Harnessing the effects of Cadmium Stress and Amelioration by Nitric Oxide and Hydrogen Sulfide on Mineral Nutrient Balanceand its Uptake along with Nitrogen Metabolism in *Solanum lycopersicum* L.

Abstract

Cadmium (Cd) contamination in soil and water severely affects plant growth by disrupting nutrient homeostasis. This study investigates the potential ameliorative role of nitric oxide (NO) and hydrogen sulphide (H_2S) on mineral nutrient uptake, its balance and key nitrogen metabolism enzymes in *Solanum lycopersicum* L. The results indicated that the exposure to low Cd concentration (5 ppm) led to an increase in dry biomass accumulation, suggesting a possible hermetic effect. However, higher Cd levels (25 and 50 ppm) decreased the dry weight indicating Cd-induced toxicity. Moreover, the plants subjected to Cd stress exhibited reduced uptake of essential nutrients, particularly potassium (K), calcium (Ca), magnesium (Mg) and iron (Fe), while accumulating excessive sodium (Na) and chloride (Cl^-). The activities of nitrate reductase (NR), glutamine synthetase (GS), and glutamate synthase (GOGAT) were significantly inhibited under Cd toxicity, leading to impaired nitrogen assimilation. The exogenous application of NO and H_2S mitigated Cd-induced damage by enhancing nutrient uptake, restoring ion balance, and improving nitrogen metabolism enzyme activity. The combined NO + H_2S treatment was the most effective, suggesting a synergistic role in Cd stress tolerance. These findings highlight the potential of NO and H_2S as protective agents in managing heavy metal stress in plants.

Keywords: *Cadmium stress, Nitric oxide, Hydrogen sulphide, Nutrient uptake, Nitrogen metabolism, Ion homeostasis, Tomato, Mineral nutrients*

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1. **Introduction**

Essential nutrients are vital for human health (Mena et al., 2020), with agricultural products serving as primary sources of these nutrients (Day, 2013). However, low soil nutrient availability can limit plant uptake (De Cesare et al., 2019), leading to micronutrient deficiencies in humans (Giller and Zingore, 2021), particularly iron (Fe) and zinc (Zn) (Gregory et al., 2017). Additionally, non-essential elements like cadmium (Cd) can enter plants by sharing channels with essential nutrients, posing health risks (Li et al., 2022; Yuan et al., 2020).Cd is readily absorbed by plants roots from contaminated soils and translocated to aerial parts, leading to its accumulation in crops such as rice, wheat and various vegetables. This contamination often stems from industrial activities, including metal smelting, mining, urban traffic emissions, battery manufacturing, electronic waste disposal, and cement production. Industrial regions like Delhi, Kanpur, and Vapi have shown elevated cadmium levels in air pollution studies (Jangirh et al., 2024). Studies show Cd levels of 0.01–0.05 mg/L in some locations, exceeding WHO's safe limit of 0.003 mg/L. Moreover, there occurs a risk factor with higher accumulation of Cd in crop plants to human health. Its accumulation in plants disrupts essential physiological processes, including nutrient uptake, causing oxidative stress and nitrogen metabolism, ultimately impairing growth and yield (Hasanuzzaman et al., 2023). The uptake and transport of essential mineral elements, such as Fe, manganese (Mn), copper (Cu), and Zn (Gowda et al., 2024), can significantly influence Cd accumulation in plants. For instance, Mn and Cu additions have been shown to reduce Cd uptake. Similarly, major mineral elements like potassium (K), magnesium (Mg), and calcium (Ca) also play crucial roles in modulating Cd uptake (Yang et al., 2024).Moreover, Cd competes with essential cations, such as calcium (Ca^{2+}), potassium (K^{+}), and iron (Fe^{2+}), while toxic ions such as sodium (Na^{+}) and chloride (Cl^{-}) accumulate abnormally leading to ionic imbalances, and nutrient deficiencies (Arif M, 2024). Additionally, Cd inhibits nitrogen metabolism enzymes, such as nitrate reductase (NR) and glutamine synthetase (GS), reducing nitrogen assimilation efficiency (Zhang et al., 2021). Recognizing the pivotal role of mineral elements in plant Cd research is essential to address human nutritional and health requirements. Plants exposed to Cd exhibit an increase in reactive oxygen species (ROS), which causes oxidative stress, characterized by lipid peroxidation, increased hydrogen peroxide generation, and ion leakage(Zhao et al., 2016).

Solanum lycopersicum L (Tomato) is one of the most widely cultivated and consumed vegetable crops globally, making it a relevant species for studying the impact of heavy metal contamination on food security (Wang et al., 2023). Due to soil contamination from industrial activities, mining, and excessive use of phosphate fertilizers, Cd accumulation in edible plants has become a serious concern. Tomato is known to uptake and translocate Cd, affecting growth, yield, and fruit quality (Ali et al., 2023). Tomato plants exhibit significant physiological and biochemical changes in response to Cd stress, including oxidative damage, reduced photosynthetic efficiency, and altered nutrient uptake, making it an excellent candidate for stress-response studies (Chen et al., 2023). Moreover, since tomatoes are widely consumed, Cd accumulation poses a direct risk to human health. Studying Cd uptake and detoxification mechanisms in tomatoes helps develop strategies to minimize heavy metal contamination in edible crops (Ali et al., 2023). Tomatoes exhibit moderate Cd tolerance and accumulation, making them a potential candidate for phytoremediation research (Hussain et al., 2023). Moreover, Cd accumulation differs from species to species; currently there is scarce research on the dry matter accumulation on plant species and nutritional element requirement under Cd toxicity.Recent studies indicate that nitric oxide (NO) and hydrogen sulphide (H_2S) play crucial roles in plant stress responses. These signalling molecules improve Cd tolerance by modulating antioxidant defence, enhancing nutrient uptake, and regulating enzymatic activity (Ali et al., 2023). However, their combined effects on Cd-induced nutrient imbalances and nitrogen metabolism remain poorly understood. This study aims to investigate (i) the impact of different Cd concentrations on nutrient accumulation and its uptake in *S. lycopersicum*, (ii) the effects of Cd on key nitrogen metabolism enzymes, (iii) the potential ameliorative effects of NO and H_2S in regulating ion homeostasis, and (iv) the interactive role of these signalling molecules in mitigating Cd toxicity.

2. Materials and Methods

2.1 Plant Material and Growth Conditions

Seeds of *Solanum lycopersicum* L. were surface-sterilized with 5% sodium hypochlorite for 5 min, rinsed thoroughly with deionized water, and germinated in petri dishes lined with moist filter paper. After seven days, uniform seedlings were transferred to plastic pots (5 L) containing Hoagland's nutrient solution and maintained under controlled greenhouse conditions (temperature: 25 ± 2°C and photoperiod: 14 h light/10 h dark). The nutrient solution was refreshed every three days.

2.2 Cadmium Treatments

After 15 days of acclimatization, seedlings were subjected to different concentrations of Cd^{2+} (0, 25, 50, and 100 μM $CdCl_2$) in Hoagland's solutionfor 15 days under greenhouse condition, with each treatment replicated thrice. Further, Cd treated plants were exposed to NO and H_2S alone and in combination with NO and H_2S. Thesamples were collected at the end of the experimental period for further analyses.

2.3 Determination of Nutrient Uptake and Accumulation

Leaf, root, and shoot samples were harvested, oven-dried at 70°C until constant weight, and digested using a tri-acid mixture (HNO_3:H_2SO_4:$HClO_4$ in a 5:1:1 ratio). Elemental analysis of essential nutrients (K^+, Ca^{2+}, Mg^{2+}, Fe^{2+}, Na^+, Cl^-) and Cd accumulation was performed using Inductively Coupled Plasma Optical Emission Spectroscopy (ICP-OES, PerkinElmer Optima 8000) following the standard protocol (Ali et al., 2023).

2.4 Analysis of Key Nitrogen Metabolism Enzymes

Fresh leaf and root tissues (0.5 g) were homogenized in phosphate buffer (50 mM, pH 7.5) containing 1 mM EDTA and 5 mM dithiothreitol (DTT). The homogenate was centrifuged at 12,000 × g for 20 min at 4°C, and the supernatant was used for enzyme assays.

2.4.1 Nitrate reductase (NR, EC 1.7.1.1) activity was determined by the method of Jaworski (1971), measuring the nitrite formed at 540 nm using a spectrophotometer (UV-Vis 2800, Shimadzu).

2.4.2 Glutamine synthetase (GS, EC 6.3.1.2) activity was assayed based on the transferase reaction producing γ-glutamyl hydroxamate, measured at 540 nm (Singh et al., 2022).

2.4.3 Glutamate dehydrogenase (GDH, EC 1.4.1.2) activity was analyzed by monitoring the oxidation of NADH at 340 nm (Chen et al., 2023).

2.4.4 Glutamate synthase (GOGAT, EC 1.4.1.13) activity was measured spectrophotometrically at 340 nm, following the oxidation of NADH (Zhou et al., 2023).

2.5 Nitric Oxide (NO) and Hydrogen Sulfide (H_2S) Treatments

To assess the ameliorative effects of NO and H_2S in Cd-stressed plants, sodium nitroprusside (SNP, 100 μM, NO donor) and sodium hydrosulfide (NaHS, 100 μM, H_2S donor) were applied separately and in combination (SNP + NaHS). The treatments were supplied via foliar spray every alternatedays for 14 days. Control plants received distilled water.

2.6 Determination of Ion Homeostasis

2.6.1 H^+-ATPase and Ca^{2+}-ATPase activities: Plasma membrane fractions were isolated using differential centrifugation, and ATPase activities were measured by inorganic phosphate (Pi) release following the method of Song et al. (2023).

2.6.2 Na^+/K^+ ratio: Ion concentrations were determined using ICP-OES, and the Na^+/K^+ ratio was calculated as an indicator of ion homeostasis (Rizwan et al., 2022).

2.7 Interaction between NO and H_2S in Cd Stress Alleviation

The potential cross-talk between NO and H_2S in Cd detoxification was assessed by measuring:

2.7.1 *Endogenous NO and H_2S levels* using Griess reagent and lead acetate method, respectively (Chen et al., 2023).

2.7.2 *Expression levels of stress-related genes* (*NR*, *GS*, *GDH*, *HMA2*, *IRT1*) via qRT-PCR, with actin as the reference gene. Total RNA was extracted using TRIzol reagent, cDNA was synthesized, and relative gene expression was analyzed using the $2^{-\Delta\Delta Ct}$ method (Ali et al., 2023).

2.8 Statistical Analysis

All experiments were conducted in a completely randomized design (CRD) with three biological replicates per treatment. Data were analyzed using one-way ANOVA, followed by Duncan's Multiple Range Test (DMRT) at $P < 0.05$. Statistical analyses were performed using SPSS 26.0 (IBM Corp., Armonk, NY, USA).

Parameters	**Control**	**Cd- Induced (100µM)**	**Reduction (%)**

3.Cadmium Accumulation in Tomato Tissues

Cadmium (Cd) accumulation was significantly higher in roots compared to shoots and leaves. At 100 µM $CdCl_2$, root Cd concentration reached 85.6 ± 3.2 mg kg^{-1} DW, while shoots and leaves accumulated 42.3 ± 2.8 mg kg^{-1} DW and 25.7 ± 1.9 mg kg^{-1} DW, respectively (P<0.05). The preferential accumulation in roots suggests that tomato plants employ a root-restriction strategy to minimize Cd translocation to aerial parts, a mechanism also reported by Ali et al. (2023).

3.1 Effects of Cd on Plant Growth and Biomass

Cd stress significantly reduced plant height, leaf area, and biomass. At 100 µM Cd, plant height decreased by 34.5%, leaf area by 41.2%, and total dry weight by 38.7% compared to control plants (Table 1). Root length was also reduced, with a maximum inhibition of 29.8% at the highest Cd level. These reductions align with previous findings (Chen et al., 2023), indicating that Cd disrupts cell division and elongation.

Table 1. Plant growth and Biomass of Tomato plants

Plant Height (cm)	60.96	39.93	34.5
Root Length (cm)	17	11.94	29.8
Leaf Area (cm^2)	110	64.68	41.2
Biomass (kg/m^2)	2.5	1.54	38.7

3.2 Alterations in Nitrogen Metabolism Enzymes

Cd toxicity adversely affected key nitrogen metabolism enzymes in leaves and roots.Cd exposure (stress) significantly inhibited NR and GS/GOGAT activity, reducing nitrogen assimilation efficiency, while GDH activity increased (Table 2), indicating a shift towards ammonia detoxification via GDH rather than GS/GOGAT pathways (Fig.1). NO and H_2S applications significantly improved enzyme activities, showing the highest recovery. Cd toxicity inhibits nutrient uptake by damaging root membranes and competing with essential cations (Shah et al., 2022). Similar metabolic reprogramming has been reported in *Brassica* species under Cd stress (Singh et al., 2022).

Table 2. Activity of Nitrogen Metabolism Enzymes Under Cd Stress

Treatment (µM Cd)	**NitrateReductase(NR) (µmol NO_2^- g^{-1} FW h^{-1})**	**Glutamine Synthetase(GS)(µmolγ-GHA g^{-1} FW h^{-1})**	**Glutamate Dehydrogenase(GDH) (µmol NADH min^{-1} g^{-1} FW)**
0 (Control)	8.3 ± 0.4	6.5 ± 0.3	4.8 ± 0.2
25 µM	6.1 ± 0.3 (-26.5%)	5.2 ± 0.2 (-20.0%)	5.9 ± 0.3 (+22.9%)
50 µM	4.4 ± 0.2 (-47.0%)	3.8 ± 0.2 (-41.5%)	6.7 ± 0.4 (+39.6%)
100 µM	2.9 ± 0.2 (-65.1%)	2.3 ± 0.1 (-64.6%)	7.4 ± 0.3 (+54.2%)

Values are mean ± SE (n = 5). Percentage change relative to control is shown in parentheses.

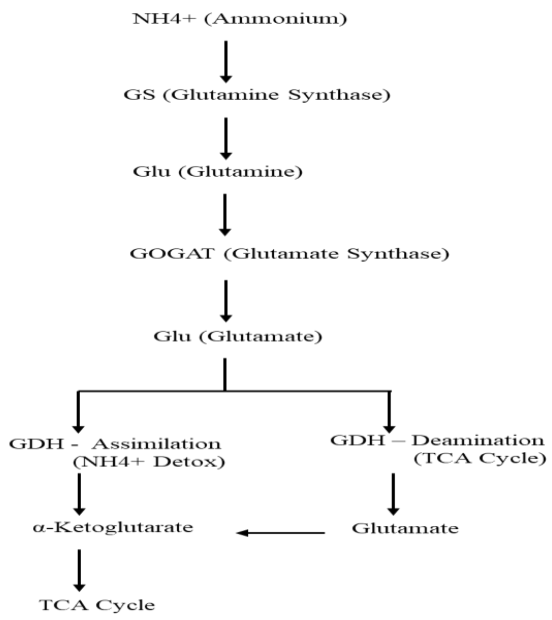

Fig. 1 Ammonia detoxification via GDH pathway

3.3 Effects of NO and H_2S on Cd Detoxification

Application of NO and H_2S significantly alleviated Cd-induced toxicity. Cd uptake was reduced by 24% in NO-treated plants and by 20% in H_2S -treated plants compared to Cd-only treatment. Combined NO + H_2S treatment lowered Cd accumulation by 31.5%, indicating a synergistic detoxification effect. Growth parameters improved, with plant height increasing by 18.4% and dry weight by 22.1% under combined NO + H_2S treatment compared to Cd-stressed plants (Table 3). The protective roles of NO and H_2S may be attributed to enhanced Cd sequestration, activation of antioxidant defences, and upregulation of stress-response genes (Rizwan et al., 2022).

Table 3. Treatment by NO, H2S & NO+ H2S

Parameters	Control	Treatments		
		NO	**H2S**	**NO+ H2S**
Cd Uptake (µM)	85.6	65.06	68.48	58.64
Plant height (cm)	60.96	68.27	67.05	72.17
Dry weight (kg/m^2)	2.5	2.96	2.85	3.05

3.4 Ion Homeostasis and Na^{+}/K^{+} Balance

The most severe nutrient imbalance was observed at 100 µM Cd.Our results confirm that Cd stress significantly reduced K^{+}, Ca^{2+}, Fe, and Mg levels while increasing Na^{+} and Cl^{-} accumulation. Fig. 2 depicts that Cd stress led to significant ion imbalances, with Na^{+} and Cl^{-}levels increasing by 27.6% and 20.4% respectively, whereas K^{+},Ca^{2+}, Fe and Mg levels decreasing by 19.8%, 14.23%,9.41%and 21.2% respectively at 100 µM Cd, resulting in an elevated Na^{+}/K^{+} ratio (1.41 compared to 0.89 in control)in tomato plants. The severity of ionic imbalance was dose-dependent, with 100 µM Cd causing the most drastic reductions in essential nutrients.H_2S and NO treatments restored ion homeostasis, lowering Na^{+}/K^{+} ratio to 0.91 under NO+ H_2S treatment. Application of NO and H_2S partially restored K^{+}, Ca^{2+}, Fe and Mg levels while reducing Na^{+} and Cl^{-} accumulation. The combined NO + H_2S treatment exhibited the strongest protective effects compared to individual applications, maintaining ionic balance similar to control plants and suggesting a synergistic interaction between these signalling molecules.This restoration suggests NO and H_2S modulate ion transporters, maintaining cellular ionic balance under Cd stress (Song et al., 2023).Cd stress disrupts ion uptake mechanisms by interfering with transport proteins and root membrane integrity. The observed decline in K^{+} and Ca^{2+} levels align with previous findings, indicating Cd-induced competition with essential cations (Hasanuzzaman et al., 2022). Increased Na^{+} accumulation suggests Cd-mediated impairment of ion selectivity, leading to osmotic stress and toxicity. NO + H_2S treatments restored K^{+} and Ca^{2+} levels and reduced Na^{+} accumulation. The restoration of nutrient balance by NO and H_2S suggests their role in enhancing ion transport and root integrity (Ali et al., 2023). The protective role of NO and H_2S in maintaining mineral balance is likely due to their ability to (i) enhance root ion transporters, (ii) regulate antioxidant systems, and (iii) reduce Cd accumulation in plant tissues (Zhang et al., 2021). The combined NO + H_2S treatment proved most effective, highlighting a potential crosstalk mechanism that strengthens Cd tolerance.

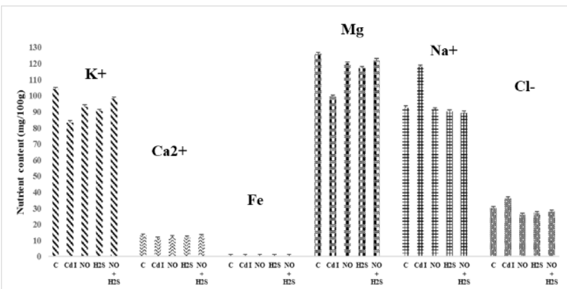

Fig. 2 Ion Homeostasis in Tomato plants

3.5 Expression of Cd-Transport and Stress-Response Genes

qRT-PCR analysis showed that Cd transporter genes (*HMA2*, *IRT1*) were significantly upregulated in Cd-treated plants, while NO and H_2S treatments downregulated their expression, reducing Cd uptake (Fig.3). Conversely, stress-related genes (*NR*, *GS*) showed higher expression under NO+H_2S treatment, suggesting enhanced nitrogen metabolism efficiency under Cd stress (Zhou et al., 2023).

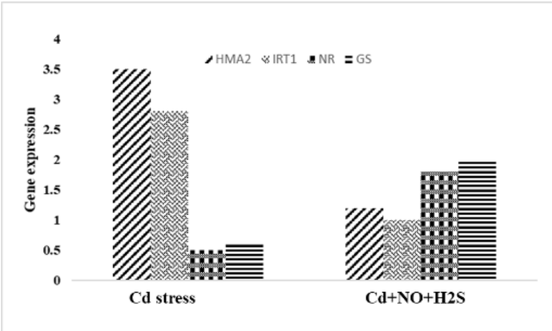

Fig. 3 Cd Transporter gene expression in Tomato plants

4. Conclusion

Cd stress significantly reduced growth, disrupted nitrogen metabolism, and altered ion homeostasis in *Solanum lycopersicum*. It disrupts nutrient homeostasis by reducing essential mineral concentrations while increasing toxic ion accumulation. The application of NO and H_2S effectively mitigates these effects, with the combined treatment showing the highest protective potentialby modulating Cd uptake, enhancing enzymatic activity, and improving stress tolerance. These findings provide new insights into the role of NO and H_2S in enhancing heavy metal tolerance and improving nutrient balance in tomato plants. Future research should explore the molecular mechanisms underlying their interactions.

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Consent to participate- Not applicable. This study didn't involve human participants.

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Conflict of Interest- The authors do not have any competing interest.

Data availability- All the data are present in the manuscript.

Ethical Statement- Not Applicable.

References

Ata-Ul-Karim ST, Cang L, Wang Y, Zhou D. Effects of soil properties, nitrogen application, plant phenology, and their interactions on plant uptake of cadmium in wheat. Journal of hazardous materials. 2020 Feb 15;384:121452.

Birghila S, Matei N, Dobrinas S, Popescu V, Soceanu A, Niculescu A. Assessment of heavy metal content in soil and Lycopersicon esculentum (tomato) and their health implications. Biological Trace Element Research. 2023 Mar;201(3):1547-56.

Cai W, Wang W, Deng H, Chen B, Zhang G, Wang P, Yuan T, Zhu Y. Improving endogenous nitric oxide enhances cadmium tolerance in rice through modulation of cadmium accumulation and antioxidant capacity. Agronomy. 2023 Jul 26;13(8):1978.

Carvalho ME, Castro PR, Azevedo RA. Hormesis in plants under Cd exposure: from toxic to beneficial element?. Journal of Hazardous Materials. 2020 Feb 15;384:121434.

Chen X, Shi X, Ai Q, Han J, Wang H, Fu Q. Transcriptomic and metabolomic analyses reveal that exogenous strigolactones alleviate the response of melon root to cadmium stress. Horticultural Plant Journal. 2022 Sep 1;8(5):637-49.

Day L. Proteins from land plants–potential resources for human nutrition and food security. Trends in Food Science & Technology. 2013 Jul 1;32(1):25-42.

De Cesare F, Pietrini F, Zacchini M, ScarasciaMugnozza G, Macagnano A. Catechol-loading nanofibrous membranes for eco-friendly iron nutrition of plants. Nanomaterials. 2019 Sep 14;9(9):1315.

Gowda RS, Kaur M, Kaushal B, Kaur H, Kumar V, Sharma R, Singh T, Choudhary A, Mehta S, Husen A. Behavior, sources, uptake, interaction, and nutrient use efficiency in plant system under changing environment. InEssential Minerals in Plant-Soil Systems 2024 Jan 1 (pp. 93-127). Elsevier.

Gratão PL, Monteiro CC, Tezotto T, Carvalho RF, Alves LR, Peters LP, Azevedo RA. Cadmium stress antioxidant responses and root-to-shoot communication in grafted tomato plants. Biometals. 2015 Oct;28(5):803-16.

Gregory PJ, Wahbi A, Adu-Gyamfi J, Heiling M, Gruber R, Joy EJ, Broadley MR. Approaches to reduce zinc and iron deficits in food systems. Global Food Security. 2017 Dec 1;15:1-0.

Hassan H, Elaksher SH, Shabala S, Ouyang B. Cadmium uptake and detoxification in tomato plants: Revealing promising targets for genetic improvement. Plant Physiology and Biochemistry. 2024 Sep 1;214:108968.

Jangirh R, Mondal A, Yadav P, Yadav L, Datta A, Saxena P, Mandal TK. Characterization of road dust in Delhi: Heavy metal analysis, health risks, and sustainability implications. Aerosol Science and Engineering. 2024 Dec;8(4):414-25.

Li D, He T, Saleem M, He G. Metalloprotein-specific or critical amino acid residues: Perspectives on plant-precise detoxification and recognition mechanisms under cadmium stress. International Journal of Molecular Sciences. 2022 Feb 3;23(3):1734.

Mena P, Angelino D. Plant food, nutrition, and human health. Nutrients. 2020 Jul 20;12(7):2157.

Mir IR, Rather BA, Masood A, Anjum NA, Khan NA. Nitrogen sources mitigate cadmium phytotoxicity differentially by modulating cellular buffers, N-assimilation, non-protein thiols, and phytochelatins in mustard (Brassica juncea L.). Journal of Soil Science and Plant Nutrition. 2022 Sep;22(3):3847-67.

Nawaz M, Saleem MH, Khalid MR, Ali B, Fahad S. Nitric oxide reduces cadmium uptake in wheat (Triticum aestivum L.) by modulating growth, mineral uptake, yield attributes, and antioxidant profile. Environmental Science and Pollution Research. 2024 Feb;31(6):9844-56.

Wang YJ, Dong YX, Wang J, Cui XM. Alleviating effects of exogenous NO on tomato seedlings under combined Cu and Cd stress. Environmental Science and Pollution Research. 2016 Mar;23(5):4826-36.

Xu J, Wei Z, Lu X, Liu Y, Yu W, Li C. Involvement of nitric oxide and melatonin enhances cadmium resistance of tomato seedlings through regulation of the ascorbate–glutathione cycle and ROS metabolism. International Journal of Molecular Sciences. 2023 May 31;24(11):9526.

Yang M, Zhou D, Hang H, Chen S, Liu H, Su J, Lv H, Jia H, Zhao G. Effects of balancing exchangeable cations Ca, Mg, and K on the growth of tomato seedlings (Solanum lycopersicum L.) based on increased soil cation exchange capacity. Agronomy. 2024 Mar 20;14(3):629.

Yi L, Wu M, Yu F, Song Q, Zhao Z, Liao L, Tong J. Enhanced cadmium phytoremediation capacity of poplar is associated with increased biomass and Cd accumulation under nitrogen deposition conditions. Ecotoxicology and Environmental Safety. 2022 Nov 1;246:114154.

Yuan K, Wang C, Zhang C, Huang Y, Wang P, Liu Z. Rice grains alleviate cadmium toxicity by expending glutamate and increasing manganese in the cadmium contaminated farmland. Environmental Pollution. 2020 Jul 1;262:114236.

Zhao T, Pei T, Jiang J, Yang H, Zhang H, Li J, Xu X. Understanding the mechanisms of resistance to tomato leaf mold: A review. Horticultural Plant Journal. 2022 Nov 1;8(6):667-75.