Review article

Silicon mediated heavy metal stress amelioration in fruit crops

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A B S T R A C T

Fruit crops are essential for human nutrition and health, yet high level of heavy metal levels in soils can degrade fruit quality. These metals accumulate in plant roots and tissues due to factors like excessive fertilizer and pesticide use, poor waste management, and unscientific agricultural practices. Such accumulation can adversely affect plant growth, physiology, and yield. Consuming fruits contaminated with toxic metals poses significant health risks, including nervous system disorders and cancer. Various strategies, such as organic manuring, biomaterials, and modified cultivation practices have been widely researched to reduce heavy metal accumulation. Recently, silicon (Si) application has emerged as a promising and cost-effective solution for addressing biological and environmental challenges in food crops. Si, which can be applied to the soil, through foliar application or a combination of both, helps reduce toxic metal concentrations in soil and plants. Despite its potential, there is currently no comprehensive review that details Si's role in mitigating heavy metal stress in fruit crops. This review aims to explore the potential of Si in reducing heavy metal-induced damage in fruit crops while enhancing growth by alleviating heavy metal toxicity.

1. Introduction

Fruit crops are a cornerstone of agricultural GDP in many developing and underdeveloped countries, valued for their delicious taste and numerous health benefits. Ripe fruits are composed primarily of carbohydrates, followed by proteins and fats, and are rich in essential vitamins and minerals crucial for human health [1]. The sweetness of fruits comes from their high sugar content, including fructose, glucose, sorbitol, and starch, with fructose, being notably sweet despite having the same caloric content as sucrose [2]. In addition to their nutritional value, fruits are prized for their unique flavor and diverse applications across various industries.

Fruit crop production faces numerous challenges, including biological and environmental factors such as pest attacks, long life cycles, climate change, heavy metal toxicity, highly heterozygous genomes, and improper farming practices. In recent years, non-degradable heavy metals from industrial waste, inorganic fertilizers, and pesticides have contaminated fertile lands, transforming them into wastelands [3]. These persistent heavy metals are significant concern, as plants can inadvertently absorb excessive amounts from the soil, leading to fruit contamination that exceeds safe levels. Elevated heavy metal concentrations in plants adversely affect soil biological activity, plant metabolism and growth, biodiversity, and fertility, as well as the animals that depend on these crops. These

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effects manifest through disruptions in physiological functions, binding to protein sulfhydryl groups, interference with metal transporter activities, and destabilization of cellular equilibrium [4,5].

To improve the effectiveness of heavy metal stress mitigation in fruit crops, various strategies have been evaluated, including organic manuring, crop residue application, biochar treatment, multi-cropping systems, balanced micronutrient supplementation, and modified irrigation practices. However, these methods have demonstrated limited success in significantly reducing heavy metal stress in plants [6]. In contrast, several studies have shown that Si applications in various formulations can enhance the regulation of heavy metal stress in fruit crops. This improvement is achieved by maintaining normal root architecture, vascular bundle structure, and photosynthetic activity.

Si, the second-most abundant element on Earth, acts as a quasi-essential nutrient for plants, playing a crucial role in mitigating abiotic stresses, including heavy metal toxicity. Its involvement in metal detoxification includes altering plant cell mechanisms, regulating hormones, reduced fatty acid desaturation and lipid peroxidation, and interacting with the environmental [7]. Externally, Si application enhances heavy metal tolerance by increasing soil pH through silicate application, leading to the formation of metal silicate precipitates that reduce metal phytoavailability.

Soil Si content varies, ranging from 200 to 350 g kg-1 in clay soils to 450–480 g kg-1 in sandy soils, with most of it present as insoluble oxides or silicates. Some Si is also found in a water-soluble form. Despite its abundance, the amount of Si available to plants is often limited. Plants absorb Si from the soil solution as silicic acid (H_4SiO_4), typically at concentrations ranging from 0.1 to 0.6 mmol L-1 [8]. Plant Si content varies significantly among species due to differences in uptake and transport capacities mediated by specific Si transporters [9]. This review examines how Si enhances heavy metal tolerance in fruit crops and the potential mechanisms behind this phenomenon.

The role of silicon (Si) in plant stress regulation has been widely investigated globally, with over 250 studies published in the last five years alone on Si and its interactions with metalloids. While numerous reviews discuss Si's effectiveness in alleviating heavy metal stress in cereal and pulse crops, most research has been descriptive with limited focus on the mechanical principles underlying Si's function [10–12]. The role of Si in managing heavy metal stress in fruit crops, however, remains underexplored. This review addresses the gap by providing a comprehensive analysis of Si's potential as an environmentally friendly and progressive approach to mitigating heavy metal stress in horticultural crops.

2. Si and its importance in fruit crops

Si is not considered as an essential element for plant nutrition based on the traditional criteria proposed by Arnon and Stout [13]. Nevertheless, extensive documentation exists on the biostimulator effects of Si, which positively influence the growth and development of higher plants [14]. Although Si's is not essential for plant nutrition, it can affect physiological processes, thereby enhancing growth, development, and stress responses. This categorizes Si as a bio stimulant.

Table 1
Silicon mediated plant growth and development in fruit crops.

S. No.	Crop	Concentration	Mechanisms	References
1	Apple	150 ppm	In addition, silicon increased the accumulation of total phenolic and total anthocyanin compounds in the various apple tissues.	[19]
2	Apple	50 ppm	Increase the fresh weight and dry weight, chlorophyll index, and number and length of shoots	[20]
3	Grape	250 ppm	Enhances the bunch weight, TSS content, berry crunchiness, berries number, and fruit yield.	[21]
4	Pineapple	50 ppm	Reduces the fruits collapse incidence	[22]
5	Mango	1 ppm	Significantly reduces the decay percentage and fruit weight loss	[23]
6	Citrus	500 ppm	Enhances the antioxidants activities	[24]
7	Pomegranate	1–2 ppm	ameliorate the shoot diameter, length, and juice content and reduces the total acidity content in harve3sted fruits	[25]
8	Peach	10 ppm	Enhances water use efficiency net photosynthetic rate, antioxidant capacity and inhibit the stomata closer under drought stress condition	[26]
9	Peach	10 ppm	enhances the fruit quality parameters like fruit wt, titrable aciduty, soluble solid content, and reduces the fruit loss	[27]
10	Peach	50 ppm	reduces the negative effect of sewage water on plant growth and development	[28]
12	Grape	600 kg per ha SiO2	increase fruit yield by improving berry weight and size	[29]
13	Grape		Extend the fruits self life	[30]
14	Citrus	0.01 % potassium silicate	Significantly enhances the fruit quality parameters	[31]
15	Navel orange	0.10 %	improves vegetative, growth, leaf pigmentation, fruit setting and fruit yield	[32]
16	Mango	5ppm	increases leaf area, fruit yield, fruit thickness, fruit weight, TSS, and reduces total acidity	[33]
17	Mango	1.50 %	Improves fruit size and firmness	[34]
18	Sapota	8 ppm	improves chlorophyll content, number of shoots and flowers, and reduce mummified fruit number	[35]
19	Avocado		improves the fruit storage and marketing by regulating ethylene evolution and carbon dioxide production	[36]
20	Avocado	1470 ppm	reduces the storage pest infection	[37]
21	Banana	100 ppm	improves pulp/peel ratio, self life, acidity, and sugar content	[38]

Studies demonstrate that Si is essential for fruit trees, as it enhances leaf chlorophyll content, improves photosynthesis, prevents root rot and premature aging, promotes root growth and development, and regulates the absorption of major and micro-essential nutrients. Si also effectively prevent early defoliation, cracking, and other physiological disorders, enhance the resilience by inhibiting moisture evaporation in leaves and fruits. Additionally, Si improves storage and transportation conditions [15,16]. This section explores how Si contributes to the growth and quality of various fruit trees.

Si enhances fruit production quality by forming a cuticle-Si double layer beneath the leaf cuticle layer, which ultimately slows down respiration and fruit transpiration [17]. It regulates nutrient assimilation and plant metabolism, leading to significant improvements in fruit yield [18]. Research indicates that Si promotes seed germination and seedling establishment by increasing biomass accumulation. Additionally, foliar application of Si boosts overall plant growth and fruit yield by influencing antioxidant and hormonal levels, stomatal movement, respiration, transpiration rates, root biomass, quality parameters, and mitigating environmental stresses (see Table 1).

Optimal preharvest and postharvest practices are enhancing for maintain fruit quality and durability during storage, which in turn enhances consumer confidence. Si plays critical role in improving fruit quality by increasing free phenol levels. It facilitates the releases of free phenols [39] from membrane-bound forms, thereby boosting the antioxidant capacity in fruits. This is crucial for enhancing postharvest fruit quality. Fruits treated with Si demonstrate lower mass loss, likely due to improved moisture retention facilitated by Si accumulation in fruit peels [40], which covers the stomata and reduce respiration and weight loss. Additionally reduced polyphenol oxidase activity leads to less mesocarp browning, helping cut fruits stay fresh for a longer period [41].

Si's ability to bind cellular oxygen helps reduces oxidant accumulation, which is crucial for maintaining membrane integrity and inhibiting lipid peroxidation under stress. This results in improved fruit firmness, and decreased fruit firmness and decreased mass loss, likely due to enhanced cell membrane stability [42]. Similar benefits are observed in apples, where Si-enriched cell walls protection against pathogens, enhancing fruit firmness, and increase pest resistance. Si treatments also lower polygalacturonase activity, a key enzyme in fruit softening, thus extending apple storage life, and improving yields [43]. Additionally, Si supplementation in acidic soils reduces titratable acid content while increasing total soluble solids and vitamin C levels in fruits, understanding its positive impact on fruit quality and yield. Overall, silicate fertilization proves to be a promising strategy for enhancing fruit quality, increase yield, and prolonging storage life.

3. Impact of heavy metal consumption on plant health

Excessive accumulation of heavy metals in plants can cause a variety of toxic symptoms, including stunted growth, chlorosis
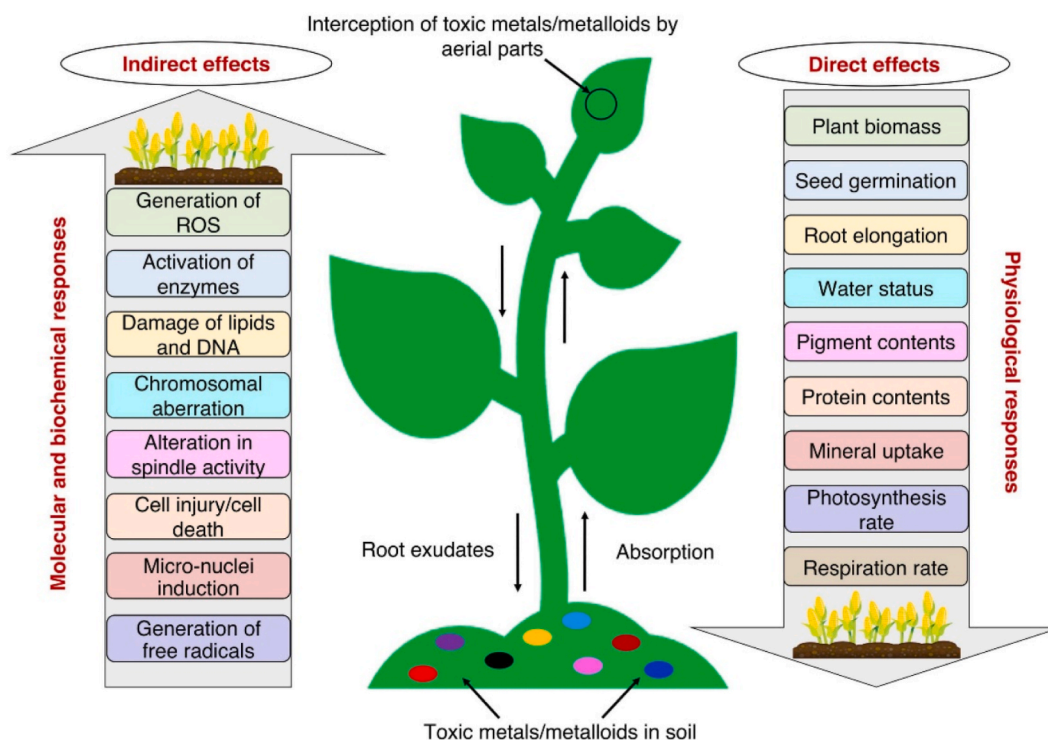

Fig. 1. Illustrates plant responses to toxic metals/metalloids, impacting crop productivity directly or indirectly. Plants encounter these substances through both above-ground and below-ground pathways. The toxic nature of various metals/metalloids diminishes physiological reactions while amplifying molecular and biochemical responses (Source: Raza et al. [47]; CC BY).

(yellowing), root browning, decline, and even death [44]. Fig. 1 illustrates the diverse responses of plants to toxic metal/metalloid toxicity, highlighting the potential direct and indirect effects on crop productivity. Heavy metal stress can lead to the generation of harmful reactive oxygen species (ROS) such as superoxide radicals (O_2^-), hydroxyl radicals (^-OH), hydrogen peroxide (H_2O_2), and singlet oxygen ($^1O_2$). These ROS can negatively impact essential biological processes, including photosynthesis, respiration, plasma membrane function, and fatty acid integrity [45]. To mitigate ROS damage, plants employ various defense mechanisms. Enzymatic antioxidants such as ascorbate peroxidase (APX), catalase (CAT), peroxidase (POD), superoxide dismutase (SOD), and glutathione reductase (GR) work in conjunction with non-enzymatic antioxidants such as ascorbic acid (AsA), carotenoids (Car), and glutathione (GSH) to regulate ROS levels and protect plant cells from heavy metal-induced damage [46].

Heavy metals exert their harmful effects at the cellular level by interacting with both intra- and intercellular DNA and protein molecules. These interactions can lead to cross-linking, deletion, modification, rearrangement, breakage, and depurination of DNA bases. Furthermore, these metals can generate a harmful compound known as 8-oxoG (7,8-dihydro-8-oxoguanine), which disrupts normal DNA replication by incorrectly pairing with adenine, ultimately causing mutations such as cytosine to thymine conversions. Cation Diffusion Facilitators (CDFs) and the Natural Resistance-Associated Macrophage Protein Family (NRAMPs) are crucial for maintaining cellular metal homeostasis and developing plant strategies to withstand heavy metal stress [45]. However, the capacity to absorb, transport, and accumulate varies significantly among different plant species.

4. Impact of heavy metal contaminated fruit consumption on human health

Consuming fruits contaminated with heavy metals can significantly impact human health, potentially causing both acute (short-term) and chronic (long-term) toxicity through various mechanisms (see Fig. 2 and Table 2 for details). For example, lead exposure can negatively affect the circulatory and renal (kidney) systems. In the kidneys, it can lead to mild excretion of glucose (glucosuria), amino acids (aminoaciduria), and phosphates (hyperphosphaturia). Of particular concern is leads potential damage the central nervous system, especially in children. Lead can inhibit enzymes, such as δ-aminolevulinic acid dehydratase [ALA-D] and haem synthetase in the blood, leading to the accumulation of ALA-D and free erythrocyte protoporphyrin (FEP), which can cause anemia [48].

Another concerning heavy metal is cadmium (Cd), which primarily affects kidney function. People exposed to Cd may have proteins like $\alpha2$-, $\beta2$-, and γ-globulin in their urine. Prolonged Cd accumulation can also lead to cancer development, as it is classified as a carcinogen. Conversely, Nickel (Ni) is an essential trace element found in various organisms and is involved in redox metabolism (electron transfer) and the ROS generation. However, studies on laboratory animals suggest that Ni exposure can induce cancer. Ni subsulfide and β-nickel monosulfide have been identified as potent carcinogens [63]. These examples highlight the complex and
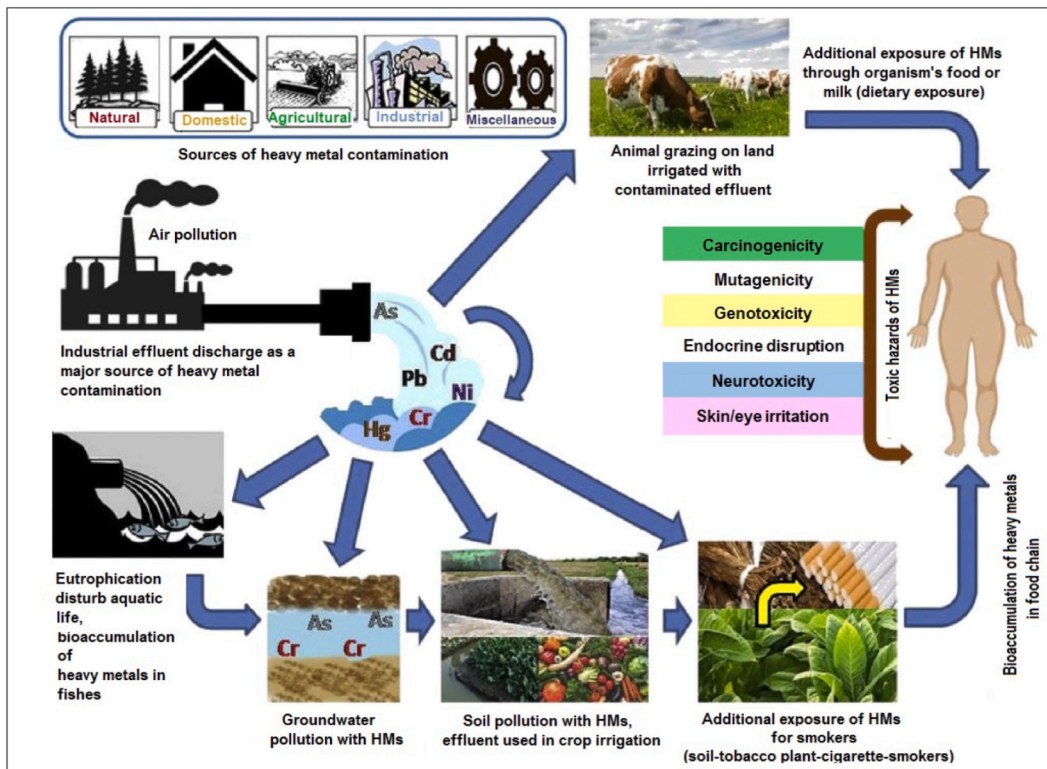

Fig. 2. Sources of heavy metal contamination in food plants and transfer to humans (Source: Afonne et al. [49]; Licence No: 5861300445650, Accessed on June 15, 2024).

Table 2
Dietary limit of heavy metal intake to maintain safe human health.

S. No	Heavy metal	Dietary limit	Potential toxicity	Reference
1	Cd	0.003 ppm (WHO); 0.005 ppm (EPA)	damage to the hemopoietic and adrenals systems, testicular damage, and pulmonary edema	[50]
2	Hg	0.001 ppm (WHO); 0.002 ppm (EPA)	heart stroke, cardiovascular disease, and hypertension	[51]
3	Co	0.000003 ppm (ATSDRS); 0.000005 ppm (Cal EPA)	endocrine and hematological dysfunctions, with major health hazards	[52]
4	Cr	0.003 ppm (WHO)	Muscular cramps, toxic nephritis, renal failure, liver damage, acute multisystem organ failure.	[53]
5	Pb	0.01 ppm JECFA; 0.025 ppm (PTWI)	Loss of sex drive, fatigue, headaches, muscle and joint paining	[54]
6	As	0.01 ppm USEPA	vomiting, nausea, severe diarrhoea, abdominal pain	[55]
7	Sb	5 ppm (WHO)	increase the risk of carcinogenicity, and disturb the reproductive health	[56]
8	Mg	350 ppm (WHO)	Diarrhea followed by abdominal cramping	[57]
9	Mn	11 ppm (NAS)	Nausea, hypotension, retention of urine, facial flushing, depression, ileus, and lethargy	[57]
10	Fe	0.8 mg kg^{-1}/bw/day	Cause neurodegenerative diseases	[58]
11	Ba	2 ppm (EPA)	Kidney and cardiovascular diseases, mental, neurological and metabolic disorders.	[59]
12	Be	0.004 ppm (EPA)	Carcinogenicity and genotoxicity	[60]
13	Cu	1.5 ppm (WHO)	Cancer or arthritis, cognitive decline, and cardiovascular diseases	[61]
14	Zn	5 ppm (WHO)	Dysfunction of cell-mediated immunity, and increases the pathogen infection	[62]

potentially harmful effects of heavy metals exposure on human health. This emphasizes the critical need to reduce heavy metal stress in fruit crops to protect human health.

5. Si-mediated mechanisms of metal detoxifications

Si plays a key role in enhancing plant tolerance to heavy metals through various mechanisms. Initially, the application of silicate increases soil pH levels, leading to the formation of less soluble metal-silicate complexes that are less readily absorbed by plants. Si also plays a crucial role in the internal distribution of metals within plants, aiding their resilience under high metal stress conditions [64]. Fig. 3 provides an overview of the Si's intricate involvement in plants facing heavy metal stress. Si nanoparticles significantly contribute significantly to plant tolerance by boosting the activity of antioxidant enzymes, facilitating the development of physical barriers, reducing metal uptake, and modulating gene expression associated with stress responses. This multi-faceted approach highlights Si's potential as a robust strategy for alleviating heavy metal stress in plants. While the capacity for Si accumulation may vary among different plant species, both monocots (known for higher Si accumulation) and dicots can benefit from Si-mediated mitigation of metal toxicity. Additionally, Si application has been found to alleviate lipid peroxidation and fatty acid desaturation
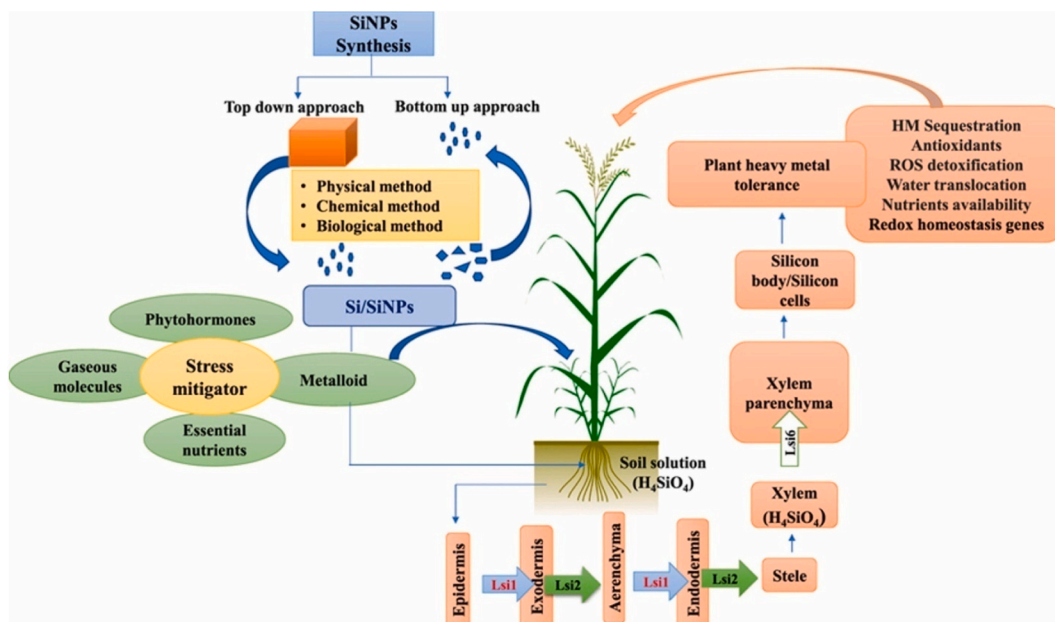

Fig. 3. Silicon-mediated mechanisms of metal detoxification (Source: Asgher et al. [67]; Licence No: 5861300748532, Accessed on June 15, 2024).

in plant tissues, thereby promoting overall growth and biomass production under heavy metal stress [65]. Given the depletion of Si reservoirs in agricultural soils due to the removal of Si-rich organic matter during harvests, the necessity for external Si application in agriculture is evident [66]. This trend is expected to gain prevalence in the future as a means to enhance plant growth and combat heavy metal toxicity. The detailed discussion of Si-mediated mechanisms for metal detoxification is outlined in the following sub-section headings.

5.1. Si-induced immobilization of heavy metals in soil

Several studies demonstrate that applying Si to soil can immobilize toxic metals through two primary mechanisms: increased soil pH and alterations in metal speciation via silicate complex formation. For example, in banana cultivation, Si application to Pb-contaminated soil reduced Pb uptake by significantly increasing soil pH and decreasing the amount of exchangeable Pb [68]. Similarly, in Si-amended soils, Cd was primarily found as oxides or adsorbed onto Fe-Mn oxides [69,70]. Soluble silicate in aqueous solutions hydrolyzes to form metasilicic acid (H_2SiO_3), which can directly adsorb heavy metals or facilitate their incorporation into silicates, thereby reducing metal availability for plant uptake [71].

Although Si in soil is primarily bound in silicates, limiting its availability to organisms, pre-treatment with Si has been shown to stimulate phenolic root exudation. This mechanism contributes alleviating manganese toxicity in citrus plants [72]. Si further promotes the exudation of phenolics and organic acids, influencing the availability of metals like aluminum (Al) by immobilizing them on root surfaces through the formation of Al-Si complexes outside root tissues and reducing metal binding within cell walls. Additionally, applying Si as calcium silicate can modify Cd and Zn distribution in soil, stabilizing these metals in complexed forms with organic matter and iron oxides [69,70].

The studies primarily focused on metal speciation and pH changes in bulk soil following Si application. However, further research is needed to understand Si-mediated metal immobilization specially the orchid's rhizosphere and soil solution, especially concerning the role of root secretions and associated microorganisms. Additionally, evaluating the effects of various Si amendments on metal speciation in soil is essential for gaining a comprehensive understanding of this process.

5.2. Si-mediated co-precipitation of heavy metals

Silicon co-precipitation with heavy metals can alleviate metal stress in plants by primarily localizing metalloids in the apoplastic sap and cell walls, with maintain lower concentrations within the protoplast. Si treatments reduce the protoplast/apoplast ratio, thereby minimizing the presence of toxic metals in critical cell components. This process can help restore vacuolization in root cells, improve mitochondrial membrane integrity, enhance chloroplast structure, and increase the density of starch grains and grana. In C4 plants, Si may also protect mesophyll chloroplasts from metal induced damage.

Several studies provide evidence for Si forming complex with metals in roots. For instance, da Cunha and do Nascimento [73] observed silica, cadmium, and Zn in root mesophyll cells, indicating Si-metal complexes formation. Oliva et al. [74] found Cu within phytoliths of plant shoots, suggesting that Si reduces free Cu concentrations and alleviates Cu stress in shoots. Janeeshma et al. [75] identified Zn-Si precipitates in less bioactive plant tissue cell walls. Zhang et al. [76] reported Si and Cd co-deposition in the root endodermis, proposing co-precipitation as a potential mechanism. Additionally, Tubaña and Heckman [77] suggested that Si treatments under metal stress conditions lead to hydrated amorphous silica (HAS) complexes formation within the root apoplast, aiding metal detoxification. These findings indicate that Si co-precipitation with heavy metals may be a significant detoxification mechanism, through further research is required to fully understand its prevalence and effectiveness.

5.3. Si-enhanced antioxidant defense against heavy metal stress

Si application enhances both enzymatic and non-enzymatic antioxidant activity in plants subjected to heavy metal stress. These antioxidants-such as non-protein thiols, glutathione, and ascorbic acid-play a crucial role in mitigating oxidative damage by reducing ROS levels. Research indicates that Si treatment effectively decreases MDA, H2O2, and EL in both shoots and roots under Cd, Pb, and Zn stress [78,79].

Pre-treatment with Si often enhances the activity of both antioxidant enzymes and non-enzymatic antioxidants in plants, thereby aiding in stress management. For instance, Si application significantly increased the activities of POD, SOD, and CAT in banana plants under lead (Pb) stress. Additionally, Si improved levels of non-enzymatic antioxidants such as GSH, NPT, and AsA under Cd and Mn stress [68]. Similar enhancements have also been observed in plants exposed to other heavy metal toxicities [80].

Some studies have indicated that Si application can suppress antioxidant activity under Cd stress. This suppression may result from a reduced stress response induced by Si, which lowers the plant's need for antioxidant synthesis [81]. When metal stress levels are higher, this mechanism might become less effective, and other detoxification pathways could play a more significant role. Consequently, the enhancement of antioxidant activities through Si seems to be most beneficial primarily under mild metal stress conditions.

5.4. Si-promoted chelation mechanisms for heavy metal detoxification

Si promotes heavy metal detoxification primarily by chelating metals through flavonoid phenolics and organic acids. Phenolic compounds known for their high Al-chelating activity; help alleviate Al toxicity in root tip apoplasts [82]. Si also influences the release of organic acids from roots. Fan et al. [83] demonstrated that Si affects the exudation of oxalic and acetic acid, which can alleviate

toxicity from various heavy metals, particularly Zn and Cd. Additionally, Bali et al. [84] found that Si-induced oxalate exudation reduces Cd phytotoxicity.

Si also impacts Fe dynamics in the rhizosphere. Sharma et al. [85] highlighted how organic ligands exuded from roots in mobilizing Fe, and Si influences these exudates, thereby affecting the availability of both heavy metals and essential nutrients such as phosphorus (P). Although some mechanisms, such as co-precipitation, are still debated and require further research, understanding the complex interplay between Si and heavy metals at the molecular and genetic levels is crucial for fully elucidating Si's role in mitigating heavy metal toxicity in plants.

5.5. Regulation of Si-induced genes expression and metal transport proteins performance under heavy metal stress condition

Silicon (Si) is pivotal in mitigating heavy metal stress in plants through multiple mechanisms. One major strategy involves the downregulation of metal transporter genes, such as Nramp5 and HMA2, which are responsible for the uptake of metals like Cu and Cd [86,87]. By reducing the expression of these genes, Si decreases the influx of these potentially toxic elements into plant cells. Additionally, Si upregulates genes related to its own transport, such as *Lsi1* and *Lsi2*, particularly in members of the Poaceae family, thereby enhancing Si uptake and stress tolerance [88]. Si also aids in sequestration of excess metals in vacuoles, limiting their movement to the shoot and mitigating their disruptive effects on cellular processes [89]. Research has demonstrated that Si promotes the accumulation of metals like Cu and Cd within vacuoles, reducing their potential for harm. Moreover, Si's regulatory effects extended to metalloids such as arsenate (As(III)) and antimonite (Sb(III)), where its upregulation of *Lsi1* and *Lsi2* transporters to lower As(III) concentrations in plant tissues [90]. Interestingly, Si application can also enhance the expression of transporter genes for essential mineral nutrients, understanding its multifaceted role in plant stress responses and nutrient acquisition. Fig. 4 depicts the interaction between Si and other heavy metals at the molecular level within plant root cells.

The transportation of Cd, Fe, Mn, and Zn is facilitated by transporters within the *ZIP* gene family, suggesting that regulating *ZIP* gene expression could manage the accumulation of these metals. ZIP family proteins typically feature eight transmembrane domains with both termini exposed to the apoplast. *ZIP1* and *ZIP3*, mainly expressed in roots, show peak activity under Zn stress conditions [92]. *NRAMP* metal transporters, present in both the plasma membrane and tonoplast membrane, regulate Cd and Fe transportation
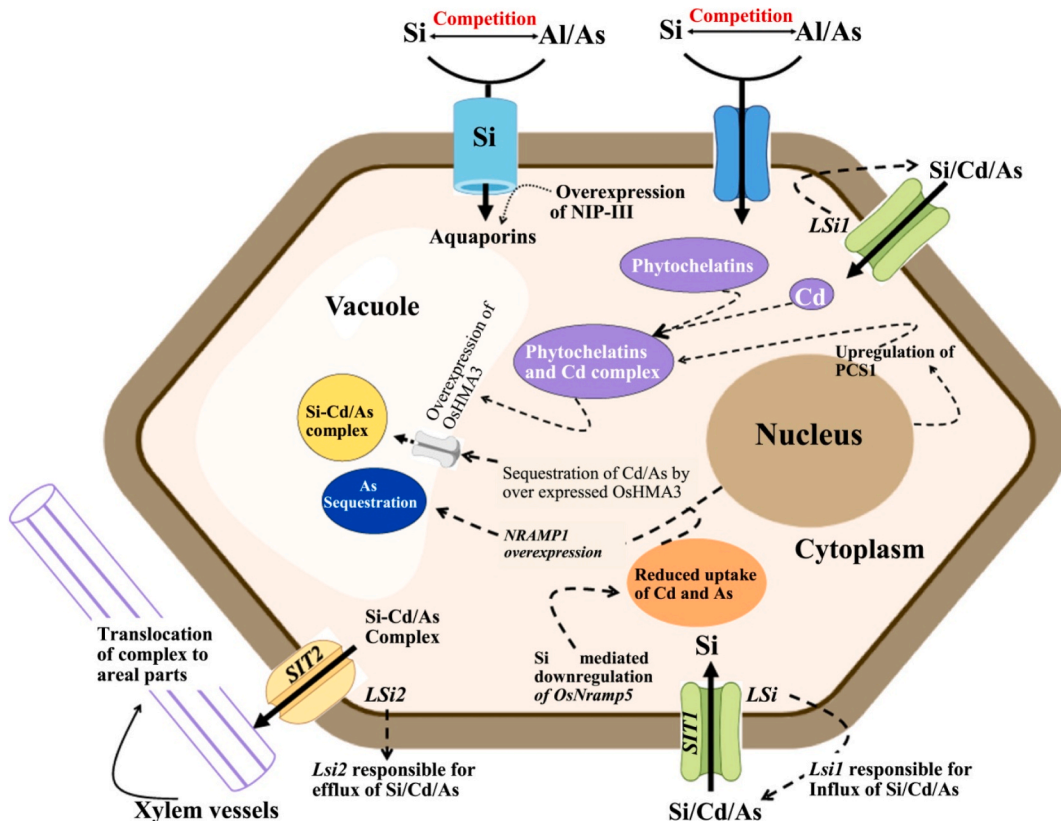

Fig. 4. Illustrates the molecular-level interaction between silicon (Si) and heavy metals in plant root cells. It shows the competition for cellular entry among heavy metals and Si via different transporters and aquaporins. The *SIT2* transporter genes aid Si efflux, while vacuolar transporters help sequester heavy metals in vacuoles, reducing their cellular impact. The figure also indicates the transport of Si-heavy metal complexes from roots to xylem vessels for translocation to above-ground plant parts (Source: Khan et al. [91]; Licence No: CC BY).

[93]. Similarly, Cu transporters (CTR), located in the cell membrane are upregulated when plants require Cu [94]. Smooth metal transporters like HMAs and CPx-type ATPases act as efflux pumps, removing excess metal ions from cells and facilating Cd and Zn transfer into xylem. Overexpressing *AtHMA4* improves plant tolerance to Cd and Zn stress [95]. The MATE transporter group aids moving multidrug and harmful substances out of cells [96]. To detoxify, metal ions are transported into vacuoles for storage as complex compounds under neutral conditions, with specific transporters in the tonoplast regulating this process. ABC family transporters chelate and sequester excess heavy metals before transporting them to vacuoles [97]. The CDF and MTP families transfer heavy metals to the endoplasmic reticulum or apoplast and also serve as metal sensors [98]. MHX and CAX transporters, from the CaCA family, maintain metal homeostasis by counter-transporting $Mg2+$ and $Zn2+/H+$ and are involved in Cd transport [99,91]. Besides these transporter proteins, various other cellular biomolecules and structural components also play roles in regulating heavy metal balance.

6. Importance of Si in regulation of heavy metal accumulation in fruit crops

In vitro studies of Si-mediated metal precipitation reveal that Si can reduce the availability of toxic metals to plants through precipitation processes. Under specific conditions, Si decreases metal bioavailability but it can also mobilize previously immobilized metals to address nutrient deficiencies through reversible processes induced by Si [91,100]. In the soil environment, Si increases soil pH by forming silicate precipitates, further reducing heavy metals availability. Additionally, exogenous Si application mitigates lipid peroxidation and fatty acid desaturation in plants, thereby enhancing physiological activity under heavy metal stress [101].

It is widely accepted that Si aids in heavy metal detoxification through several mechanisms, including immobilizing metals in the soil before plant uptake, stimulating both enzymatic and non-enzymatic antioxidants, co-precipitating metals, chelating metal ions, and facilitating compartmentalization. One possible explanation for the reduction of heavy metals is that Si forms strong complexes with cell wall molecules, which alters structural integrity and blocks apoplastic transport, thereby limiting metal into the plant [102]. Si is well recognized for its beneficial effects on plant growth and development, particularly in mitigating heavy metal stresses. In the following discussion, we will explore the detailed mechanisms by which silicon-induces mitigation of heavy metal toxicity in plants.

6.1. Si mediated arsenic (As) metal stress regulation in fruit crops

Arsenic, a non-essential element, can significantly disrupt soil health, plant growth, and reproduction, and pose serious risks to human health through contaminated produce. High arsenic levels in soil impede nutrient absorption by plants, compromising their physiological functions [103]. Are mimics potassium (K) for cell membrane transporters, reducing K influx. As a semi-metal, As exists in both organic and inorganic arsenic compounds-arsenite (As(III)) and arsenate (As(V))- being more detrimental to plants. Arsenite primarily enters plants via nodulin 26-like intrinsic proteins (NIPs), whereas arsenate is absorbed through phosphate transporters from the rhizosphere. Arsenic exposure induces oxidative stress by generating ROS [104]. Plants attempt to mitigate this stress using enzymatic and non-enzymatic biomolecules, although the effectiveness of these detoxification mechanisms is influenced by factors such as arsenic availability, toxicity, its movement within the plant, and the presence of other ligands.

Si can mitigate the harmful effects of As by enhancing photosynthesis and carbohydrate accumulation. Research indicates that Si application not only improves seed germination but also reduces As accumulation in tomato cultivars. Plants treated with both As(III) and Si show upregulated expression of *OsLsi1*, *OsLsi2*, and *OsLsi6* genes compared to those treated with As(III) alone, suggesting that *OsLsi* gene expression plays a role in reducing As accumulation when Si is present. Additionally, Si activates GSH-dependent peroxide scavenging mechanisms under As stress, increasing the activity of GPX and GST enzymes. This reduces oxidative damage and prevents membrane damage [105].

Recent studies by Khan et al. [106] and Zaheer et al. [107] have highlighted the potential of Si to alleviate As toxicity in date palm and *Gladiolus grandiflora*, respectively. These studies demonstrated that Si application not only reduced As accumulation in both roots and shoots but also enhancing antioxidant enzyme activities (POD, PPO, GSH, CAT). Additionally, Si application decreased the levels of ROS and lipid peroxidation. It also modulated plant hormone signaling by lowering ABA levels under normal conditions and SA and JA hormonal levels under As stress. Moreover, Si was found to upregulate genes related to ABA biosynthesis and cellular homeostasis during stress conditions.

Dogan et al. [108] investigated the effects of Si application combined with humic acid on Cd stress in strawberries, finding that it alleviated the negative impacts of Cd. Similarly, Treder and Cieslinski [109] observed that pre-planting Si application reduced Cd uptake in strawberries. These findings suggest that Si might also reduce As translocation to edible fruit tissues.

Overall, these studies underscore the potential of Si to enhance growth, manage As translocation, and promote As tolerance in fruit crops by affecting antioxidant activity and hormonal signaling. However, the role of Si in reducing As toxicity during germination in fruit crops is still underexplored and warrants further investigation.

6.2. Si mediated aluminum (Al) metal stress regulation in fruit crops

Aluminum (Al) toxicity significantly hampers crop growth in acidic soils. Lower pH levels increase Al solubility as Al^{3+}, which negatively impacts several physiological processes and reducing plant growth. This toxic form disrupts cell wall functions, nutrient homeostasis, plasma membrane properties, and signal transduction pathways [110,111].

The initial evidence of Si alleviating Al toxicity was observed in soybean studies by Hodson and Evans. Si mitigates Al toxicity through three main mechanisms: (i) increasing solution pH, (ii) reducing Al availability by forming hydroxyaluminosilicate complexes

in the external solution, and (iii) enhancing the plant's Al detoxification mechanisms. To counteract Al toxicity, plants have developed strategies such as Al exclusion and internal tolerance. Specific membrane transporter gene families, including *ALMT* (aluminum-activated malate transporter) and *MATE*, play crucial role in regulating the efflux of organic acid anions to mitigate Al toxicity [112].

Bilal et al. [113] conducted a study on date palms that demonstrated the significant benefits of combining silicon (Si) and boron (B) applications. This approach notably improved plant growth and reduced aluminum (Al) accumulation in both roots and shoots. The observed improvement was linked to increased exudation of organic acids in the rhizosphere, which immobilized Al in the soil. The study also reported an upregulation of genes related to Si transport (*Lsi2*) and Al transporters (*ALMT1, ALMT2, PMMA1, PMMA3*), which may affect Pb uptake and translocation. Additionally, the co-application of Si and B enhanced antioxidant enzyme activity (CAT, Cyt-Cu/Zn SOD) while downregulating stress hormones (ABA), suggesting improved stress tolerance. These findings underscore the potential of Si application to enhance the growth and productivity in fruit crops in Al-contaminated soils. However, further field trials are needed to assess its effectiveness in mitigating Al stress, particularly in orchid settings.

6.3. Si mediated nickel (Ni) metal stress regulation in fruit crops

Nickel (Ni) is essential for normal plant physiological functions at low concentrations but can become toxic at levels exceeding 0.05–5 µg g−1 dry weight, impairing growth and yield. Ni acts as a cofactor for enzymes, including hydrogenase, glyoxalase, methyl-CoM reductase, superoxide dismutase, urease, and peptide deformylase activities. Elevated Ni concentrations can disrupt normal stomatal activities and stomatal conductance, affecting photosynthesis, transpiration rates, and CO_2 concentration. Excessive Ni in soil often causes plant symptoms such as necrosis, chlorosis, and nutrient deficiency. Abd Allah et al. [114] observed that excessive Ni accumulation significantly decreased plant growth, total chlorophyll content, and relative leaf water content (RLWC), while increasing levels of H_2O_2, malondialdehyde (MDA), and electrolyte leakage in plant cells.

Si-mediated activation of defense systems, particularly the AsA-GSH cycle, plays a vital role in managing ROS and detoxifying methylglyoxal (MG) under Ni stress [115]. Research suggests that Si creates a reducing environment, thereby lowering natural Ni levels in plants. In Ni-stressed plants, a 10 ppm Si treatment significantly alleviated the adverse effects. Additionally, Si improved dry matter content by promoting Si-Ni precipitation in the root zone [116]. Foliar Si application also reduced electrolyte leakage and proline content, helping to restore normal growth processes and enhancing alkaloid content. The role of Si in regulating Ni stress in fruit crops warrants further research to better understanding mechanisms and to optimize Si application strategies for effective mitigation.

6.4. Si mediated lead (Pb) metal stress regulation in fruit crops

Among the various soil types, heavy metals, particularly lead (Pb), are highly toxic environmental contaminants. Pb poses lethal threats to both plant and animal health., with its toxicity being influenced by the amount absorbed by plants and the specific soil type. Once absorbed into plant cells, Pb disrupts hormonal balance and compromises cell membrane integrity. It also inhibits the activity of enzymes containing sulfhydryl groups, leading to reduction in water and mineral content in cells. Physiologically, Pb adversely affects photosynthesis pathways by impeding essential pigments like chlorophyll and carotenoids. It further inhibits the Calvin cycle and electron transport chain, ultimately reducing stomatal conductance. Studies have shown that Pb tends to accumulate predominantly in roots, followed by petioles and leaf tissues [117].

The study by Giannakoula et al. [118] highlighted the detrimental effects of Pb and Cu exposure on sour orange (*Citrus aurantium* L.) plants. These adverse impacts include oxidative stress, disrupted membrane integrity, hindered growth and photosynthesis, and potential disruption in on nutrient uptake. In mango plants, lower Pb concentrations interfere with the water-to-nutrient ratio, hinder photosynthesis, and cause hormonal imbalances, leading to a decrease in fruit production. Conversely, higher concentrations of these heavy metals heavy metals are associated with carcinogenic, teratogenic, and mutagenic effects, which can result in complete seed viability [65]. Additionally, research by Orisakwe et al. [119] demonstrates that excessive Pb retards intrauterine growth and weakens the immunological defense mechanisms in *Ananas comosus* (pineapple), *Citrus reticulata* (mandarin orange), and *Canarium schwein-furthi* (African elemi) plants.

Si application in lead (Pb)-contaminated soil significantly reduced Pb uptake, translocation, and electrolyte leakage in plants. Additionally, it decreased H_2O_2 and MDA levels, and even increased biomass yield when Pb contamination in seeds was low [120]. Similarly, Shi et al. [121] found that Si mitigated Cd toxicity by reducing Cd absorption from the soil.

Li et al. [122] explored the effects of Si amendment on Pb-contaminated soil and its impact on banana growth and tolerance to Pb toxicity. Their study demonstrated that the addition of 800 mg kg^{-1} Si (Na$_2$SiO$_3$•9H$_2$O) to Pb-contaminated soil significantly increased banana biomass across various growth stages. This Si amendment also elevated soil pH and reduced exchangeable Pb content, thereby decreasing Pb availability. Pb fractionation analysis showed a shift towards Pb bound in carbonate and residual fractions in Si-amended soils, with the ratio of Pb-bound carbonate to total Pb increasing as the plants grew. Furthermore, Si addition enhanced the activities of antioxidant enzymes) POD, SOD, and CAT) in banana roots by 14.2 %–72.1 %, suggesting that Si-mediated Pb tolerance in banana seedlings is due to Pb immobilization in the soil, reduced Pb translocation from roots to shoots, and improved detoxification mechanism within the plants. This research underscores the potential of Si amendments in mitigating Pb toxicity in plants by alternating soil properties and bolstering antioxidant defenses.

6.5. Si mediated cadmium (Cd) metal stress regulation in fruit crops

For orchids, soil with cadmium (Cd) levels exceeding 100 mg kg-1 is deemed unsuitable for cultivation. Cd toxicity can cause several detrimental effects, including chlorosis (yellowing of leaves), stunted growth, altered enzyme activity, excessive accumulation of ROS, and protein denaturation. Additionally, Cd disrupts the activity of Fe+3 reductase, resulting in iron (Fe+2) deficiency. It also interferes with the uptake of essential nutrients such as calcium (Ca), phosphorus (P), potassium (K), and magnesium (Mg), and inhibits nitrate absorption and translocation by affecting nitrate reductase activity.

Baryla et al. [123] found that even low concentrations of Cd (5 μM) negatively impacted plant growth, photosynthesis, and transpiration due to stomatal closure. Similarly, Cd adversely affected root structure. However, Kim et al. [124] reported that Si application significantly mitigated the harmful effects of Cd's, improving biomass and chlorophyll content. Typically, Cd accumulates in the endodermis and epidermis of the root. By acting as a barrier in the endodermis, Si prevents Cd from being transported to the shoot. Additionally, Si enhances cell wall extensibility, water- and light-use efficiency, RuBisCO carboxylation, and antioxidant activity. Huang et al. [125] reported that Si application increased the activities of CAT, APX, and SOD enzymes, while decreasing MDA and H2O2 concentrations.

Ahmad et al. [126] reported that sprays containing Si and Si-NPs effectively mitigated Cd toxicity in fruit crops. This mitigation was achieved by enhancing antioxidant activities, osmolytes, and photosynthetic pigments, ultimately lead to improved growth, yield, and fruit quality. Similarly, Khan et al. [127] found that Si treatment under Cd stress in date palm seedlings increased the transcript accumulation of genes encoding proline transporter 2 and GAPDH, while simultaneously downregulating the expression of the ABA receptor gene.

Understanding how silicon (Si) reduces Cd toxicity is crucial for improving fruit crop production. Nwugo and Huerta [128] examined the leaf proteome of plants grown in Cd-contaminated soil with and without Si supplementation. They identified 60 proteins involved in mitigating Cd toxicity, associated with key plant functions such as photosynthesis, protein synthesis regulation, redox homeostasis, and pathogen response. Furthermore, Si enhances the activity of class III peroxidases, which are critical for plant defense mechanisms [129].

Song et al. [130] further established that Si application under Cd stress conditions increases the levels of GSH, AsA, and NPT in the cell membrane. These molecules act as antioxidants, scavenging harmful free radicals generated by Cd exposure. Numerous studies have highlighted the role of *HMAs* in plant detoxification. *HMAs* including *AtHMA1*, *AtHMA2*, *AtHMA3*, and *AtHMA4* are involved in Zn detoxification in chloroplasts and regulate Cd accumulation in various cell organelles, primarily vacuoles and the plasma membrane. A study by Song et al. [129] demonstrated that Si treatment significantly increased the expression of *OsHMA2* and *OsHMA3* genes under Cd stress one day after treatment (1-DAT). This suggests that Si may enhance HMA activity, facilitating the sequestration of Cd into vacuoles and thereby mitigating its harmful effects on plant cells.

While the precise molecular mechanisms by which Si promotes growth in Cd-stressed fruit crops remain under investigation, numerous studies have demonstrated its beneficial effects in mitigating Cd toxicity in various cereal crops [130]. These findings suggest that Si application could be a valuable tool for alleviating Cd toxicity and improving fruit crop production in Cd-contaminated soils. Further research is needed to fully elucidate the mechanisms of Si-mediated Cd detoxification in fruit crops and to optimize Si application strategies for different fruit species and soil conditions.

6.6. Si mediated mercury (Hg) metal stress regulation in fruit crops

Mercury (Hg) does not play a role in any plant biochemical or physiological activities and offers no beneficial effects. It exists in various forms in the soil, including methylmercury (MeHg), cinnabar (HgS), and the ionic form Hg^{2+}. Mercury can persist in the soil for extended periods by forming chelates with carbonates, hydroxides, sulfides, and phosphates. Anaerobic bacteria present in the soil can convert precipitated Hg into its MeHg [131]. Plants absorb MeHg along with water through their roots, where it binds to water channel proteins, impending water movement within the plant. Consequently, Hg disrupts chloroplast and mitochondrial functions, leading to oxidative stress, membrane degradation, and oxidation of biomolecules. The presence of Hg impairs cellular functions and hampers the normal growth and development of plants [132]. Our understanding of Hg's impact on fruit crops and their defense mechanisms against its toxic effects is still limited. Further research is necessary to explore whether and how Si can help mitigate Hg stress in fruit crops.

6.7. Si mediated chromium (Cr) metal stress regulation in fruit crops

Chromium (Cr) contamination is a critical environmental issue, primarily originating from industrial and sewage water. Recent years have seen a significant increase in global chromium emissions due to industrialization. Among its various forms, Cr(VI) is the most toxic to living organisms. Its ability to pass freely through cell membranes allow it enter the cytoplasm easily, where it disrupts metabolic processes. Cr adversely affects plant growth by degrading photosynthetic pigments such as anthocyanin, disrupting water balance, and impending nitrogen metabolism within cells. These disruptions ultimately lead to a drastic reduction in seed germination rates [133].

Cr disrupts plant growth and development through multiple mechanisms. It inhibits amylases activity during seed germination, reducing sugar availability for seedlings. Cr also impairs enzymes crucial for carbon fixation and electron transport [134]. Additionally, Cr induces the production of metabolites such as glutathione and ascorbic acid, which, while beneficial in moderation, can hinder plant growth at elevated levels. In peach plants, Cr exposure notably retards growth by compromising cellular functions,

damaging cell membranes, and affecting root cell function. It also impairs photosynthesis by reducing photosynthetic pigment deposition and affects sap ascent by disrupting vascular bundle function. Studies utilizing laser-induced breakdown spectroscopy (LIBS) and inductively coupled plasma atomic emission spectroscopy (ICP-AES) indicate that Si application can reduce Cr accumulation in plant tissues. Si also enhances the absorption of essential nutrients like potassium, calcium, magnesium, and sodium. Under Cr stress, silicon application improves transpiration rates and chlorophyll fluorescence efficiency. However, while Si offers some protective benefits, it may cause structural changes in plants such as swollen chloroplasts, damaged thylakoid membranes, increased plastoglobuli, vacuole damage, and nuclear disruption [135].

In their study, Ding et al. [97] demonstrated that that the addition of Si reduced exchangeable Cr concentrations by promoting Cr binding to organic matter. Moreover, Si-treated plants showed improved growth and development, even under high Cr stress. The inhibition of Cr absorption in growing seedlings by Si can be attributed to two primary factors: first, Si-induced lignin deposition in cell walls binds Cr, thereby reducing its translocation from root to shoot [136]; Second, the formation of Si-Cr complexes also plays a role. Additionally, plants employ various strategies to minimize Cr uptake and transport. Consequently, externally applied Si effectively mitigates Cr toxicity [137]. However, the precise physiological mechanisms by which Si regulates Cr toxicity in horticultural crops are yet to be fully understood.

6.8. Si mediated iron (Fe) metal stress regulation in fruit crops

Iron (Fe) plays a crucial role in plant metabolism, but its presence requires careful regulation. Excess Fe accumulation in plants induces the production of ROS through Fenton and Haber-Weiss reactions. These ROS damage plants by degrading cell wall components, exacerbating nutritional disorders, and forming iron plaques in roots to immobilize Fe ions. This accumulation disrupts carbon metabolism by inhibiting ATP and NADPH synthesis, consequently reducing the efficiency of the Calvin-Benson cycle [138]. Conversely, Fe deficiency also imposes significant stress on plants. Symptoms of Fe deficiency is commonly observed in calcareous soils, where high bicarbonate accumulation elevates the soil pH to a range of 7.5–8.5. These deficiency symptoms, such as interveinal leaf chlorosis and necrosis, manifest during the plant's growth period, and ultimately result in decreased quality and yield [139].

Studies have confirmed that silicon enhances the transport of Fe from plant roots to shoots. One proposed mechanism involves the upregulation of Si transporters following Si supplementation in the nutrient solution. This upregulation can influence Fe uptake and translocation, thereby mitigating Fe deficiency in plants [140]. Si likely plays a role in regulating micronutrient balances, such as the Fe/Mn ratio, which is crucial for promoting chlorophyll synthesis and stimulating the growth of Fe-deficient plants. Additionally, Si promotes iron mobilization, facilitating its movement through the xylem and increasing the accumulation of Fe-mobilizing compounds like citrate and catechins in roots and xylem sap [141].

The increase in citrate levels, particularly after excluding Fe from the nutrient solution, suggests that Si promotes long-distance Fe transport and utilization in leaves. Si treatment influences the expression of genes related to Fe uptake and mobilization, enhancing Fe distribution within plants and mitigating Fe deficiency [142]. Furthermore, Si indirectly impacts gene activation linked to improved Fe acquisition and mobilization in both roots and shoots. Additionally, Si can also alleviate Fe toxicity by reducing the root's oxidizing capacity, thereby limiting excessive Fe uptake and precipitation. In rice, Si application effectively mitigates Fe toxicity by increasing Fe precipitation on the root surface or within the growth medium. This effect is likely due to pH alteration and co-precipitation with Si, preventing excessive Fe absorption and depletion from the solution.

6.9. Si mediated zinc (Zn) metal stress regulation in fruit crops

Zinc (Zn) is crucial for normal plant functions and is considered indispensable. It participates in various physiological processes, including auxin synthesis, carbohydrate metabolism, and protein metabolism. Additionally, Zn serves as a cofactor for several enzymes, particularly those essential for pollen formation. Similar to iron, Zn availability is limited in calcareous soils and decreases with increasing soil alkalinity. However, plants require Zn in smaller amounts, as excessive accumulation can hinder plant growth and even lead to complete senescence. Plants exhibit Zn deficiency when concentrations fall below 15–20 mg per kg of dry plant mass [143].

Excessive Zn accumulation disrupts the function of membrane transporters and ion channels in banana plants. This leads to increased non-specific membrane permeability and subsequent nutritional imbalances [102]. Similarly, high Zn levels in guava plants significantly reduce stomatal conductance, photosynthesis, transpiration, non-photochemical quenching (NPQ) under dark-acclimated conditions, and leaf chlorophyll fluorescence in both light (Fv'/Fm') and dark-acclimated (Fv/Fm) states [112].

When zinc concentration exceeds plant threshold limits, it manifests as visible symptoms such as phosphorus deficiency, inhibited photosynthesis, reduced floral fertility subsequent flower and fruit drop. Elevated Zn levels can decrease the activity of Cu/Zn superoxide dismutase (Cu-Zn-SOD), impairing ATP synthesis and increasing the production of ROS. Normalizing Zn concentration can reverse these symptoms; however, prolonged stress persists, the effects of zinc toxicity may become permanent. For instance, excess zinc ions can replace magnesium ions in the enzyme RUBISCO (ribulose-1,5-bisphosphate carboxylase/oxygenase), thereby inhibiting carbon fixation and causing plant death [105]. Zinc is stored in cell vacuoles, which help regulate zinc content its content by immobilizing and detoxifying it. Sinclair and Kramer [144] note that shoot tissue vacuoles act as reservoirs for metals, farming organic acid complexes based on the concentration of organic acids in various plant tissues.

Si plays a crucial role in influencing Zn nutrient uptake in plants under deficiency stress. Zinc availability in the rhizosphere is primarily controlled by two factors: the release of low-molecular-weight chelating agents and the root-induced acidification of the growth medium [145]. Consistent research shows that Si application in hydroponic and soil cultures affects Zn distribution, leading to the accumulation of both elements in similar plant regions [146]. Si strengthens cell walls, which can delay the transport of Zn ions to

shoots. Importantly, both Siand Zn predominantly accumulate near the root endodermis, where they forming zinc silicate precipitates. These precipitates can obstruct the loading and translocation of Zn through the xylem.

6.10. Si mediated copper (Cu) metal stress regulation in fruit crops

Copper (Cu) is an essential element with critical **roles** in plant biochemistry, including photosynthesis, carbon assimilation, and ATP synthesis. It is a key constituent of cytochromes, plastocyanin, and cytochrome oxidase-important components of both the respiratory and photosynthetic electron transport systems [147]. In the rhizosphere, only 1–20 % of Cu is available in a form that readily uptake, while the remainder is bound to organic matter in the soil [148]. Due to its limited mobility within the plant, Cu deficiency symptoms typically manifest first in young leaves and reproductive parts.

Excessive Cu in orchard soils can severely impact plant health by impairing root and shoot growth, inhibiting photosystem II activity, disrupting protein synthesis and enzyme functions, reducing carbohydrate concentrations, and inducing plant senescence and death, ultimately leading to decreased fruit productivity [149]. Recent studies underscore the significance of subcellular distribution in plants for Cu accumulation, migration, and detoxification [150]. Detoxification strategies, however, differs among plant species: cell wall immobilization is critical for Cu detoxification in apple trees [151], while vacuolar sequestration is the main mechanism in tomatoes [152]. Kiwifruit plants exposed to excess Cu show diminished antioxidant properties and reduced pigment deposition. Although there is limited research on the interaction between Si and Cu in fruit crops, it is known that Cu toxicity typically results in leaf chlorosis and reduced root biomass. Si application has been found to alleviate some toxic symptoms by binding Cu in the cell wall, but it does not significantly reduce the overall Cu content in leaves.

Cu deficiency at the physiological level leads to decreased respiration, inhibited photosynthetic electron transport, and stunted growth [153]. However, the application of Si mitigates the toxic symptoms induced by Cu binds with the Si deposited on the cell wall, despite this, the Cu content in the leaves remains relatively unchanged with external Si application.

6.11. Si mediated manganese (Mn) metal stress regulation in fruit crops

Manganese (Mn) is an essential element for normal enzyme function, but it is required only at low levels. Certain plant species, including peach, are highly susceptible to Mn deficiency, which can lead to significant yield reductions in winter crops when Mn levels fall below a critical threshold. Plants grown in Mn-deficient soil often exhibit symptoms such as reduced dry matter accumulation, decreased photosynthesis, and lower chlorophyll content [154]. Specifically, dicotyledonous plants show interveinal chlorosis in younger leaves, while cereals may develop gray specks. These symptoms are most commonly observed in sandy or calcareous soils.

Studies have investigated the interaction between Si and Mn in various plant species, revealing several key insights. Si enhances rice root oxidation capacity, which increases Mn oxidation in the root zone and leads to Mn deposition outside the plant. This deposition helps alleviate Mn deficiency symptoms temporarily. Additionally, Si promotes a more uniform distribution of Mn within leaves, preventing its accumulation in damaged tissues. The Introduction of Si into the plant growth medium has been shown to significantly reduce Mn levels in outer cell layers [155], likely due to Si facilitating metal adsorption onto cell walls. Soluble Si appears to influence Mn's oxidation state, encouraging its precipitation. Furthermore, research indicates that Si indirectly decreases leaf apoplastic OH- levels by reducing unbound apoplastic Mn^{2+} concentrations, thus regulating the Fenton reaction and protecting from Mn toxicity [156].

Emamverdian et al. [157] conducted a tissue culture study to investigate the effects of silicon dioxide nanoparticles on *Arundinaria pygmaea*, a bamboo species, under various heavy metal stresses (copper, manganese, and cadmium). Their findings reveal that SiO2 nanoparticles significantly impact plant growth and stress tolerance. Specifically, exposure to Cu and Mn led to enhanced plant growth, characterized by increased biomass, shoot length, protective enzyme activity, chlorophyll content, and fluorescence. Conversely, under cadmium stress, treatment with 100 μM SiO_2 nanoparticles resulted in reduced biomass and shoot length, suggesting limited effectiveness in mitigating Cd accumulation in leaves. The study concludes that 100 μM SiO_2 nanoparticles are effective in improving tolerance to Cu and Mn stresses, facilitating plant growth through mechanisms such as metal ion adsorption, increased protective enzyme levels, and enhanced photosynthetic efficiency. It proposes that a combination of 100 μM SiO_2 nanoparticles with 100 and 200 μM concentrations of Cu and Mn, respectively, optimizes the plant's tolerance to heavy metal-induced stresses in bamboo species, offering valuable insights for enhancing plant growth and stress resilience.

7. Boosting Si content in fruit crops: strategies for enhanced resilience

Crops that accumulate significant levels of Si in their shoots typically show enhanced resistance to the harmful effects of heavy metals. This section explores various strategies to increase Si accumulation in crop plants, aiming to improve their overall health and stress resilience.

7.1. Si fertigation to improve Si availability to plants

Supplying Si at appropriate levels, while staying below toxic thresholds, through various fertilization techniques has emerged as a promising method to enhance plant health and alleviate heavy metal stress in fruit crops. The application of readily absorbable silicic acid has shown beneficial effects in several cases. For instance, in strawberries, Si application improved tissue strength and durability during post-harvest handling, thereby reducing losses [158]. In gerberas, soil application of Si fertilizers led to enhanced flower quality

[159]. Research on sapota suggested that soil application of calcium silicate is a cost-effective alternative to foliar Si applications [160]. Moreover, foliar application of Si, often as potassium silicate, has proven advantages; in bananas, it improved shelf life, sugar content, and other quality parameters [161].

Slow-release Si fertilizers, such as potassium silicate encapsulated in an alginate matrix, provide sustained Si release and enhanced water retention [162], which can significantly boost crop yields, particularly in long-term field applications [163]. Additionally, steel slag, a silicon-rich by-product, offers a cost-effective and abundant Si source. Research has demonstrated its effectiveness in correcting soil acidity and benefiting low Si accumulators, such as oranges. Specially Si fertilization at 0.8 % (w/w) has improved soil physicochemical properties under heavy metal contamination and supported bacterial communities associated with heavy metal resistance [164]. These findings highlight the versatility of Si fertilization techniques in improving fruit crop health and resilience to heavy metal stress, with the optimal method based on crop type, soil conditions, and economic considerations.

7.2. Modifying soil properties to improve Si availability to plants

Intensive horticultural practices and monoculture cropping systems, particularly in tropical and subtropical regions, can lead to "desilication" – the depletion of plant-available Si in the soil. Although numerous soil remediation techniques exist for reducing heavy metal mobility and availability [165], Si's potential is often underutilized. This is despite most soil Si existing in unavailable, polymerized forms that require biological or chemical processes for conversion to plant-absorbable silicic acid (H_4SiO_4). This readily absorbed form originates from mineral weathering and maintains a dynamic balance in the soil solution, influenced by factors such as pH [166].

Adding crop residues, manure, and compost can contribute Si to the soil, though its conversion to a plant-available form can be slow. The increased biological activity associated with organic matter can, however, enhance Si solubility through microbial mineral breakdown [167]. Recent research underscores the role of microbial communities in solubilizing minerals, including Si, for plant uptake. Practices that promote beneficial soil microbes can improve Si availability for fruit crops. Additionally, maintaining optimal soil pH is crucial, as Si availability is influenced by pH. Basic conditions favor the formation of less soluble Si forms, whereas silicic acid breakdown is more prevalent under acidic conditions [168].

By implementing these strategies, we can unlock the potential of Si to enhance plant health and resilience against heavy metal stress in fruit crops. The choice of the most suitable approach depends on factors like soil type, existing Si levels, and overall farm management practices.

7.3. Identifying Si transport genes in fruit crops

Identifying Si transport genes in various fruit crops is crucial for understanding how Si alleviates heavy metal stress. Researchers can utilize a homology-based approach, comparing known Si transporter sequences from model plants with genomic data [169] from fruit crops such as apple, grape, and citrus. Bioinformatics tools assist in identifying potential Si transport genes for further investigation [170]. Functional characterization involves expressing these genes in model systems to assess their Si transport capabilities and examining their expression patterns under both normal and heavy metal stress conditions using techniques like qPCR and RNA sequencing. Genetic and genomic methods, such as GWAS [171], QTL mapping [172], and CRISPR-Cas9 gene editing [173], validate gene functions and link specific genetic regions to Si uptake traits. High-throughput transcriptomic [174] and proteomic analyses [175] provide comprehensive insights into Si transport mechanisms, identifying differentially expressed genes and transporter proteins. Case studies in various fruit crops have successfully identified Si transport genes, demonstrating the effectiveness of these methods in enhancing fruit crop resilience to heavy metal stress.

8. Future directions and challenges

As the application of Si for protecting fruit crops against various heavy metal stresses gains momentum, several promising research avenues and significant challenges require attention. Ongoing studies are broadening our understanding of Si-based crop protection, focusing on evaluating different Si sources, and their effectiveness, and refining application methods and dosages. Additionally, current research is exploring the potential of nanoscale Si in mitigating heavy metal stress in crops, along with the development of Si-based technologies to promote sustainable large-scale agriculture.

Despite the well-documented benefits of Si in alleviating heavy metal stress, several key questions remain. Uncertainties persist regarding the precise mechanisms by which Si interacts with heavy metals, its impact on heavy metals, its impact on heavy metal bioavailability, and how these interactions vary across different plant species. Addressing these gaps will enhance our understanding and enable more effective use of Si in crop protection. Si presents great promise as an eco-friendly strategy for protect horticultural crops from heavy metal stress offers great promise for a sustainable and secure agricultural future. By exploring these future possibilities and addressing associated challenges, Si can become a viable solution for improving crop resilience and food production.

9. Conclusion

Heavy metal contamination poses a global threat to fruit production, but Si has emerged as a valuable tool to mitigate this challenge. Si's effectiveness in reducing heavy metal stress is well-established, functioning through mechanisms like antioxidant enzyme stimulation and metal transport protein regulation. However, its impact can vary depending on factors such as plant species and stress

duration.

This review underscores silicon's potential to enhance fruit quality under heavy metal stress. Nevertheless, knowledge gaps persist. Future research should delve deeper into Si's role in plant biology and its interaction with stress responses. A Comprehensive understanding of silicon uptake and transport in fruit crops is crucial. Recent advancements in the characterization of silicon transporter genes are promising but they require further exploration.

While Si's stress-alleviating effects are evident, the underlying mechanisms require further exploration. This includes understanding Si's role in metal detoxification and its potential interaction with heavy metal transport systems within the plant cell. The majority of Si research has been conducted in controlled agricultural settings. Future studies should investigate Si's effectiveness in fruit crops grown in naturally contaminated soils with mixed metals, considering long-term application effects. Large-scale field trials are necessary to validate Si's ability to mitigate heavy metal stress in fruit crops. These trials should assess Si's impact on pollutant uptake, transport, and overall soil health. By prioritizing these research areas, we can fully realize Si's potential as a sustainable solution for safeguarding fruit crop production and ensuring food quality.

Ethical approval

Not required.

Ethical statement

Not applicable.

Data availability statement

All data utilized and analyzed in this study are included within the article and its supplementary materials. We obtained permission to use Figs. 2 and 3 from previously published articles through the Copyright Clearance Center. The specific license numbers are as follows: Fig. 2 (License No. 5861300445650) and Fig. 3 (License No. 5861300748532).

CRediT authorship contribution statement

Vinaykumar Rachappanavar: Writing – original draft, Conceptualization. **Satish K. Gupta:** Writing – review & editing. **Gururaj Kudur Jayaprakash:** Writing – review & editing, Validation. **Mohamed Abbas:** Supervision, Funding acquisition.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:Mohamed Abbas reports article publishing charges was provided by King Khalid University. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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