of the Cd from the seed coat to the seed itself; 91% of Cd is remobilized into the seeds before maturity, with only 9% remaining in the seed coat before the fermentation process.

As a cauliflorous tree—flowers and pods develop on the trunk and thicker branches of the plant—cacao has unique mechanisms for loading Cd into developing seeds. Cadmium translocation involves direct xylem transport and source-to-sink remobilization via the phloem [65], with this mobility varying according to plant species and age. Initially, it was suggested that a significant portion of Cd taken up by cacao bypassed the leaves, traveling directly from roots and branches to beans, suggesting the branches as relevant Cd storage [54,55,65]. However, isotope tracing studies confirmed that Cd can reach beans via phloem tissues in the branches. More recent research using hydraulic pulse monitoring indicated that most Cd in beans originates from leaf redistribution, particularly during the final stages of bean development, highlighting the mobility of Cd in phloem tissues [55,69].

Cacao tree age also influences Cd accumulation. Although data are still scarce, younger plants are found to accumulate less Cd than older ones [31,48]. The causes are unknown, but Ortiz-Alvarez et al. [48] discuss factors such as deeper roots reaching soil depth with low Cd, higher Ca concentration, more lignin in root tissues, or even a dilution effect due to higher biomass accumulation. This highlights that Cd accumulation in cacao trees involves complex interactions between soil characteristics, plant growth, and genetic and environmental variables.

Understanding the mechanisms of Cd uptake, transport, and storage in cacao remains incomplete. Identifying the genes and regulatory pathways involved in these processes is essential for developing agronomic and breeding strategies to produce low-Cd cacao. Future studies should address knowledge gaps to better elucidate these mechanisms and improve cacao management in Cd-contaminated areas.

In this context, a recent study has identified Cd binding to calcium oxalate (CaOx) crystals in roots and branches of the high-Cd genotype NA-132. These crystals may limit Cd translocation to leaves and beans, suggesting a potential detoxification mechanism [61]. In

soils with low and high cadmium, Ca-oxalate crystals binding to Cd were also identified in two other cacao genotypes (Nacional and CCN-51) [70]. Cacao can be considered an extreme accumulator of CaOx, and these crystals seem to be correlated with Cd detoxification. However, the role of CaOx in Cd dynamics remains unclear, as plants with higher CaOx and Cd concentrations sometimes exhibit enhanced Cd in beans.

4. Potential Strategies for Cadmium Mitigation in Cacao

4.1. Agronomic Management: Soil Amendments, Nutrients, and Beneficial Elements

Agronomic practices, such as applying soil amendments, can reduce cadmium (Cd) availability in the soil. Applying lime, biochar, and gypsum has been shown to reduce Cd solubility. Lime enhances soil pH, increasing Cd sorption to soil particles, as H^+ ions are the main competitors of Cd^{2+} for sorption sites. This effect has been demonstrated in cacao experiments; however, the field results remain inconsistent [31,71]. Several implications must be considered.

Surface lime applications raise soil pH only in the topsoil, and applying lime to deeper soil layers is impractical in cacao farms [36]. Interestingly, Cd uptake in the lower soil layers has been shown to increase when liming is applied to the surface, suggesting compensatory mechanisms for Cd uptake or nutrient deficiencies, such as reduced zinc (Zn) concentrations in cacao leaves caused by liming [56]. Additionally, liming may increase Cd levels in beans, necessitating a careful evaluation of its applicability based on soil characteristics and the type of liming material used [72]. The use of gypsum or a combination of lime with compost may serve as alternative strategies for cacao areas; however, the mechanism by which gypsum reduces Cd uptake remains unclear, and preliminary results in cacao systems have been inconsistent, as is the case with biochar [71,73].

The use of nutrients—essential elements for plants to complete their growth cycle—has also been shown to reduce Cd in plants and can be associated with soil amendments (Figure 2). Studies in other crops suggest that nitrogen fertilizers, particularly in the ammonium form (NH_4^+), can increase Cd accumulation, while nitrate forms (NO_3^-) may reduce Cd bioavailability by raising soil pH [74–78]. Conversely, phosphorus-deficient soils increase Cd bioavailability due to root-induced acidification, which solubilizes Cd bound to soil components [79,80]. Applying phosphate fertilizers under such conditions can reduce Cd uptake [51,81], but it is crucial to account for the potential presence of Cd in phosphate fertilizers.

Potassium (K) alleviates Cd toxicity by strengthening the xylem cell walls and enhancing plant antioxidant activity, thereby reducing Cd translocation to shoots. In sweet potato, potassium supply has been shown to inhibit the expression of *IRT1* and *YSL3* (responsible for Cd uptake in roots) while downregulating *COPT5* and *Nramp3*, leading to increased Cd retention in root vacuoles. Potassium also upregulates genes like *POD*, *CAD*, *INT1*, and *SUS*, which contribute to lignin and cellulose biosynthesis, thickening the root xylem cell walls and further limiting Cd translocation [82]. Additionally, the synergistic interaction between K and calcium (Ca) enhances growth, enzymatic antioxidant activity, and the production of secondary metabolites under Cd stress [83,84].

Sulfur (S) plays a crucial role in the formation of organic compounds like cysteine (Cys) and glutathione (GSH) [85,86], which are vital for the biosynthesis of phytochelatins (PC) [87]. Phytochelatins facilitate the formation of PC-Cd complexes, providing a vacuolar sequestration mechanism that reduces Cd mobility from roots to stems and leaves [88]. Moreover, increased Ca availability in the growth medium has been linked to the enhanced expression of LCT1, a non-selective transmembrane transporter for Na, K, and Ca, which reduces Ca uptake and accumulation [67].

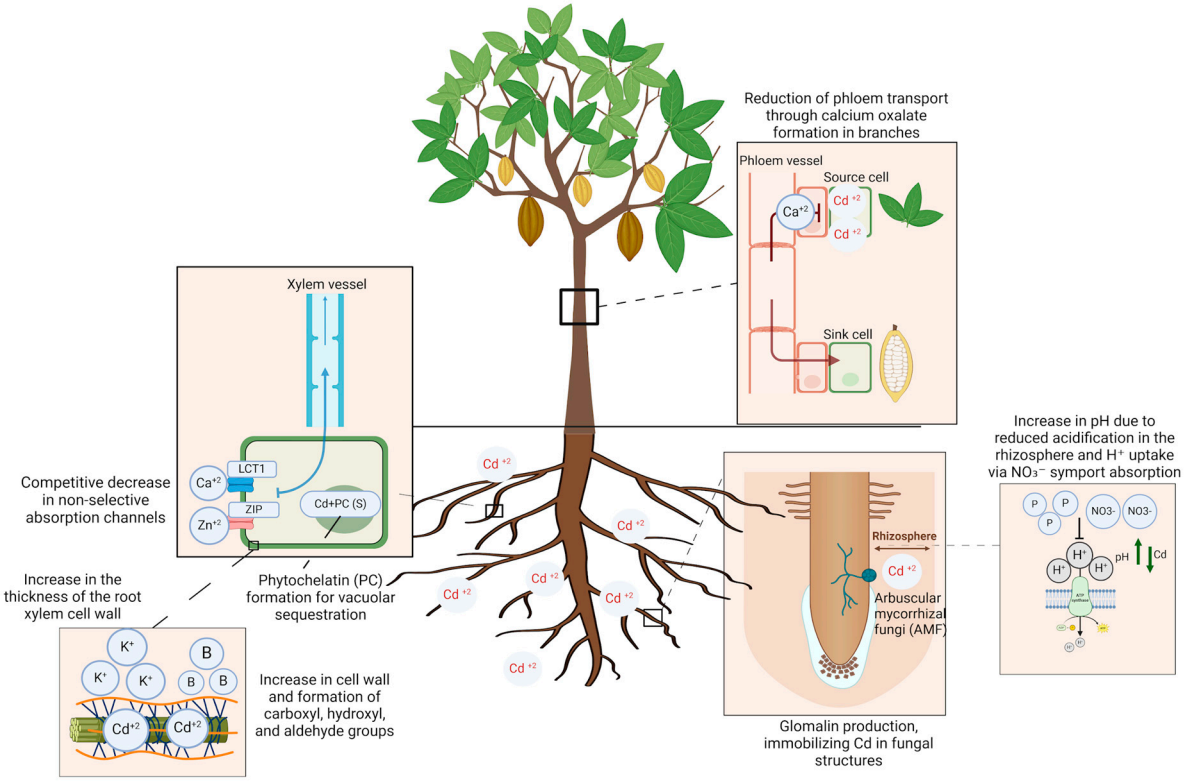


Figure 2. Potential strategies for mitigation of Cd in cacao. Garcia, G. (2024) https://BioRender.com/x50a576.

Regarding micronutrients, zinc (Zn) and manganese (Mn) compete with Cd for absorption due to shared transport pathways, thus reducing Cd uptake and translocation [89,90]. Zinc and manganese also mitigate Cd toxicity by regulating proteins involved in stress defense and photosynthesis [91]. Insights into their common transporter genes, such as those in the NRAMP family, suggest that regulating Mn-Cd interactions and the expression of NRAMPs could help minimize Cd accumulation in plants [92].

Recent studies in cacao reveal that Zn and Mn can reduce cadmium toxicity. Soil Zn deficiency correlates with increased Cd absorption in cacao, while foliar Zn applications promote Cd sequestration in vegetative tissues, reducing its allocation to beans [21]. In experiments with young CCN-51 cacao plants, Zn application decreased Cd uptake and oxidative stress while promoting the expression of genes related to photosynthesis and antioxidant metabolism [90]. Manganese, on the other hand, increased protein accumulation and induced detoxification-related proteins [91].

Other nutrients, including iron (Fe), boron (B), and molybdenum (Mo), though not studied in cacao, play critical roles in Cd mitigation in other crops. For example, Fe deficiency increases rhizosphere acidity, enhancing Cd solubility [79,93]. Boron promotes pectin synthesis in root cell walls, immobilizing Cd and preventing its cytoplasmic entry, as demonstrated in *Brassica napus* [94]. Exogenous Mo can reduce Cd toxicity by immobilizing soil Cd and improving plant physiology in rape [95].

While not essential for plants, selenium (Se) and silicon (Si) are beneficial elements that promote plant growth, productivity, and stress tolerance, including Cd mitigation [96]. Selenium reduces Cd translocation from roots to shoots and enhances antioxidant defenses by forming Cd–thiol complexes [97–99]. As observed in rice, silicon leads to Cd retention in roots, minimizing its movement to aerial tissues [100–102]. Applying Se and Si represents a practical short-term strategy for mitigating Cd accumulation in cacao. However, further research is required to expand our understanding of these elements in cacao systems, particularly for underexplored nutrients and beneficial elements. These findings underscore

the importance of tailored agronomic management strategies to effectively minimize Cd accumulation in crops [103].

4.2. Genetic Improvement: Selection of Genotypes and Rootstocks

Given the high natural cadmium (Cd) concentration in agricultural soils across cacao-producing regions in Latin America, genetic improvement programs have emerged as a promising strategy to reduce Cd accumulation in cacao. Countries such as Brazil, Ecuador, Peru, and Colombia have been actively evaluating genotypes for their potential to limit Cd absorption and translocation [21].

A study of 100 cacao cultivars conserved in the International Cacao Genebank (Trinidad) revealed significant variations in Cd concentrations among cultivars. Under uniform soil conditions, bean Cd content varied 13-fold, and leaf Cd content varied 7-fold [104]. The genotypes were categorized into low accumulators (e.g., IMC-67 and ICS-1) and high accumulators (e.g., NA-312 and SCA-5). These findings underscore the influence of genetic traits, including cultivar-specific absorption capacities and growth-related factors, on Cd uptake rates [30].

Fifty-three Peruvian wild and domesticated cacao genotypes were evaluated, revealing genotype-dependent responses to Cd stress. Eleven genotypes, including the THS-565 and the widely cultivated CCN-51, were identified as having lower Cd concentrations, making them potential candidates for future use as low-Cd cultivars or rootstocks [105]. CCN-51, a genotype from Ecuador, is of paramount economic importance across Latin American countries. It is self-compatible, resistant to fungal diseases, and can produce approximately four times more than other varieties, like Nacional [106]. Due to its widespread use and desirable agronomic traits, CCN-51 is the most frequently studied genotype in Cd-related research [29,106].

Rootstock–graft combinations offer a promising approach to reduce Cd uptake, using low-Cd genotypes as rootstock to limit Cd translocation, thereby enabling cacao cultivation in areas with elevated Cd levels. These combinations are selected not only for their agronomic advantages—such as tolerance to abiotic and biotic stresses—but also for their ability to restrict Cd movement to the aerial parts of the plant [107]. Similar strategies have been successfully employed in other species, including apple, citrus, and tomato [108–111]. For instance, specific combinations like CCN-51/BN-34 and CCN-51/PH-16 have demonstrated a capacity to sequester higher Cd levels in the root system, thereby reducing Cd concentrations in leaves and beans, even under high soil Cd exposure (up to 150 mg Cd kg^{-1}). This highlights their potential to mitigate Cd bioaccumulation [112]. Another study tested IMC-67 and PA-121 progenies as rootstocks in grafts with two commercial genotypes (ICS-95 and CCN51). It was observed that ICS-95 (low-Cd genotype), grafted on IMC-67, accumulated less Cd compared to CCN-51 grafted on the same rootstock [113].

While genotypic differences in Cd uptake efficiency in cacao have been demonstrated, further studies are required to assess the impact of soil types, nutrient availability, plant age, and cacao growing regions on this genetic control. Some genotypes, such as TSH-565, ICS-1, CCN-51, and PS13-19, have been reported as low-Cd accumulators under certain conditions and high-Cd accumulators under others [10,29,30,104]. These variations highlight the complexity of Cd accumulation in cacao and emphasize the need to consider multiple variables when interpreting Cd distribution patterns across different plant tissues. Genetic improvement programs that harness cacao's genetic diversity represent an effective medium- and long-term strategy. These programs focus on developing low-Cd varieties and rootstocks suitable for cultivation in areas with naturally high Cd levels.

Table 2 summarizes mitigation strategies evaluated in cacao. By combining genetic improvement with agronomic management, cacao-producing countries can address reg-

ulatory food safety requirements while sustaining productivity in Cd-affected regions.

Table 2. Cadmium effects in cacao plants and responses to mitigation strategies.

Cd Effect	Mitigation Approach	Response	Reference
Cd-contaminated soil	Liming	Increase in soil pH; reduction in Cd in topsoil and increase in the lower layer; Cd, Zn, and Mn decreased in cacao leaves.	[56]
Cd-contaminated soil	Liming and biochar	Increase in soil pH; reduced Cd soil phytoavailability and leaf Cd level.	[68,71]
Cd-contaminated soil	Commercial liming	Increase in soil pH; mineral uptake, except Mg and Ca; and increase in Cd uptake for some materials.	[72]
Cd-contaminated soil	Liming, gypsum, and liming + compost	Increase in topsoil pH; reduced Cd in leaves, but not in beans.	[73]
Reduction in mesophyll thickness; photosynthesis reduction; hormesis effect in lower Cd concentration	Soil Zn application	Increase in antioxidant enzymes and proline content; reduction in lipidic peroxidation; decrease in Cd uptake and transport to leaves.	[90]
Induction of proteins involved in the oxidoreduction process, defense, and stress response; increase in antioxidant enzyme activity	Soil Mn application	Repression of enzyme activity and proteins related to stress, induced by Cd, and the induction of detoxification proteins.	[91]
Alterations in the leaf proteome		Cd detoxification by the antioxidant system and protein accumulation.	[112]
Reduction in plant growth, photosynthesis, and water use efficiency; oxidative stress; reduction in nutrient content.	Rootstock combination	Decrease in Cd translocation to shoots; minimization of physiological alterations caused by Cd.	[113]
Physiological and biochemical perturbations	Rootstock combination	Higher Cd accumulation in the roots; increase in carbon assimilation, antioxidant enzymes, and water use efficiency.	[114]

5. Conclusions and Future Perspectives

In recent years, studies related to mitigation strategies in cacao plants have been undertaken. The strategies considered by this avenue of research include the following: (i) the application of soil amendments and essential micronutrients such as zinc and manganese, and (ii) using low-Cd cacao cultivars as rootstocks or for breeding. Other potential strategies have also been proposed to reduce or immobilize Cd concentrations in soil and plant tissues. These alternatives warrant further investigation into cacao-growing areas to guide the development of viable and safe solutions for cacao farmers worldwide.

Bioremediation, which involves using living organisms to eliminate or neutralize high Cd concentrations in soils, may present a promising approach [115]. Although the use of microorganisms has been explored in cacao, these studies remain in the early stages, and experimental results in the published literature are still limited.

A newly identified fungal species, *Talaromyces santanderensis* sp. nov., has demonstrated remarkable Cd tolerance, with a tolerance index of 0.81 at 300 mg kg^{-1} of Cd. This fungus was isolated in Santander, a region of Colombia where Cd concentrations can reach up to 27 mg kg^{-1}. Additionally, a decrease in Cd uptake by cacao cultivar IMC-67 was reported in the presence of a native arbuscular mycorrhizal fungus (AMF) in Colombia [116]. Similarly, a mixture of organic amendments with spores from AMF species such as *Glomus hoi*, *Rhizoglomus* sp., *Diversispora aurantia*, and *Acaulospora* sp. reduced Cd concentration in plant tissues [117]. Cadmium-tolerant bacteria, which participate in metabolic pathways affecting Cd content in soils, may also have the potential for bioremediation in cacao-growing areas and merit further exploration [50].

Moreover, some authors have proposed post-harvest strategies for mitigating Cd levels. For example, removing cacao beans' testa (seed coat) has been suggested for specific genotypes that preferentially store Cd in this part [104]. Another practical approach involves mixing cacao beans from regions with varying Cd levels (low and high) to reduce the overall Cd concentration in cocoa products [17].

For now, there is no general magical solution for Cd in all cacao-producing areas. Further research is required to thoroughly assess the effectiveness of existing strategies and develop new approaches tailored to the specific soil and plant conditions of each cacao-producing country. This effort calls for the active involvement of various stakeholders to evaluate local socioeconomic constraints, the likelihood of farmers' adoption of these measures, and the integration of these measures into comprehensive management plans.

Ultimately, the goal is to achieve high-quality cacao production that benefits producers and consumers while safeguarding the sustainability of this vital agroecosystem.

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