Review

Advances in Plant Science and Environment

Melatonin-Mediated Alleviation of Heavy Metal Toxicity in Horticultural

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Highlights

- Melatonin enhanced heavy metals stress tolerance in horticultural crops.
- Melatonin efficiently restricted heavy metals accumulation from root to shoot.
- Melatonin protected photosynthetic efficiency under heavy metals stress environment.

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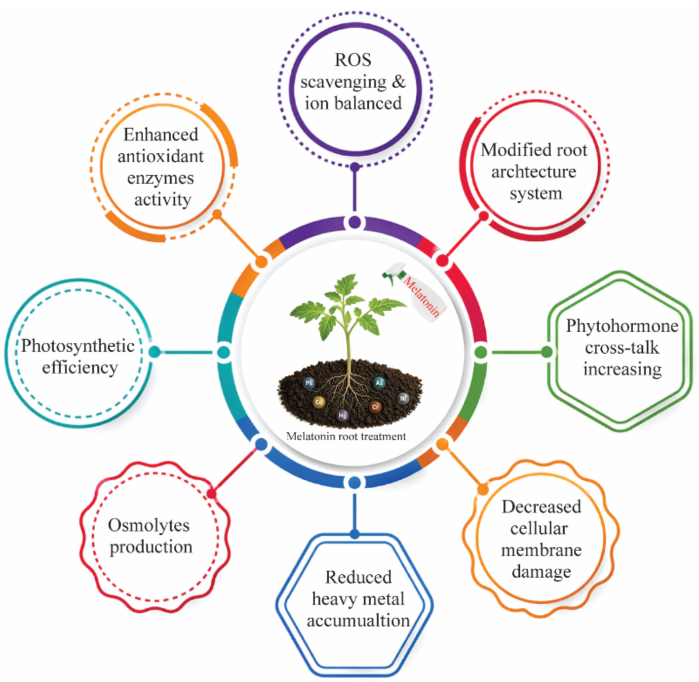
Graphical Abstract



Abstract

Human activities have caused heavy metal (HM) pollution to become a major agricultural and environmental challenge worldwide. Scientists worldwide investigate strategies to decrease the toxicity of HMs in agricultural land and their detrimental effects on plant growth. Melatonin (MT), a multifunctional molecule with strong antioxidant properties, has gained recognition as a stress-alleviating agent that works particularly well against HM-induced stresses. MT functions as a recently recognized signaling molecule and plant growth regulator that plays an essential role in strengthening plant resistance against abiotic stress. MT effectively mitigates HM stress in horticultural crops as scientists identify it as a promising solution to manage HM contamination in plant species. The review article evaluates MT's function in decreasing HM toxicity levels in horticultural plants through the identification of associated physiological, biochemical, and molecular mechanisms and minimizing rhizosphere HM concentrations and MT-mediated metal sequestration while maintaining nutrient levels and activating defense systems and hormone pathway involvement. This review article establishes a theoretical framework for regulating HM ion accumulation in horticultural plants grown in contaminated soils.

Keywords: Melatonin, Heavy metals, Photosynthesis, Root growth, Contaminated soil

1. Introduction

Global food, nutrition, and economic sustenance depend heavily on horticultural crops. However, as these crops face high levels of biotic and abiotic stressors, both production and quality are severely affected (Parmar et al., 2017). Increasing levels of HMs in fertile soils pose a serious global risk to crop growth, development, and yield (Fargasová et al., 2015). Elements are designated as metals or metalloids if their densities exceed 5 g cm^{-3}; among these, some are required by plants at very low concentrations (Madanan et al., 2021). Plants require certain metals in very low concentrations as micronutrients, including nickel (Ni), iron (Fe), manganese (Mn), copper (Cu), and molybdenum (Mo) (Page and Feller, 2015). These metals play roles in redox reactions and are essential for plant metabolism at optimal concentrations (Ghori et al., 2019). Pollutants such as arsenic (As), lead (Pb), mercury (Hg), chromium (Cr), strontium (Sr), thallium (TI), vanadium (V), titanium (Ti), lanthanum (La), and cadmium (Cd) are well known (Edelstein and Ben-Hur, 2018). Anthropogenic and natural activities release large amounts of these toxic compounds into the atmosphere, thereby increasing HM levels in soils (Morkunas et al., 2018). HM are stable and non-degradable, with no natural means of removal from the environment. HM can be either immobile, remaining in place once accumulated, or mobile, allowing plants to absorb them from soil and water through diffusion, or metal transporters (Ashfaque et al., 2016). Thus, plants are natural bio accumulators, absorbing and accumulating different HM in soil and water, some of which may be necessary for optimal growth (Ghori et al., 2019).

HMs cause phytotoxic effects on physiological, biochemical, and molecular processes in plants. As a result, HMs induce the production of reactive oxygen species (ROS) in plants, which can accumulate, leading to lipid peroxidation as a marker of ROS-caused cellular injury (García-Caparrós et al., 2020 Hassan, 2024). A variety of defensive or detoxification mechanisms have evolved in plants, conferring tolerance to HMs (Xie et al., 2019). Scavenging of ROS in plants to resist oxidative stress is mainly controlled by enzymatic and nonenzymatic antioxidants (Sharma et al., 2019). Therefore, an effective approach is needed to improve stress tolerance and crop yield (Behera et al., 2022).

A promising approach to regulate gene expression and assist in stress tolerance in horticultural crops under harsh conditions has been identified as melatonin (MT) (Tiwari et al., 2020). MT is an essential biomolecule that is involved in plant growth and developmental processes. It is similar to auxin in function, promoting root and hypocotyl growth and increasing seedling biomass (Byeon and Back, 2014). Both MT and indoleacetic acid (IAA) are involved in plant physiological processes and are structurally and biosynthetically similar (Arnao and Hernández-Ruiz, 2006). It has been reported that MT participates directly or indirectly in the biosynthesis pathways of phytohormones such as gibberellin (GA) and abscisic acid (ABA), acting as an endogenous regulator of the gene expression involved in their synthesis (Li et al., 2015). Recently, MT has emerged as a potential strategy to promote postharvest preservation of fruits and vegetables (Chen et al., 2020). Given the significance of the many functions that MT, as a hormone, plays in plants, it is necessary to understand the role of MT in plant-environment interaction. This book chapter summarizes the emerging role of MT in the physiological and molecular basis for the improvement of horticultural crop growth and development exposed to HM stress.

2. Effects of Heavy Metals on Plants

The presence of HMs in the soil inhibits plant growth and development, resulting in a reduction in horticultural crop production. Oxidative stress initiated in plant cells under HM stress involves various signaling pathways and plant antioxidant defense responses.

2.1. Morphological and Physiological Changes

Plant productivity and growth are reduced due to altered plant morphological, biochemical, and physiological responses under severe environmental conditions (Sandeep et al., 2019). As in Table 1, the pronounced effects of HMs on plants, including stunted growth and impaired physiological processes, are described. Direct contact of roots with the HM-polluted soil limits the water and nutrient availability for the plant, causing restricted growth (Nawaz et al., 2018). Consequently, the transport of HM to the upper part of the plant is harmful to productivity and fruit quality of horticultural crops (Ashfaque et al., 2016).

At the early stages of development, seedlings show high sensitivity to environmental factors (Singh and Prasad, 2014). Plants show an unregulated water response as the primary effect of HMs because these pollutants disrupt aquaporins in cellular structures. Aquaporin proteins (AQPs) experience inhibition in the epidermal cells of onion bulbs, which leads to decreased cell water permeability due to HM (Przedpelska-Wasowicz and Wierzbicka, 2011). Research shows that rising Cr levels in plants result in reduced water potential, together with increased transpiration rate and higher relative water content and diffusive resistance (Zewail et al., 2020). Like Co and Mn, Zn, P, and Cu also affect the transport of these metals from root to shoot in cauliflower. It reduces the concentration of Fe and decreases enzymatic activity and chlorophyll content (Chatterjee, 2000). During lipid peroxidation, HM disturb the composition of the plasma membrane by causing it to lose its integrity and create a water imbalance (Alaraidh et al., 2018). HMs harm cellular membranes by altering their composition and disrupting transporter functions, which lowers the intake of necessary nutritional substances (Iti, 2013). HMs harm the photosynthetic system and block Calvin cycle enzyme function, which leads to CO_2 shortage triggered by stomatal closures (Lalelou et al., 2014) (Fig. 1). The stomatal regulation and closure induced by metals' disturbance in the photosystem were found to directly affect the K^+ flux in guard cells (Fargasová et al., 2015). The toxicity of HM toward plant growth and development in horticultural crops is detailed in Table 1.

2.2. Oxidative stress

Metabolic processes produce ROS through the formation of three recognized natural byproducts: the hydroxyl radical, superoxide radical, and hydrogen peroxide (H_2O_2) (Gupta et al., 2016). Cells produce these compounds inside chloroplasts, peroxisomes, mitochondria, and plasma membrane organelles. ROS generation and the consequent redox imbalance state of the cell are associated with the toxic effects of HM (Feki et al., 2021). Oxygen is reduced to H_2O_2 by HM stress in the cell, and H_2O_2 can form OH•, causing oxidative damage (Chaki et al., 2020). HM-induced stress results in both direct and indirect ROS production, which disturbs metabolic pathways and disables enzymes required for antioxidant defense (Ramakrishna and Rao, 2015). Under prolonged environmental stress conditions, plants generate an excessive amount of ROS that exceeds the oxygen-scavenging mechanisms' ability to neutralize it. The interaction of ROS with lipids and the subsequent process of lipid peroxidation, together with the denaturation of proteins involved in cellular processes (Fig. 2), results in DNA and cellular functional damage (Ali et al., 2019).

Several studies have shown that H_2O_2 plays a role in stress-signaling pathways and can trigger a range of defense responses that enhance resistance to stress caused by HM. For instance, the overexpression of pepper CaWRKY41 causes the activation of HM transporters, thereby reducing Cd tolerance in *Arabidopsis thaliana* and increasing H_2O_2 and Cd content. On the other hand, silencing CaWRKY4 results in increased tolerance to Cd as well as a decrease in the concentration of H_2O_2 in pepper plants. Likewise, Al toxicity generates ROS, such as O_2, H_2O_2, which disrupts redox homeostasis and engages in lipid peroxidation that in turn brings about oxidative stress in plants (Ali et al., 2019). Microarray analysis of C. sinensis leaves and roots shows that Al treatment increases the activity of ROS-scavenging enzymes, catalase (CAT) and superoxide dismutase (SOD), in the tolerant genotype C. sinensis more than in the sensitive genotype *C. grandis* (Jiang et al., 2015).

ROS produced in excess, directly or indirectly, causes oxidative stress in plant structures. Plants have developed many strategies to face stress. Oxidative stress occurs when the concentration of ROS in plant cells exceeds the defensive capacity of the internal defense system (Xie et al., 2019). It further damages macromolecules and disturbs metabolic pathways (Chaki et al., 2020). Hg affects mitochondrial and chloroplast activities, which disrupts the electron transport chain, thus causing oxidative stress through biomolecule oxidation and membrane degradation (Ghori et al., 2019). With increasing Cu concentrations, there is a direct relationship with increasing ROS activity, which ultimately results in increased cellular damage and oxidative stress in basil (*Ocimum basilicum* L.) plants (Georgiadou et al., 2018). Excess iron absorption also results in the production of ROS that damage cellular structures, membranes, proteins, and DNA (Asati et al., 2016). In addition, HM toxicity disturbs enzyme activity, damages cellular structures, decreases membrane permeability, and interferes with mineral nutrition in *S. longena*, S. lycopersicum, and *P. persica* (Shah et al., 2021; Noor et al., 2022). This leads to an increase in ROS production and triggers oxidative stress. Thus, under normal conditions, oxygen utilization during metabolic reactions can lead to excessive ROS production, disturbing the balance of the antioxidant system toward oxidants and resulting in oxidative stress caused by HMs.

Table. 1. Effects of heavy metals/metalloids on plant growth and metabolism.

Heavy metals	Inhibitory Effects on Morphology and Physiology	Crops	HM Concentration	References
Chromium (Cr)	• Decreases the transpiration rate and water potential • Lowers the amylase activity that affects sugars transport • Alters pigments synthesis, along with anthocyanin and photosynthesis • Reduces plant biomass	Fenugreek (*Trigonella foenum-graecum* L.) Cauliflower (*Brassica oleracea*) Malabar spinach (*Basella alba*)	25 µM $K_2Cr_2O_7$ 0.5 mM $Cr_2(SO_4)_3$ 400 µM $K_2Cr_2O_7$	(Chatterjee, 2000; Alaraidh et al., 2018; Zewail et al., 2020)
Cadmium (Cd)	• Shows the symptoms of stunted growth, yellowing of leaves, and browning of root tips that lead to plant death • Causes fruit stem-end yellowing • Hampers the Fe(III) reductase in roots, which causes the lack of Fe(II) and affects photosynthesis • Prevents chlorophyll biosynthesis which alters the chloroplast metabolism • Blocks CO2 fixation by reducing enzymes activity	Tomato (*Solanum lycopersicum*) Pea (*Pisum sativum*) Eggplant (*S. melongena*) Radish (*Raphanus sativus*) Black nightshade (*S. nigrum* L.) Tomato (*S. lycopersicum*) Petunia (*Petunia hybrid*)	1 mM $CdCl_2$ 50 µM $CdCl_2$ 10 µM $CdCl_2$ 50 µM $CdCl_2$ 600 µM $Cd (NO_3)_2$ 500 µM $CdCl_2$	(Gratão et al., 2008; Varalakshmi and Ganeshamurthy, 2013; Singh and Prasad, 2014; Li 2020)
Nickel (Ni)	• Causes plant ultrastructural changes • Restricts the functions of respiration and transpiration • Decreases the carbonic anhydrase activity • Degrades chlorophyll pigments • Disrupts membrane stability by lowering enzyme activity	Tomato (*S. lycopersicum*) Petunia (*Petunia hybrid*)	75 µM $NiCl_2$ 75 µM $NiCl_2$	(Kumar et al., 2015; Khan et al., 2019)
Arsenic (As)	• Reduces shoot and root elongation • Decreases the uptake of other essential nutrients	Pea (*P. sativum*) Black nightshade (*S. nigrum* L.)	50 µM Na_2HAsO_4 500 µM Na_2HAsO_4	(Iti, 2013; Li 2020)
Lead (Pb)	• Inhibits the enzyme activities of the Calvin cycle and causes CO2 deficiency due to stomatal closure by affecting photosynthetic machinery • Reduces plant growth and biomass	River tamarind (*Leucaena leucocephala*) Black nightshade (*S. nigrum* L.) Weeping willow (*Salix babylonica*) Eggplant (*S. melongena*) Petunia (*P. hybrid*) Sunflowers (*Helianthus annus*)	300 µM $Pb(NO_3)_2$ 3 mM $Pb(NO_3)_2$ 100 µM $Pb(NO_3)_2$ 800 µM $Pb(NO_3)_2$ 100 µM $Pb(NO_3)_2$ 600 µM $Pb(NO_3)_2$	(Alaboudi et al., 2018; Kabir et al., 2018; Khan et al., 2019; Topal et al., 2019; Li 2020; Xue et al., 2018)
Copper (Cu)	• Lowers seed germination rate • Alters photosynthetic machinery • Inhibits enzymatic activity • Denatures DNA and destroys membrane stability • Reduces inflorescence number and plant biomass • Enhances suberin lamellae deposition • Increases lateral root numbers	Cherry Plum (*P. cerasifera*) Tomato (*S. lycopersicum*) Cucumber (*C. sativus* L.) Stone-head Cabbage (*B. oleracea*) Chinese cabbage (*B. pekinensis*) Shiny Elsholtzia (*Elsholtzia splendens*) Radish (*R. sativus*)	100 µM $CuSO_4$ 120 µM $CuSO_4{\cdot}5H_2O$ 22 µM $CuSO_4{\cdot}5H_2O$ 5–10 µM CuCl2 5–10 µM $CuCl_2$ 136 µM $CuSO_4{\cdot}5H_2O$ 60 µM $CuSO_4$	(Lombardi and Sebastiani, 2005; Shahbaz et al., 2010; Adrees et al., 2015; Jin et al., 2015; Kovac et al., 2018)

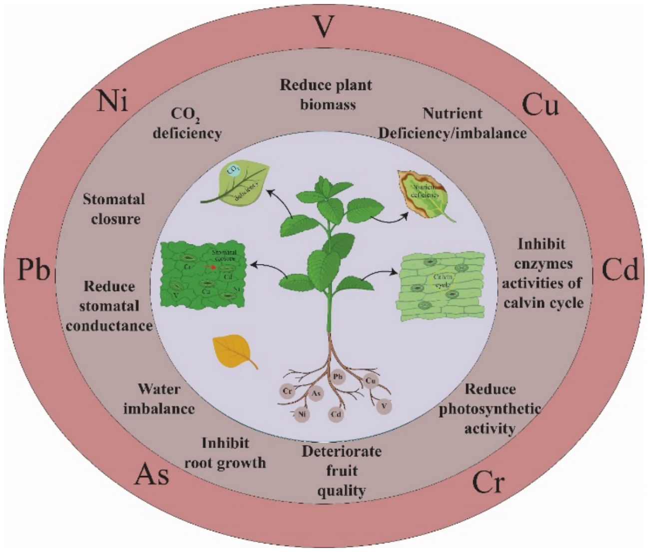


Fig. 1. Morphological and physiological responses of plants under heavy metal/metalloid toxicity.

3. Melatonin Biosynthesis and Signaling and Its Role in Stress Responses in Horticultural Crops

In plants, biosynthesis of MT starts with the conversion of tryptophan to tryptamine by tryptophan decarboxylase (TDC). Tryptamine is then converted to serotonin by tryptamine 5-hydroxylase (T5H) (Lee and Back et al., 2016). The key intermediate in the MT biosynthesis pathway is serotonin, which is subsequently converted into MT through the action of the enzyme serotonin N-acetyltransferase (SNAT) (Hwang and Back, 2020). The process happens predominantly in chloroplasts; however, it can also occur in various plant tissues, including the cytosol, nucleus, and mitochondria (Tan and Reiter, 2020). Therefore, Zheng et al. (2021) performed a study to determine and clarify the genes involved in MT biosynthesis. The results of the study show that MnSNAT5, MnT5H2, MnTDC, and MnASMT12 play important roles in MT biosynthesis in mulberry.

Liu et al. (2023), Khan et al. (2020), and Li et al. (2019) have reported that light, temperature, drought, and salinity are environmental factors that can induce modulation of enzymes controlling the biosynthesis of MT. However, the precise mechanisms by which these factors affect the MT biosynthesis pathway remain unclear. MT molecules interact with plant cell surface receptors upon activation of certain receptors referred to as MT signaling (Zhao et al., 2023a). When MT binds to its receptors, it triggers downstream signaling cascades that are involved in stress responses and the regulation of gene expression (Zhang et al., 2022). Activation of these receptors stimulates cellular biochemical reactions that initiate different metabolic pathways inside the plant.

Several reports have indicated that MT has promising effects in boosting crop growth, yield, and quality of horticultural crops. For instance, research on tomato plants shows that MT has a twofold effect: accelerating fruit ripening and increasing antioxidant activity (Li et al., 2015). MT is also believed to improve grape quality and enhance resistance of the fruit to fungal pathogens according to studies (Li et al., 2022). Furthermore, MT delays yellowing of broccoli through its ability to control chlorophyll breakdown and preserve chloroplast structure during storage, leading to better color quality (Wu et al., 2021). Regulation of chlorophyll degradation and maintenance of chloroplast structure enables this effect. MT prevents plants from degrading chlorophyll, which gives them their green color, and helps restore normal chloroplast function. Due to this, broccoli maintains its green color and overall quality for a longer period in the presence of MT. MT treatment improves the growth rate and production of strawberry plants (Hayat et al., 2022). MT application in horticultural crops has shown promising results; however, there are possible drawbacks and limitations. For example, it is still not well understood to what extent MT use for agricultural purposes has environmental impacts, and further research is needed (Arnao and Hernández-Ruiz, 2006).

The effect of MT on the stress response of plants occurs through enhancing stress-responsive gene expression, such as genes coding for ROS-removing enzymes, which are beneficial for plant stress tolerance (Ayyaz et al., 2022). Treatment of tomato plants with MT can increase the activity of antioxidant enzymes such as superoxide dismutase (SOD), which helps limit oxidative damage resulting from heat, drought, and cold stress (Altaf et al., 2022). MT also enhanced photosynthetic efficiency and alleviated salt stress-induced oxidative damage, as well as upregulated genes encoding antioxidant enzymes in cucumber plants (Sun et al., 2021). Additionally, MT is involved in Cd stress–induced expression of a set of genes encoding chaperones, including heat shock proteins (HSPs), which are responsible for protective and repair functions for damaged proteins in tomato plants (Cai et al., 2017). Moreover, MT increases photosynthetic efficiency in tomato plants by controlling the expression of photosynthesis-related genes such as *SBPase*, *FBPase*, *RCA*, *rbcS*, *psaA*, *rbcL*, *psbB*, and *psaB* (Jahan et al., 2021). These upregulations enhance photosynthetic efficiency, which is conducive to plant growth and productivity under heat stress. Thus, modulation of stress-responsive gene expression through MT can be considered a promising strategy to achieve enhanced stress tolerance in horticultural crops. MT can increase the expression of ROS-scavenging enzymes and chaperones and enhance photosynthetic efficiency, among other beneficial effects, under stress conditions.

MT signaling works directly with stress responses but also interacts with other pathways, such as phytohormone signaling, to achieve proper regulation of plant stress responses and development (Zhang et al., 2022). For instance, MT is known to interact with the ABA signaling pathway to improve stress tolerance and fruit quality in strawberries, tomatoes, and many other horticultural crops (Zahedi et al., 2020; Jahan et al., 2021a). Moreover, MT has been demonstrated to trigger the salicylic acid signaling pathway, which helps enhance defense mechanisms in cherry tomato (Li et al., 2022).

4. Melatonin Mitigates Heavy Metal Toxicity in Plants

Melatonin serves multiple functions in protecting plants from harmful HMs present in soil. Plants easily absorb HM that commonly exists in the soil–water environment. These disturbances modify plant ion homeostasis, disrupt osmotic balance, and cause oxidative damage to tissues as well as to primary and secondary metabolic processes (Altaf et al., 2023). Among horticultural crops, tomato and leafy vegetables are highly sensitive to HM toxicity (Naz et al., 2022). MT acts as a detoxification agent in plants, helping to mitigate the harmful effects of HM toxicity (Table 2). Moreover, MT accelerates the production of secondary metabolites, promotes osmolyte accumulation, enhances antioxidant enzyme activity, and prevents the excessive production of malondialdehyde (MDA) and ROS (Nawaz et al., 2018). The application of MT also improves the photosynthetic performance of leaves, along with increased activity of RuBisCO and FBPase enzymes. Through these collective functions, MT enhances plant cellular processes under HM stress conditions.

4.1. Cadmium

Plants translocate and distribute Cd as a major pollutant that easily enters the food chain (Tran and Popova, 2013). Cd uptake in plants leads to growth inhibition, disruption of mineral nutrient balance, and alterations in root development (Ahmad et al., 2023). Reduced growth of many plant species exposed to Cd stress, such as Brassica juncea, tomato, and banana, has been reported (Cai et al., 2017). Studies on different tomato cultivars reveal that Cd toxicity reduces root length and affects mineral content in the roots. However, MT supplementation significantly promotes root morphology and maintains ion homeostasis (Altaf et al., 2022). Strawberry and eggplant seedling growth and biomass yield are impeded by Cd toxicity due to inhibition of the antioxidant enzyme system. However, MT effectively strengthens the plant antioxidant defense system and reduces Cd uptake from root to shoot (Wu et al., 2021; Lema et al. 2024).

Table 2. Effects of heavy metals/metalloids on plant growth and metabolism.

Plant	Application	MT conc.	HM	HM conc.	MT pretreatment duration	Stress duration	Reference
Tomato	Sprayed	100 µM	Ni	35 µM	7 days	14 dyas	Jahan et al. (2020)
Safflower	Root/Sprayed	300 µM	Pb	50 µM	6 days	14 days	Namdjoyan et al. (2020)
Cabbage	Seed treatment	100 µM	Cu	0.5 µM			Posmyk et al. (2008)
Pepper	Root	5 µM	Cr	40 mg	3 days	14 days	Altaf et al. (2023)
Cucumber	Root	10 nM	Cu	80 µM	12 h	14 days	Cao et al. (2019)
Fava bean	Root	50 µM	As	5 µM	3 days	7 days	Siddiqui et al. (2020)
Watermelon	Root	0.1 µM	V	40 mg	3 days	7 days	Nawaz et al. (2018)
Tomato	Root	100 µM	Cd	35µM	3 days	14 days	Altaf et al. (2022)

The positive effect of MT has also been observed by Menhas et al. (2022), who reported that MT improved the growth, yield, and quality of Brassica napus seedlings subjected to Cd toxicity. Moreover, leaves of Brassica napus showed higher content of photosynthetic pigment, proline, and phenolic compounds when treated with MT under mild Cd stress. In addition, MT positively correlates with the growth of apple plants and effectively decreases Cd accumulation from root to shoot (He et al., 2020), radish (Xu et al., 2020), and Chinese cabbage (Wang et al., 2021). MT has also been proven to enhance photosynthetic efficiency, strengthen antioxidant enzyme activity, and improve Cd stress tolerance in tomato plants (Umapathi et al., 2018).

Previous studies have shown that MT application greatly increases Cd stress tolerance in many plant species (Amjadi et al., 2021). According to Saqib et al. (2023), foliar spray of MT protects leaf photochemical performance in Cd-treated plants by regulating antioxidant enzymes while decreasing Cd levels and preventing oxidative damage. MT treatment also enhanced the growth of Perilla frutescens under Cd toxicity (Xiang et al., 2019). Cd toxicity in Platycladus orientalis caused cellular membrane damage, imbalance of mineral uptake, and increased ROS production. In contrast, MT supplementation triggered the accumulation of mineral nutrients, increased osmolyte production, and reduced oxidative damage (Ou et al., 2023). The application of MT also played a positive role in the development of root hairs, accumulation of secondary metabolites, glandular trichomes, and antioxidant metabolism in tobacco under Cd toxic conditions (Song et al., 2022). Exogenous application of MT significantly decreased oxidative damage and Cd uptake in shoots while enhancing antioxidant enzyme activity and improving Cd stress tolerance in tomato plants (Hasan et al., 2019). In addition, foliar application of MT (0.1 mM) improved the photosynthetic capacity of leaves and enhanced Cd tolerance in both lettuce plants and Catharanthus roseus (Tang et al., 2023).

4.2. Chromium

The second most common metal pollutant found in groundwater, soils, and sediments as a result of widespread industrial use is chromium (Cr), which poses a major environmental threat (Hayat et al., 2012). Since plants do not require Cr as an essential element, there is growing concern regarding Cr contamination in soil and water (Shahid et al., 2020). Cr accumulation in plants is highly damaging to growth and biomass production and causes structural changes in plants (Hayat et al. 2012). Cr toxicity significantly decreases biomass yield, disrupts ion homeostasis (K, Na), and reduces pigment content, relative water content, enzyme activities, and ascorbic acid (AsA) levels in pepper. However, under Cr toxicity, the leaves of marjoram show enhanced activity of antioxidant enzymes and higher Cr levels. The application of MT (100 µM) significantly increases growth and other physiological functions. Furthermore, MT treatment also inhibits the accumulation of Cr in the pepper leaves (Rizwan et al. 2024).

Treatment with MT under Cr toxicity significantly promotes the growth of Brassica napus seedlings, increases the efficiency of photosystem II and the antioxidant enzyme system, and reduces ROS production (Ayyaz et al., 2020). According to Ayyaz et al. (2020), Cr toxicity affects B. napus growth by decreasing photosynthetic pigment content and altering chlorophyll parameters. Nevertheless, under Cr toxicity, exogenous application of MT improves the growth of Brassica napus. Moreover, MT application promotes increases in soluble protein concentration, proline concentration and antioxidant enzyme activity in rapeseed (Ayyaz et al., 2021).

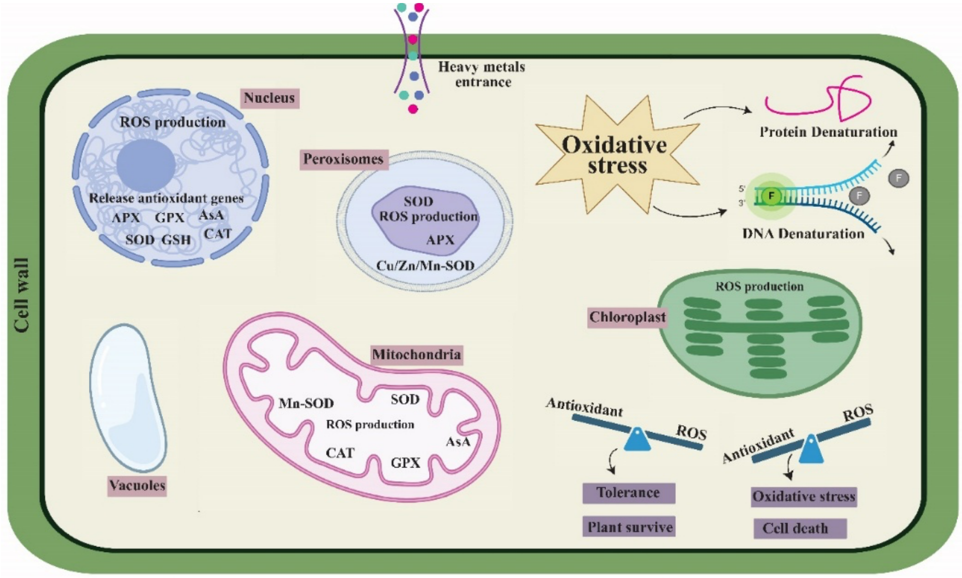


Fig. 2. Schematic illustration of reactive oxygen species production sites and defense mechanisms in different cell organelles (nucleus, mitochondria, chloroplasts, and peroxisomes) during heavy metal/metalloid stress.

A recent study showed that Cr toxicity reduced growth, decreased biomass production, and adversely affected the pepper leaf photosynthetic system. Conversely, MT application strongly promoted the growth of pepper plants and improved the photosynthetic efficiency of their leaves (Altaf et al., 2023). Additionally, MT treatment significantly reduced the overproduction of ROS and high MDA levels, enhanced the accumulation of secondary metabolites, and efficiently inhibited Cr accumulation in tomato leaves (Sun et al., 2023).

4.3. Arsenic

Arsenic (As) is one of the most widely distributed and concerning toxic metalloids in the environment (Finnegan and Chen, 2012). This natural element, although a metalloid, is not required for plant development but can accumulate to lethal concentrations in plants. Consequently, it may enter the food chain and pose a potential hazard to human health (Altaf et al. 2023). The growth of spinach is greatly inhibited by As toxicity. However, MT supplementation successfully alleviates As toxicity by reducing stress effects, improving growth traits, increasing antioxidant enzyme activity, enhancing chlorophyll content, and lowering lipid peroxidation in spinach (Asif et al., 2020).

Similarly, the growth of pepper seedlings is suppressed under As stress, leading to reduced photosynthetic pigment content and oxidative damage. However, MT supplementation mitigates the effects of As toxicity in pepper seedlings. Under As stress conditions, MT treatment markedly decreases MDA and electrolyte leakage (EL) while reducing As accumulation in pepper leaves. In addition, it increases proline, total soluble sugars, glycine betaine content, and the activity of antioxidant enzymes (Kaya et al., 2022).

As toxicity also induces excessive production of ROS, leading to oxidative damage in tea seedlings. In contrast, MT application alleviates As-induced oxidative damage by enhancing the antioxidant enzyme system (Fig. 3). Moreover, MT treatment following As exposure improves anthocyanin content and related gene expression in tea leaves under As toxicity. Results show that As concentration in tea leaves is significantly reduced by MT (Li et al., 2021).

As stress also inhibits the growth of Vicia faba seedlings. MT treatment mitigates As toxicity by improving growth characteristics, chlorophyll content, leaf photosynthesis, proline levels, and the AsA–GSH cycle while reducing ROS accumulation in Vicia faba seedlings (Siddiqui et al., 2020). Furthermore, As stress stimulates the production of osmolytes, secondary metabolites, antioxidant enzymes, and ROS. MT application significantly promotes the growth of rosemary, improves pigment content, enhances osmolyte production, and increases essential oil yield. Additionally, MT preserves cellular membrane integrity, prevents oxidative damage, and strengthens the antioxidant defense system of pepper plants (Rizwan et al., 2024).

4.4. Lead

Lead (Pb) is a potential contaminant that easily accumulates in sediments and soils. However, Pb is not an essential element for plants, and it is readily absorbed and accumulated in various parts of plants (Zulfiqar et al., 2019). Excessive Pb in plants leads to a series of toxic effects such as stunted growth, decreased seed germination, decline in photosynthesis, and disruption of root architecture (Sharma and Dubey, 2005). MT supplementation significantly improves growth, chlorophyll content, the antioxidant enzyme system, and the glyoxalase enzyme system, while lowering the contents of MDA and H_2O_2 in safflower seedlings (Haghi et al., 2022).

Eruca vesicaria exposed to Pb toxicity shows reduced growth parameters, pigment content, leaf gas exchange, and activity of photosynthetic enzymes. However, exogenous application of MT considerably reduces Pb toxicity in Eruca vesicaria by promoting growth characteristics and improving the leaf photosynthetic apparatus under Pb stress (Mohamed et al., 2021). Under Pb toxicity, MT application also reduces Pb accumulation and increases the growth of Medicago truncatula (Zhang et al., 2020). In addition, Tang et al. (2021) reported that MT treatment increases the activity of antioxidant enzymes and decreases Pb accumulation in radish leaves.

4.5. Nickel

Nickel (Ni) functions as an essential micronutrient for plants; however, at higher concentrations it becomes highly phytotoxic (Bhalerao et al., 2015). Therefore, Ni toxicity poses a serious threat to the sustainable future of agriculture (Yusuf et al., 2011). The effects of Ni toxicity on plant physiology vary depending on Ni concentration, exposure duration, environmental conditions, plant species, and developmental stage (Shahzad et al., 2018). Ni exposure adversely affects the growth and photosynthetic activity of tomato seedlings and disrupts mineral nutrient uptake, while also stimulating excessive ROS production and increasing EL. However, MT application significantly promotes the growth of tomato seedlings, enhances photosynthetic efficiency, induces the accumulation of secondary metabolites, maintains ion homeostasis, and further increases the activity of antioxidant enzymes. Moreover, MT decreases Ni accumulation from root to shoot in tomato plants (Jahan et al., 2020).

It has also been observed that MT application under Ni toxicity significantly enhances growth traits, pigment content, and root morphological characteristics of tomato seedlings. Furthermore, MT treatment reduces elevated ROS levels and boosts the antioxidant enzyme system. Ni uptake in leaves is considerably reduced by MT, while the accumulation of other mineral nutrients in tomato leaves is enhanced (Altaf et al., 2021a). In addition, eggplant seedling growth parameters, photosynthetic assimilation rate, glutathione content, and antioxidant enzyme activities are significantly increased by 4-hydroxymelatonin supplementation under Ni toxicity, indicating that 4-hydroxymelatonin plays a central role in protecting eggplant against Ni-induced toxicity. Treatment with 4-hydroxymelatonin significantly lowers H_2O_2, MDA, and EL levels. Moreover, 4-hydroxymelatonin also decreases Ni accumulation in both the roots and shoots of eggplant (Shah et al., 2021).

4.6. Vanadium

Vanadium (V) is a naturally occurring trace metal widely distributed in air and soil (Yang et al., 2017). Low concentrations of V may positively regulate plant growth, whereas higher concentrations have deleterious effects on plant physiological mechanisms (Chen et al., 2020). V toxicity affects plant growth and impairs metabolic processes (Imtiaz et al., 2015). A recent study by Altaf et al. (2023) showed that V toxicity severely inhibits root growth, disturbs mineral accumulation, and increases V accumulation in the shoots. However, supplementation with 5 μM MT in pepper significantly decreases V accumulation in shoots and helps maintain mineral nutrient uptake.

Furthermore, V toxicity negatively affects plant growth, chlorophyll pigment content, ion homeostasis required for plant growth, and root morphological characteristics, while increasing MDA and H_2O_2 production in watermelon seedlings. Nevertheless, the application of MT considerably improves plant growth, root architecture, and antioxidant enzyme activity. In addition, MT supplementation substantially decreases ROS production and reduces the translocation of V from root to shoot in watermelon (Nawaz et al., 2018). Another study reported that V stress inhibits tomato seedling growth and increases oxidative damage. In contrast, MT supplementation enhances the accumulation of macro- and micronutrients, improves leaf photosynthesis, root structure, and strengthens the antioxidant enzyme system in tomato plants exposed to V stress (Altaf et al., 2021b).

4.7. Copper

Copper (Cu) is toxic at high concentrations but is required for normal plant growth (Yruela, 2009). Cu plays an essential role in photosynthesis and several metabolic processes in plants. However, excessive Cu accumulation can cause various morphological and physiological disorders (Khatun et al., 2008). The growth of cucumber seedlings is reduced under Cu toxicity. In contrast, MT treatment efficiently alleviates Cu-induced stress by improving plant growth and antioxidant enzyme activity while reducing ROS generation and Cu accumulation from root to shoot. Furthermore, under Cu toxicity, MT significantly alters gene expression at the transcriptome level (Cao et al., 2019).

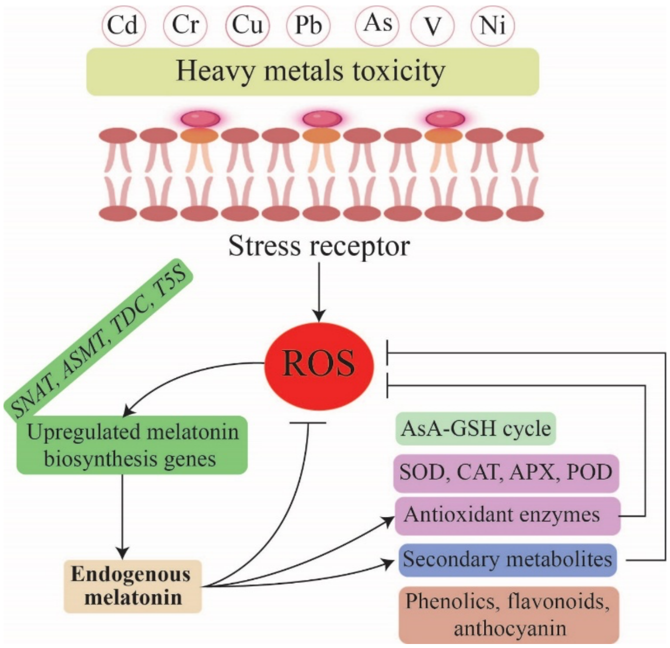


Fig. 3. Melatonin reduced oxidative damage and enhanced the antioxidant enzyme system in plants.

MT seed treatment also maintains the growth of red cabbage seedlings under toxic Cu ion concentrations (Posmyk et al., 2008). In Brassica napus, MT treatment results in lower oxidative damage, higher pigment content, and regulated proline levels (Kholodova et al., 2018). Cu toxicity also decreases antioxidant enzyme activity and root growth while increasing proline and MDA levels in melon seedling roots; however, MT application mitigates these adverse effects (Hu et al., 2020). Additionally, Zhang et al. (2022) reported that MT treatment in tomato seedlings improves the antioxidant enzyme system and reduces ROS generation. Moreover, MT enhances non-enzymatic antioxidant activity and decreases Cu accumulation in tomato leaves.

5. Melatonin-Mediated Functional Genes Under Heavy Metal Stress in Horticultural Crops

MT plays an important role in protecting plants from HM stress, and its significance in enhancing plant tolerance to toxic metals has increasingly gained attention. Evidence from several research studies highlights the role of MT in alleviating HM stress and its interaction with functional genes to enhance plant resilience (Fig. 3). For instance, Hasan et al. (2019) provided strong genetic evidence for the contribution of MT to Cd stress tolerance in tomato plants through its involvement in the effective regulation of sulfur (S) metabolism, redox homeostasis, and Cd translocation. The presence of MT together with several crucial functional genes, such as COMT and sulfate transporters, is necessary for enhancing sulfur uptake and assimilation, which ultimately results in improved plant growth and enhanced tolerance to Cd stress. Understanding the complex interaction between MT and the sulfur metabolism pathway under HM stress provides valuable insights for sustainable agriculture in HM-contaminated environments.

Similarly, Jahan et al. (2020) reported that Ni stress in tomato plants negatively affects photosynthesis, root activity, mineral homeostasis, and osmotic balance, resulting in reduced plant growth. However, the application of MT positively influences plant growth by upregulating genes responsible for chlorophyll biosynthesis, such as POR, CHLG, and CAO, thereby enhancing photosynthetic efficiency. In another study, Wang et al. (2021) reported that MT reduces Cd accumulation and nitric oxide (NO) levels in Chinese cabbage seedlings. The action of MT was associated with the downregulation of enzymes and genes involved in NO synthesis, including nitrate reductase and nitric oxide synthase. In addition, MT reduced the expression of the gene encoding the metal transporter IRT1, which is involved in Cd uptake in plants. By inhibiting IRT1 expression, MT decreases Cd accumulation in plant tissues, thereby enhancing plant tolerance to Cd stress and mitigating Cd-induced damage. These findings demonstrate that MT regulates the expression of functional genes involved in NO synthesis and metal transport, thereby playing a crucial role in plant responses to HM stress. Collectively, these studies highlight the importance of MT in conferring plant tolerance to HM stress through the regulation of genes essential for stress response and metabolic functions.

6. Conclusion and Future Perspectives

Various scientific studies performed in the last decade demonstrated that MT plays a vital role in protecting plants through their defensive mechanisms. Studies have proven MT to be effective in stress mitigation of various abiotic stressors that lead to oxidative damage if applied within proper MT concentration levels. Research has identified different protective mechanisms that explain MT's protective properties.

The present book chapter focuses on explaining the effective understanding of MT's significance to assist plants against HM exposure while also advocating for future research on its fundamental mechanisms. Environmental stress conditions trigger plants to accumulate substantial amounts of MT while also showing their capability for MT synthesis and uptake. Moreover, the use of exogenous MT enhances stress resistance in plants. Additionally, it provides a possible mechanism by which MT conferred resistance to HM stress. MT serves as a powerful growth regulator under HM stress conditions and improves plant growth and production in a general way. Application of MT exogenously enhanced the activity of synthesis enzymes and reduced the expression of genes responsible for degradation, factually increasing the photosynthetic content in plants. As a result, there is a major increase in the concentration of these pigments. Despite this, using MT resulted in improved mineral nutrient deposition and modified root system configuration of horticultural plants. MT is exogenous and functions by upregulating a variety of defensive genes that increase antioxidant capability and chelate more metals. This does help in reducing the toxic effects of HM on plants. Furthermore, MT treatment increases nonessential (osmolytes) accumulation and/or osmotically adjustment in plant cells and increases antioxidant enzyme activity in plants in exposure to HMs in order to increase the tolerance to HM stress. In this way, ROS and lipid peroxidation production are blocked, and membrane integrity is maintained, while the action is also promoted by both enzymatic and nonenzymatic antioxidants.

Although MT has been a topic of interest for plant biologists, very little is known about the intricate signaling pathways that it controls under HM stress conditions. While MT is known to regulate specific genes and pathways, we know only partially which genes, and hardly any at all, for mechanisms of MT-regulated HM transport, absorption, or sequestration. Research is required to fully understand the mechanisms of this molecule and allow the appropriate use of these processes to enhance plant productivity in the presence of high metal toxicity. They are essential phytohormones that control signals to progress plants' ability to tolerate stress. BRs mediate important physiological processes as a main protector for plants under stressful conditions of HM toxicity.

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MMA and SA; writing–original draft. SA and MS: Writing reviewing and editing; writing–original draft. MA: data collection, writing–original draft. HSH: formal analysis, writing–original draft. JW: formal analysis, funding acquisition, writing–original draft. MMA: supervision, writing–review and editing. All authors read and approved the manuscript.

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The authors have no relevant financial or non-financial interests to disclose.

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