





Effect of heavy metals on strawberry (*Fragaria × ananassa*). A review

Efecto de los metales pesados sobre la fresa (*Fragaria × ananassa*). Una revisión



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Strawberry crop in Cundinamarca (Colombia).

Photo: G. Fischer

ABSTRACT

Despite their high nutritional properties, strawberries are classified as the most contaminated fruits. Their contaminants include heavy metals (HM) such as cadmium (Cd), lead (Pb), mercury (Hg), chromium (Cr) and the metalloid arsenic (As). The sources of these contaminants are water, air and soils of geogenic and anthropogenic origin, the last of which is the biggest contributor. This situation poses a health risk to humans. Between 3 and 16% of agricultural soils are affected by excessive levels of HM, especially those near industrial and mining areas, as well as those with high concentrations of pesticides and fertilizers. There is a strong correlation between the HM content in the soil and the HM content in the strawberry plants, with the greatest accumulation of HM in the root system. HM are absorbed by the roots but also aerially by the leaves, and they are also retained in the cuticle wax of the fruits. Excess HMs, especially Cd, in strawberry plants manifest themselves in a decrease in biomass, chlorophyll, stomatal conductance, growth hormones, and leaf area, as well as in oxidative damage, lower photosynthetic efficiency, and changes in the accumulation and redistribution of mineral elements. Strategies for reducing contamination in strawberry plants include the application of silicon, humic acid, melatonin, abscisic acid, or *Bacillus* spp., as well as the use of nanoparticles (e.g. SiNPs), inoculation with arbuscular mycorrhizal fungi, biochar amendments, and planting HM hyperaccumulators, among others.

Additional key words: contamination; cadmium; oxidative damage; biomass; sewage sludge; remediation.

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RESUMEN

A pesar de sus altas propiedades nutritivas, la fresa es clasificada como el fruto más contaminado, entre sus contaminantes se incluyen metales pesados (MP) como el cadmio (Cd), plomo (Pb), mercurio (Hg), cromo (Cr) y el metaloide arsénico (As). Las fuentes de estos contaminantes son el agua, el aire y el suelo de origen geogénico y antropogénico, siendo este último el mayor contribuyente, esta situación representa un riesgo para la salud humana. Entre el 3 y 16% de los suelos agrícolas se ven afectados por niveles excesivos de MP, especialmente aquellos cercanos a zonas industriales y minería, así como aquellos con altas concentraciones de plaguicidas y fertilizantes. Existe una fuerte correlación entre el contenido de MP en el suelo y el contenido de MP en la planta de fresa, con una mayor acumulación de MP en el sistema radical. La absorción de MP es por la raíz, pero también por vía aérea a través de las hojas, y se retienen en la cera de la cutícula del fruto. El exceso de MP, especialmente Cd, en las plantas de fresa se manifiesta en una disminución de la biomasa, la clorofila, la conductancia estomática, las hormonas de crecimiento y el área foliar, así como en daño oxidativo, menor eficiencia fotosintética, y cambios en la acumulación y redistribución de elementos minerales. Las estrategias para reducir la contaminación en las plantas de fresa incluyen la aplicación de silicio, ácido húmico, melatonina, ácido abscísico o *Bacillus* spp., además del uso de nanopartículas (p.e. SiNPs), la inoculación con hongos micorrízicos arbusculares, enmiendas con biochar y la plantación de hiperacumuladores de MP, entre otros.

Palabras clave adicionales: contaminación; cadmio; daño oxidativo; biomasa; lodos de depuradora; remediación.

Received: 28-06-2025 Accepted: 03-11-2025 Published: 23-12-2025

INTRODUCTION

Fruits have many beneficial effects on human health, being an essential source of minerals, vitamins, fibers and bioactive compounds, and consumption of them is increasing in line with improvements in living conditions (Taghizadeh *et al.*, 2024; Yahia *et al.*, 2019). Moreover, the increase in world population results in a corresponding increase in the demand for fruits, which are required for a healthy diet (Homeshvari *et al.*, 2024), in which toxic heavy metals (HM) should not be a part.

The uncontrolled growth of industrialization and urbanization, in conjunction with intense agriculture, has caused remarkable pressure on the world environment (Calderon *et al.*, 2023; Shahid *et al.*, 2016). The risk of HM pollution is one of the greatest challenges to agriculture and the environment (Saqib *et al.*, 2023). In general, HM contamination not only harms crop yield and quality but also affects the ecology and biodiversity of soils (Guerra Sierra *et al.*, 2021).

Jomova *et al.* (2024) characterized HM as natural components of the Earth's crust and persistent environmental pollutants. Furthermore, according to Qi *et al.* (2025), the processes that control the availability and mobility of HM are complex, due to their climatic, geochemical, biological and anthropogenic factors.

Globally, the concentration of HM and metalloids in soils, drinking and irrigation water, and thus in fruit crops, has increased (Calderon *et al.*, 2023).

Due to their biologically toxicity, persistence and non-degradable characteristics, HM have received much interest from researchers (Calderon *et al.*, 2023). As highly stable pollutants in ecosystems, they easily accumulate in food (Melebari, 2023). Marschner (2012) mentions many studies on HM in higher plants relating to contaminants originating from environmental pollution, namely lead (Pb), cadmium (Cd), mercury (Hg), chromium (Cr) and the metalloid arsenic (As). The micronutrients iron (Fe), manganese (Mn), copper (Cu), zinc (Zn), nickel (Ni), and molybdenum (Mo) are essential for plant metabolism, but, since they are HM, in excess concentrations their overall effect can be harmful to plants (Zwolak *et al.*, 2019). For their part, lead (Pb), cadmium (Cd), mercury (Hg) and metalloid arsenic (As), are very harmful to the health of humans and animals, even at low levels (Zwolak *et al.*, 2019).

There are several factors that influence HM accumulation in fruits, that depend mainly on species and variety, but also on soil factors such as pH, organic matter contents, HM concentration and chemical

form, nutrient availability, as well as climate factors such as soil humidity and temperature (Azeez *et al.*, 2018). In general, the accumulation of each HM is specific depending on its physiological effect, chemical properties and anthropogenic load (Vetrova *et al.*, 2014). Apart from the influence of water and air pollution, soil is the most important factor favoring HM bioaccumulation in plants (Khan *et al.*, 2015).

Many fruit orchards are intensively managed, using metal-based chemical pesticides and fertilizers, fossil fuels and contaminated water for irrigation, all of which are sources of chemical elements that contaminate the plant through water and soil, harming human health (Milošević *et al.*, 2014; Castañeda *et al.*, 2025). Hussain *et al.* (2019) found that consumption of contaminated plant products is very common in underdeveloped and developing countries.

Fischer and Fischer-García (2023) report different classifications of HM based on their specific density. Lambers and Oliveira (2019) and Covarrubias and Peña (2017) classified HM as elements with a density $\geq 5 \text{ g cm}^{-3}$ while Londoño-Franco *et al.* (2016) classified them as elements with a density $\geq 4 \text{ g cm}^{-3}$, and Epstein and Bloom (2004) as toxic metals, especially in their ionic form. Metal-organic forms, such as methylated and ethylated forms of Hg, As, Pb, or Cd formed in soils and sewage sludge, could be more toxic to plants, due to ease of penetration through cell membranes during root absorption (Zhao *et al.*, 2022; Mohamed *et al.*, 2025).

HMs affect human health, mainly because of their potential to alter the antioxidant defense system (Jomova *et al.*, 2024). Harmful concentrations of HM, including Cd, Al, As, Pb, Hg, and Cr, can cause gastrointestinal, renal, pulmonary, reproductive, cardiovascular, neurodegenerative, and carcinogenic diseases (Jomova *et al.*, 2024). For example, Gong *et al.* (2020) state that Cd poses a great risk for humans considering that most cases of human intoxication (70%) come from plants, where there is a half-life of between 10 and 30 years for Cd. Also, Hou *et al.* (2025) classify Cd, which affects 9% of the global crop area, as the HM with the most detrimental impact on crops, followed by Ni and Cr, affecting 5.8 and 3.2%, respectively.

HMs are often categorized according to their toxicity and danger to human health and the surrounding environment, which means that Zn, Fe and Mn are frequently listed as low toxicity metals, Cr, Ni and

Cu as moderately toxic, and Pb, Hg, Cd and As as very toxic (Mallick *et al.*, 2024).

The production of dessert strawberry *Fragaria* \times *ananassa* (*F. virginiana* \times *F. chiloensis*) has grown steadily in recent decades, exceeding 2.5 million t year¹, especially in the northern hemisphere (98%) with possible increases in the southern hemisphere, given that there are no climatic or genetic barriers (Hancock *et al.*, 2008). In addition to its production in temperate and subtropical zones, its cultivation is also possible in tropical altitudes, for example in Colombia, where Ruiz and Piedrahita (2012) mention an adaptability between 1,800 and 3,200 m a.s.l.

Globally, strawberries are the most economically important soft fruits, as a result of their intense red color, juiciness, crunchy texture, delicious flavor, and ease of consumption (Quintero-Arias *et al.*, 2021). Strawberries stand out for their richness in vitamins, minerals, antioxidants, anthocyanins, flavonoids, and other bioactive compounds that benefit the human organism (Lidiková *et al.*, 2024). Also, the content of vitamin C in strawberries exceeds that of the citrus fruits (Quintero-Arias *et al.*, 2021), with 60-90 mg vitamin C/100 g fresh weight in strawberry and only 50 mg in orange fruits. These compounds have a synergistic and cumulative impact on the improvement of human health and well-being and, above all, on disease prevention (Cianciosi *et al.*, 2025). Epidemiological studies have found that the consumption of this fruit reduces inflammation, hypertension, cancer and cardiovascular diseases, type II diabetes, neurodegenerative diseases, and obesity (Cianciosi *et al.*, 2025).

Strawberries grown in less fertile soils, including acid soils, are highly susceptible to the uptake of high amounts of HM (Lidiková *et al.*, 2024) that impair normal plant development, production and fruit quality (Dogan *et al.*, 2022). Yang *et al.* (2022) warn of the great risk of contamination by HM in strawberries, especially in the region of central China, given that this fruit is one of the most highly-consumed in the world, not only for its rich nutritional composition, but also for its pleasant sensory characteristics.

Shao *et al.* (2021) report that the large amount of pesticides applied worldwide in the technified production of strawberries have led to this fruit being the most contaminated on the 2024 Dirty Dozen™ list (EWG's Shoppers Guide to Pesticides in Produce – EWG, 2024). For example, the average US resident

consumes about 8 pounds of fresh strawberries per year, including a dozen pesticides that cause cancer and reproductive problems or are banned in the European Union (EWG's Shoppers Guide to Pesticides in Produce – EWG, 2024). Strawberry does not count as a super HM-accumulator fruit, although its ability to absorb these ions with their associated strong risks requires more consideration by growers and consumer (Yang *et al.*, 2022).

The aim of this study was to review the principal effects of excessive HM contents on strawberry growth, production, and fruit quality as well as the main strategies to mitigate the impact of HM on strawberry plants.

METHODOLOGY

Research articles and review articles from four databases were used according to the PRISMA guide, applying a modified analytical procedure of Page *et al.* (2021). The keywords “strawberry” and “heavy metal” were applied for the years 2001 to 2025, which produced about 700 article titles in the “Google Academic” database, of which 49 were used. ScienceDirect derived 106 titles, of which 9 coincided with the objectives of this review. The 3 titles from the SciELO database were included, and the Semantic Scholar base had 120 articles, with 31 suitable for this survey.

ORIGIN OF HEAVY METAL CONTAMINATION IN CROPS

The cause of HM in the food chain, according to WHO (2020), is contamination of water, soil and air, with HM in soil being of anthropogenic or geogenic origin. HMs of geogenic origin can come from the same parent material as the Earth's crust, originating from mineral weathering or emissions from volcanoes (Zwolak *et al.*, 2019). Erosion of the Earth's crust, together with volcanic activity, constitute about 80% of the natural input of metals to the environment (Martínez-Vega, 2014). In peri-urban soils, the Pb level was elevated on land near gasoline stations (<1.5 km) and industrial enterprises (<4 km) (Wu *et al.*, 2023).

Crop contamination is diverse and can be caused by the sources shown in figure 1, according to Mallick *et al.* (2024); Rai *et al.* (2019) and Li *et al.* (2018).

Similarly, Melebary (2023) highlights irrigation water, agricultural soils, cultivation practices, air pollution and packaging, cans, and materials used in equipment as sources of food contamination by toxic metals.

A significant source of contaminants entering plants and thereby the food chain is atmospheric pollution (Rodríguez-Rodríguez *et al.*, 2023), considering that metals such as Cu, Cd, Pb, Ni and Zn are 75 to

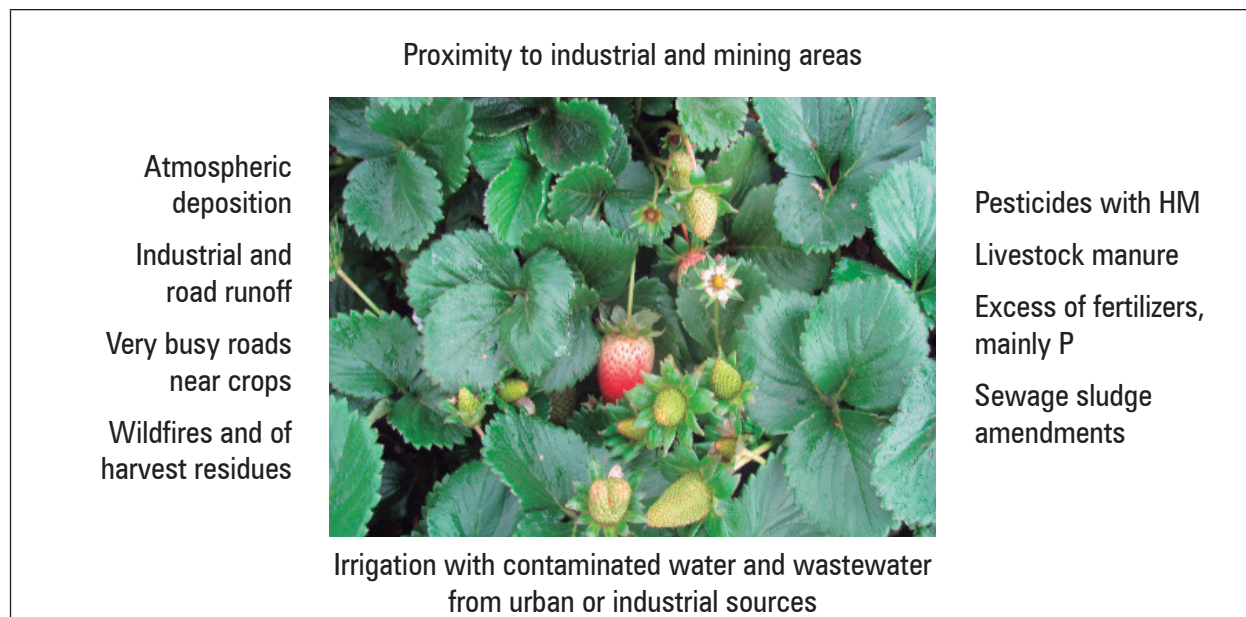


Figure 1. Main sources of contamination in strawberry crops.

90% bound to the airborne particles (Mohanraj *et al.*, 2004). HM associated with air masses can be deposited at sites far distant from their origin, on the soil or directly on plants (Fischer and Fischer-García, 2023). The physiology, biochemistry and morphology of plants are highly influenced by atmospheric pollutants and these effects vary widely depending on the species and variety (Rodríguez-Rodríguez *et al.*, 2023).

For Cd, Dogan *et al.* (2022) mention irrigation pipes, refined petroleum products, gases produced by industrial production and coal combustion, and fertilizers, particularly those containing phosphates, as important sources of contamination.

In strawberry plantations, at distances of 0-10 to 100 m from a road, near Mardan, Pakistan, Ahmad *et al.* (2022) found that Pb and Cd decreased in plants with increasing distance from the road; however, in those plants closer to the road the Cd concentrations at 1-10 m with 8.71, 8.32 and 3.81 μg in dry biomass of root, stem and leaves, respectively, surpassing the WHO permissible limit. This demonstrates that strawberry should not be planted near roads.

Moreover, concentrations of HM, especially As, can pass permissible concentrations in groundwater, resulting in increased levels in soil and plants (Panda *et al.*, 2010), as it was found for wild strawberries (*Fragaria vesca*) by Kuehnelt *et al.* (2000). Meanwhile Hou *et al.* (2025) suggest that groundwater generally contains lower levels of toxic metals than other irrigation water sources.

Hou *et al.* (2025) also relate environmental factors contributing to excess HM and their global distribution, stating that the most influential factors are near-surface temperature, potential evapotranspiration, and precipitation.

EFFECT OF HEAVY METALS ON STRAWBERRY PLANTATIONS

Effect of heavy metals in soil

According to Strumpf and Reichmuth (2009), in 97% of agricultural and horticultural zones located in rural areas in Germany, HM concentrations in harvested products do not represent a considerable risk for consumers. However, in the remaining 3% of agricultural and horticultural zones in rural areas, as

well as in urban horticultural production areas, local contamination may be above precautionary levels for soils and crops (Strumpf and Reichmuth, 2009).

In contrast to Strumpf and Reichmuth (2009), mentioned above, Hou *et al.* (2025), reviewing 1493 regional studies from a global base of soil pollution, warn that soil contamination by HM has serious effects on food production and food safety. These authors estimate that some 242 million ha (16% of the world's crop area) are affected by excessive levels of toxic metals.

In this context, soil is one of the most important sources of contamination in plantations, thus, it can be inferred that the uptake of HM through the soil-plant agri-food chain is the main cause of the increasing accumulation of HM in humans (Yang *et al.*, 2022).

Strawberries can also be grown in soils of lower fertility and in acidic soils, and these conditions can lead to higher uptake of HM (Bednarek *et al.*, 2006), except for Cr, W, V, Mo and others presenting in soil solution as anions (chromate, wolframite, vanadate, molybdate, respectively), whose mobility tends to be reduced with lower soil pH (Sparks *et al.*, 2022). HM can be released into the soil by leaching, reduction or oxidation, which would further favor their uptake by plants (Hossain *et al.*, 2008, Mohamed *et al.*, 2025). In addition, Song *et al.* (2025) state that factors such as environmental conditions, crop species, soil type, organic matter content, pH and interaction with other elements determine the HM toxicity in soil. Treder and Cieslinski (2005) found that 'Elsanta' strawberries grown in a sandy soil had a markedly higher concentration of Cd in all organs than those grown in a sandy loam-clay soil, considering that clay soils reduce the mobility and absorption of metals by retaining them strongly. Appropriate soils for strawberry cultivation are reported by González-Pedraza *et al.* (2024) with textures of loam, clay loam, silt loam, and sandy loam. HM contamination is also a significant problem in strawberry crops in soils adjacent to contaminated rivers. For example, in the case of the Bogota river in Colombia (between Villapinzón and Bosa, Cundinamarca), soil samples (0-20 cm depth) had medium to high concentrations of Cr and Cd, making remediation of these soils necessary (Lora and Bonilla, 2010). Meanwhile in the world's floodplains, not just millions of residents but also crops, such as strawberries, suffer from highly contaminated tailings from past and present metal mining activities (Macklin *et al.*, 2023).

Table 1. Effect of HM stress on strawberry plant growth and physiology.

Heavy metal	Methodology; country	Effects on growth and physiology	Author(s)
Cd	'Rubygem' exposed to 50 mg kg ⁻¹ Cd; Türkiye	Decreased plant FW ¹ and DW ² , leaf stomatal conductance, relative water content, chlorophyll, leaf area and number of leaves, leaf N, P, K and root N, P, K, Mg and Ca. Increased leaf temperature, membrane permeability, lipid peroxidation and proline level	Dogan <i>et al.</i> , 2022
Cd	The nutrient solution of 'Yellow Wonder' was used alone or enriched with 15 µM CdCl ₂ (Cd); China	Induction of oxidative damage, reduced photosynthetic efficiency, changes in the accumulation and redistribution of mineral elements. Reduction of gibberellic acid, indolacetic acid and trans-zeatinriboside concentrations, while abscisic acid concentration increased	Song <i>et al.</i> , 2024
Cd	When watering the pots, 0, 15, 30, 45 or 60 mg kg ⁻¹ CdSO ₄ × 8 H ₂ O was added 4 times during growth; Türkiye	Excessive Cd treatments on 'Camarosa' reduced chlorophyll <i>a</i> and <i>b</i> , increased malondialdehyde (MDA ³) and antioxidant enzymes (SOD ⁴ and CAT ⁵), changed nutrient concentrations in leaves and roots, and reduced plant growth by 30%	Muradoglu <i>et al.</i> , 2015
Cd	'Albion' strawberry plants were subjected to 0, 7.5, 15, 30, 60, 90 mg Cd kg ⁻¹ in soil; Colombia	Cd accumulated mainly in the root of the plant. In the 60 and 90 mg treatments there was less dry mass accumulation, due to the reduction in gas exchange. Loss of electrolytes after as few as 20 days at high Cd concentrations decreased chlorophyll	Martínez-Vega, 2014
Cd	'Elsanta' was exposed to three rates of Cd (0.3, 2.5 or 5 mg Cd kg ⁻¹) and four rates of salinity (0, 20, 40 or 60 mM NaCl) in peat substrate (pH=5.5); Croatia	Leaves and fruits accumulated 1.86 and 2.28 mg kg ⁻¹ Cd (subtoxic level), respectively, due to a lower translocation of Cd to the aerial part of the plant, with similar Cd mobility in phloem and xylem. 60 mM NaCl increased Cd accumulation in fruits. The combination of NaCl+Cd produced severe effects on vegetative growth and plant physiology	Ondrasek <i>et al.</i> , 2021
Cd, Pb	Analyzing HM content in plantations 0-10, 10-50, and 50-100 m away from a road; Pakistan	Pb and Cd decreased in the plants with increasing distance from the road; however, closer to the road the Cd passed the WHO ⁶ permissible limit. The highest concentration of Pb in the fruits was at 0 to 10 m from the road. Proline and phenol contents increased with increasing Pb and Cd in leaves and roots	Ahmad <i>et al.</i> , 2022
Pb	In 'Camarosa', when watering the pots, 0, 20, 60 and 80 mg kg ⁻¹ Pb (NO ₃) ₂ was added four times during growth; Türkiye	The two high Pb concentrations reduced chlorophyll <i>a</i> and <i>b</i> , increased MDA, lipid peroxidase and antioxidant enzymes (SOD, CAT, APX ⁷) and altered the concentrations of nutritional elements in leaves and roots. Accumulation of Pb content in the roots was about twice that of leaves	Muradoglu <i>et al.</i> , 2016
Zn, Mn	In the pots used for the 'Camarosa' 350 mg kg ⁻¹ Zn or 150 mg kg ⁻¹ Mn were added to the substrate; Colombia	In leaves, high concentrations of Zn and Mn reduced biomass, leaf area, chlorophyll and carotenes. In fruits, total soluble solids and fruit size were reduced. Zn toxicity was higher than Mn toxicity	Casierra-Posada and Poveda, 2005
Ni, Fe, Zn, Cu, Pb.	Accumulation of MP in organs of 4 varieties of strawberry in a forest soil under pollution; Russia	Mamochka, Rubinoviikulon and Bylinnaya varieties accumulated more Pb in leaves than in roots, presumably due to atmospheric foliar uptake. Pb concentration in 'Bogema' was reduced in the following order: roots > rhizomes > leaves > fruits	Vetrova <i>et al.</i> , 2014
Zn, Cu, Pb, Cd, Al, Cr, Co, Ni, K, Mn Mg, Fe, B	Plants in a closed growing chamber, with air contaminated by recirculating HM; Spain	Cd, Ni and Cr in the fruit had the highest incidence, showing that the fruit had the greatest capacity to accumulate HM inside the plant organs. The second highest contamination levels were in the leaves and the third highest in the soil affected by HM deposition	Rodríguez-Rodríguez <i>et al.</i> , 2023
Ni, Zn, Cd, Cr, Cu, Pb, Al, Fe, Mn, V, Hg, Mo, Co, As, Se, Ag, Sr, Sn, Ti, Sb	Use of a bioremediated marine sediment as a substrate, alone or in mixture with peat; Italy	Bioremediated marine sediment alone or mixed as substrate did not cause any HM accumulation in the fruit that surpassed the limits set in European legislation. In roots, leaves and stems the most abundant HM were Fe, Mn, Zn, Sr and Al. In the fruit, only Fe, Mn, Zn, Al, Mo, Ni and Mn were detected	Martínez-Nicolás <i>et al.</i> , 2020

¹FW: fresh weight; ²DW: dry weight; ³MDA: malondialdehyde; ⁴SOD: superoxide dismutase; ⁵CAT: catalase, ⁶WHO: World Health Organization; ⁷APX: ascorbate peroxidase.

The use of soilless cultivation systems has shown that composts, depending on their origin, can cause high concentrations of HM in strawberry fruits, as found by El-Sayed *et al.* (2016) for Ni and Pb HM in the Festival variety using a substrate mixture of perlite:plant compost (4:1).

In contrast, the use of dredged bioremediated marine sediment from a port in Italy as a substrate alone or mixed with peat for strawberry plantations did not cause any accumulation of HM or pesticide that surpassed European legislation limitations in the fruit (Tab. 1) (Martínez-Nicolás *et al.*, 2020), instead conferring to the substrate a lighter texture with a higher porosity and a higher organic carbon content in soil.

For the maintenance of soil structure and recycling of plant nutrients, as well as for better management of pests and diseases and detoxification of harmful substances, soil bacteria are essential, considering that acid soils in strawberry crops can limit microbial activity and increase susceptibility to HM (Quintero-Arias *et al.* (2021), and that HMs in harmful amounts in the soil impair microbial communities and enzyme activity, leading to soil degradation (Aji and Olufemi, 2024) and, in turn, affecting crop growth (Pruteanu, 2023).

Effect of heavy metals on strawberry plants

To counteract HM stress, plants consume more energy for metabolic changes, including synthesis of glutathione, phytochelatin, and metallothioneins, which affect other physiological processes such as respiration, nutrient uptake, photosynthesis, metabolism, water balance and reproduction (Pruteanu, 2023). Kumar *et al.* (2019) list the following plant reactions to HM toxicity: chlorosis, necrosis, wilting, senescence, metabolic disorders, growth slowdown, yield decrease, reduced ability to fix atmospheric nitrogen, nutrient deficiency, low seed number and, at the extreme, plant death. In addition to the physiological reactions mentioned above, Faizan *et al.* (2023) also highlight the accumulation of growth inhibitors and metabolic toxicity in the plants.

The uptake of HM by plants depends on the type of species and the physicochemical characteristics of soil (Ahmad *et al.*, 2022). Shahid *et al.* (2016) specify that the uptake of HM by roots is influenced by metal chemistry, soil cation exchange capacity, soil

particle size, organic matter content, soil pH and microbial activity.

With reference to the entry of HM into strawberry plant tissues, Rodríguez-Rodríguez *et al.* (2023) mention the two routes, their absorption from the soil or deposition from the atmosphere, however, there is also the possibility, according to Li and Chen (2009), that inorganic or organic contaminants are retained in the cuticle wax of the fruits, in general. In the case of uptake HM by leaves, these are transported via phloem to the target organs of the plant, but less than 1% of them move to the roots (Shahid *et al.*, 2016). For the uptake of HM by leaves, Schreck *et al.* (2013) mention, as results of their research with *Lactuca sativa*, the following mechanisms: (1) penetration of HM through stomatal pores and (2) absorption through the thin/underdeveloped leaf cuticles, such as those found around the trichome base or in young leaves or understory leaves underexposed to direct sunlight. Leaf uptake of HM depends mainly on the type of metal, in addition to leaf morphology and size, cuticle composition, and epidermis structure (Shahid *et al.*, 2016).

Kordrostami *et al.* (2020) point out that, in most cases, cations of HM absorbed by roots accumulate in this organ because these ions are physically absorbed by the extracellular and negatively charged regions of the roots and few of them are transported to the aerial part of the plants. According to Shahid *et al.* (2016), as a result of root uptake 95% or more of the metal is accumulated in the roots. Thus, in strawberries near a road in Pakistan, the highest Pb concentrations were observed in the order: roots > leaves > stem > fruits (Ahmad *et al.*, 2022). Tong *et al.* (2022) point out a strong correlation between the Pb content in strawberry plants and the heavy metal content in soil, with the roots being the main pathway for Pb uptake.

On the other hand, depending on the HM and variety, there are differences in the distribution of these ions to the aerial part of the plant. In the case of Cd uptake, the highest concentration was found by Treder and Cieslinski (2002) in the roots of 'Elsanta' strawberry, while in 'Senga Sengana' it was found in the leaves and fruits. These authors also observed that Cd in heavy soils have led to higher concentrations of these ions in roots and leaves, but without any effect of soil type on Cd level in fruits. The transport of HM from roots to the aerial parts of the plants is through the xylem (Shahid *et al.*, 2016). Vetrova *et al.* (2014)

emphasize that plants can regulate the penetration of toxic HMs into fruits through physiological barriers that exist between the stem and fruits, as well as barriers between the stem and leaves and between the roots and stem, meaning that, in many cases, HMs remain in the root tissues. In addition, Pruteanu (2023) concluded that strawberries can develop protective mechanisms, because at the end of the vegetative period, the HM transfer coefficient (between soil and plant) decreases as the concentration of HM (Cu, Pb, Zn) in soil increases. Due to the preference of strawberry to accumulate more HM in the roots than in other organs, Martínez-Vega (2014) assumes that the Albion variety accumulates Cd mainly in the roots, as a possible strategy to protect the photosynthetic apparatus of the plants.

Most studies on HM in strawberry have been conducted with Cd, finding that this plant contaminant reduces growth (Tab. 1), mainly due to the effect on photosynthesis (Song *et al.*, 2024; Martínez-Vega, 2014), also induced by the decrease in chlorophyll content (Martínez-Vega, 2014; Muradoglu *et al.*, 2015; Dogan *et al.*, 2022), leading to lower plant biomass accumulation (Martínez-Vega, 2014; Muradoglu *et al.*, 2015; Ondrasek *et al.*, 2021), including lower leaf area and number of leaves (Dogan *et al.*, 2022). Similar effects were caused by high concentrations of Pb (Muradoglu *et al.*, 2016) and Zn and Mn (Casierra-Posada and Poveda, 2005). By measuring chlorophyll *a* fluorescence, Martínez-Vega (2014) found that concentrations of 60 and 90 mg Cd kg⁻¹ in the plant and soil affected photosynthetic activity in 'Albion', when comparing this to photosynthetic activity under lower concentrations (Tab. 1).

These plant growth reductions also reflect the decreased levels of indoleacetic acid, gibberellic acid and trans-zeatinriboside, while increased abscisic acid in strawberries exposed to high concentrations of Cd (Tab. 1) indicates alterations in the signaling pathway in these phytohormones (phytohormone signaling pathway) (Asiminicesei *et al.*, 2024; Song *et al.*, 2024). In turn, changes in the accumulation and redistribution of mineral elements were found in strawberry plants stressed by high concentrations of Cd (Muradoglu *et al.*, 2016), as shown by reduced levels of N, P, K in leaves and N, P, K, Mg and Ca in roots (Dogan *et al.*, 2022). However, Muradoglu *et al.* (2015) observed an increase in the concentrations of Mg, K, Ca, Fe, Zn and Cu in leaves and roots under Cd stress; Fe, Zn, and Cu are constitutive parts of antioxidant enzymes such as superoxide dismutase,

which can explain their accumulation in organs exposed to Cd.

Regarding fruit quality, high concentrations of Zn and Mn reduced the size and level of total soluble solids (Casierra-Posada and Poveda, 2005) (Tab. 1). In general, the accumulation of HM in strawberry fruit is high compared to other crops, e.g. tomato (Rodríguez-Rodríguez *et al.*, 2023), although when comparing accumulation in different parts of the strawberry plant, the Pb content was the lowest in the fruits (Ahmad *et al.*, 2022), possibly due to the previously-mentioned physiological barriers between the stem and the fruits (Vetrova *et al.*, 2014), taking into account differences in this behavior depending on the plant variety (Treder and Cieslinski, 2002).

However, there are other factors that can exacerbate HM concentrations in the strawberry fruits, such as additional contamination of the plants with NaCl (60 mM) (Ondrasek *et al.*, 2021) (Tab. 1). Likewise, in air pollution, strawberry fruits showed the highest capacity to accumulate the HMs Cd, Ni, and Cr (Rodríguez-Rodríguez *et al.*, 2023) (Tab. 1), highlighting the importance of the type of pollution.

It is well known that plants generate reactive oxygen species (ROS) in response to abiotic stresses such as HM toxicity, causing severe damage to cellular structure and organelles that alters the normal function of cells (Deshmukh *et al.*, 2017). There is a complex relationship between HM and the physiological and biochemical responses of plants, highlighting how metal stress alters biosynthetic pathways, altering the concentrations of secondary metabolites (Asiminicesei *et al.*, 2024). In strawberry, high concentrations of Pb caused oxidative damage, shown by the increase in the activity of lipid peroxidase and antioxidant enzymes (SOD, CAT, APX) (Muradoglu *et al.*, 2016) (Tab. 1). Likewise, high levels of Cd in strawberry increased MDA concentrations in leaves and roots and the activities of CAT and SOD (Muradoglu *et al.*, 2015) (Tab. 1). Also, Martínez-Vega (2014) observed an early antioxidant response in 'Albion' stressed by Cd, while POD (peroxidase) and proline were not induced by Cd. Meanwhile Ahmad *et al.* (2022) detected higher phenolic and proline contents in the strawberry leaves than in the roots when Cd and Pb concentrations were high (Tab. 1).

Regarding the effect of the application of sewage sludge on the growth and physiology of 'Camarosa' strawberry, KubilayÖnal and Topcuoğlu (2012)

applied 0.15, 30 and 60 t ha⁻¹ (on a DW basis), observing that, with the increase in the rate of sludge, the levels of minerals and HM also increased, as did the concentrations of N, P, K, Fe, Mg, Zn, Cd, Cu and Pb in the fruits, in addition to an increase in plant growth. However, it is also worth mentioning that when the levels of sewage sludge exceed a certain limit, the levels of HM in the plants also increase, requiring control in the appropriate recycling of sewage sludge in strawberry crops (KubilayÖnal and Topcuoğlu, 2012).

Ceccanti *et al.* (2022) amended sewage sludge (10 and 20% of the weight of the soil) to study the photosynthesis of strawberries growing in pots, finding that the amendments increased the values of foliar net photosynthesis (Pn) and stomatal conductance (gs) due to the nutrients provided. In the fruits of plants with 10% sewage sludge, higher contents of Zn and Hg were found compared to controls, but these remained lower than the limits set by the FAO/WHO.

Christou *et al.* (2016) irrigated a strawberry crop with wastewater, tertiary treated, with different irrigation systems, sprinkling and drip, finding that the wastewater did not affect the HM content in the fruits, the antioxidant content, the flavor, or the marketability of the fruits, compared to irrigation with clean water (controlled irrigation).

In 'Yellow Wonder' wild strawberry plants, Song *et al.* (2024) found that Cd contamination affected the expression of genes such as those related to nitrogen assimilation and absorption, while this also strengthened the plant by supplying energy reserves that ensured its survival. In addition, in these plants exposed to Cd toxicity, the biosynthesis of flavonoids and anthocyanins was promoted, increasing the free radical scavenging capacity. In general, HM toxicity in plants can increase the excessive production of reactive oxygen species (ROS), which promote genotoxicity by damaging DNA, proteins, and membranes (Lin *et al.*, 2007).

In order to find HM tolerance genes Haider *et al.* (2022) conducted a gene expression analysis on strawberries intoxicated by Cd, finding that *FvMTP1*, *FvMTP1.1*, and *FvMTP4* are induced in the leaves, while in the roots *FvMTP1.1* and *FvMTP4* are induced. They also found that, in these plants, the accumulation of Cd was greater in the roots than in the leaves.

SOME STRATEGIES TO CONTROL HEAVY METAL CONTAMINATION IN STRAWBERRIES

In strawberry crops, several strategies have been used to reduce HM content in the plant, especially in the fruit (Fig. 2). In sandy soils contaminated with Cd,



- Silicon amendments or application
- Application of humic acids
- Application of melatonin
- Application of abscisic acid
- Use of nanoparticles (e.g. SiNPs)
- Biochar amendments
- Application of *Bacillus* spp.
- Inoculation with AMF (e.g. *Rhizophagus intraradices*)
- Planting of HM hyperaccumulators

Figure 2. Examples of strategies for mitigating the impact of HM on strawberry crops.

amendment with silicon before planting reduced the harmful absorption of this HM by the plants and its accumulation in leaves, stems and fruits, but this effect was not observed in the roots (Treder and Cieslinski, 2005), while these authors did not verify these beneficial effects when they applied foliar potassium silicate. Also, these positive effects of mitigating Cd stress (50 ppm in a Hoagland solution) were found by Dogan *et al.* (2022) in the Rubygem variety when applying silicon (5 mM), humic acid (5 mM) or silicon + humic acid (5 mM + 5 mM) in a Hoagland solution, thereby reducing leaf temperature, membrane permeability, lipid peroxidation and proline contents, improving physiological, biochemical, morphological parameters and mineral content. Humic acids can decrease the transport of toxic HMs by precipitating them, so the plants reduce the absorption of these harmful elements (Rose *et al.*, 2014). While silicon mitigates stress due to HM contamination through mechanisms such as metal transport protein regulation and the stimulation of antioxidant enzymes (Rachappanavar *et al.*, 2024). Zeolite also reduced the uptake of Pb by strawberry plants by as much as 1.5 times and of Cd by up to 15.0 times (Galiulin *et al.*, 2002).

In strawberry seedlings, Cd stress was mitigated by the melatonin applications, which increased biomass production, growth, photosynthetic rate, and pigment content, in addition to promoting synthesis of secondary metabolites such as anthocyanins, phenolics, and flavonoids that restricted the high accumulation of H₂O₂ (Saqib *et al.* 2023). Melatonin plays an important role in alleviating oxidative stress and modulating the expression of stress-related genes (Sati *et al.*, 2023).

Interestingly, the stress hormone abscisic acid (ABA), at a foliar application of 40 $\mu\text{mol L}^{-1}$, effectively reduced the uptake of Cr, Hg, and Cd in strawberries (Kocaman, 2023), as well as increased the glutathione (GSH) levels (Liu *et al.*, 2023).

In organic strawberry crops in Türkiye, Şener and Cantemur (2023) found a higher quality of the fruits than in crops with traditional management. In both types of crop management, Cu and Zn accumulation was observed in the fruits, but without exceeding the legally permitted limit. Likewise, Liu *et al.* (2023) report that applications of selenium (Se) fertilizers to plants with HM stress have mitigated this damage, although it should be considered that high concentrations of Se can be toxic due to changes in the

structure and function of proteins (Hasanuzzaman *et al.*, 2020), especially those that contain amino acids cysteine and methionine, where Se could replace S.

Other remedies for mitigating toxic HM concentrations in crops are the use of nanoparticles (such as biogenic silicon nanoparticles (SiNPs) in HM stress mitigation (Maqsood *et al.*, 2023) due to their ability to intercept and form stable complexes with HMs, preventing their translocation within the plant (Faizan *et al.*, 2023). Furthermore, biofertilizers that are prepared from microorganisms can be applied to the soil and/or plant and are capable of synthesizing substances that improve tolerance to HM stress, among other effects (Romero-Romano *et al.*, 2012).

For sustainable management in agricultural regions exposed to HM toxicity, the use of biochar, a product derived from pyrolysis, torrefaction, gasification and hydrothermal carbonization using plant biomass, is an important alternative (Subramanian *et al.*, 2024). This biochar, due to its excellent physical and chemical characteristics, makes it ideal for use as an adsorbent in the treatment of HM in soils and aquatic ecosystems (Aziz and Mustafa, 2023).

Another type of bioremediation to reduce HM contamination is the bacteria *Bacillus* spp., with its different strains capable of reducing Cd, Pb, Hg, As, Cr or Ni in the soil, in addition to stimulating plant growth (Wróbel *et al.*, 2023). On the other hand, inoculation with arbuscular mycorrhizal fungi (AMF), especially *Rhizophagus intraradices*, showed good results in reducing Cd absorption and thus Cd concentrations in roots and stems of plants such as soybean and rice, demonstrating that this is important strategy for healthy crop production in contaminated soils (Xin, 2024).

Additionally, HM hyperaccumulator plants are a good way of extracting HM from soils. This includes the use of Guinea grass (*Panicum maximum*) to extract Hg, Bahama grass (*Cynodon dactylon*) for Cd and Zn and sunflower (*Helianthus annuus*) for Pb (Saa-Aondo *et al.*, 2024).

Apart from these few strategies presented to manage HM stress in soil and plants, the study of plants related to their physiological, biochemical and molecular mechanisms to resist this type of stress can lead to the development of species and varieties that show low absorption and accumulation of these toxic metals (Song *et al.*, 2025). Thus, the ecological risk of HM

accumulation in fruits could be reduced by creating and selecting varieties according to their physiological characteristics to adapt to these adverse conditions (Vetrova *et al.*, 2014).

CONCLUSIONS

The uncontrolled growth of industrialization and urbanization, in conjunction with intense agriculture, has caused remarkable pressure on the world's environment, with the risk of contamination with HM being one of the greatest challenges to agriculture and the environment, harming human health.

Strawberry, a fruit with high nutritional properties, is also the most polluted fruit globally, and is susceptible to excessive levels of HM such as cadmium (Cd), lead (Pb), mercury (Hg), chromium (Cr) and the metalloid arsenic (As), among others.

The sources of these pollutants are water, air and, especially, soils of geogenic and anthropogenic origin, especially those in proximity to industrial and mining areas, and those exposed to high concentrations of pesticides and fertilizers.

HM absorption takes place mainly via the roots, with the greatest accumulation of HM in this organ. However, HM can also be absorbed from the leaves aerially and retained in the cuticle wax of the fruit.

Various studies, especially with Cd, showed that excess HM in strawberry plants reduces biomass, stomatal conductance, chlorophyll, growth hormones and leaf area, as well as causing oxidative damage, lower photosynthetic efficiency, and changes in the accumulation and redistribution of mineral elements.

Strategies to reduce contamination in strawberry plants include the application of silicon, humic acid, melatonin, abscisic acid and *Bacillus* spp. in addition to the use of nanoparticles (e.g. SiNPs), inoculation with arbuscular mycorrhizal fungi, biochar amendments and planting of HM hyperaccumulators, among others.

Conflicts of interest: The authors disclaim no conflict of financial interests or personal relationships that could have appeared to influence this work.

Funding statement: This research received no external funding.

Author's contributions: Conceptualization, GF; writing—original draft preparation, GF, SM, YR and JLV; writing-review and editing, GF, SM and YR. All authors have read and agreed to the published version of the manuscript.

Open source research data repository: not available.

AI use statement: AI was not used in this review.

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