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Harnessing the effects of Cadmium Stress and Amelioration by Nitric Oxide and Hydrogen Sulfide on Mineral Nutrient Balance and 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 (H₂S) 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 H₂S mitigated Cd-induced damage by enhancing nutrient uptake, restoring ion balance, and improving nitrogen metabolism enzyme activity. The combined NO + H₂S treatment was the most effective, suggesting a synergistic role in Cd stress tolerance. These findings highlight the potential of NO and H₂S 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

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 (H₂S) 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 H₂S 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 Cd²⁺ (0, 25, 50, and 100 µM CdCl₂) in Hoagland's solution for 15 days under greenhouse condition, with each treatment replicated thrice. Further, Cd treated plants were exposed to NO and H₂S alone and in combination with NO and H₂S. The samples 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 (HNO₃:H₂SO₄:HClO₄ 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 $12,000 \times g$ for 20 min at $4^\circ C$, 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 H₂S in Cd detoxification was assessed by measuring:

2.7.1 Endogenous NO and H₂S 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^{-ΔΔCt} method (Ali et al., 2023).

2.8 Statistical Analysis

All experiments were conducted in a completely randomized design (CRD) with three

Parameters	Control	Cd- Induced (100μM)	Reduction (%)	biolo
			135	gical
			136	replic
			137	

ates 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).

3. Cadmium Accumulation in Tomato Tissues

Cadmium (Cd) accumulation was significantly higher in roots compared to shoots and leaves. At 100 μM CdCl₂, 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	155
Root Length (cm)	17	11.94	29.8	156
Leaf Area (cm ²)	110	64.68	41.2	157
Biomass (kg/m ²)	2.5	1.54	38.7	157

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 H₂S 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)	Nitrate Reductase (NR) (μmol NO ₂ ⁻ g ⁻¹ FW h ⁻¹)	Glutamine Synthetase (GS) (μmol γ- 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.

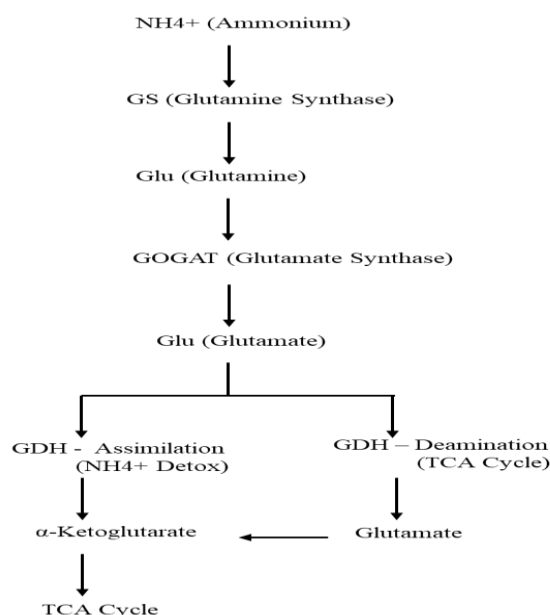


Fig. 1 Ammonia detoxification via GDH pathway

3.3 Effects of NO and H₂S on Cd Detoxification

Application of NO and H₂S significantly alleviated Cd-induced toxicity. Cd uptake was reduced by 24% in NO-treated plants and by 20% in H₂S -treated plants compared to Cd-only treatment. Combined NO + H₂S 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 + H₂S treatment compared to Cd-stressed plants (Table 3). The protective roles of NO and H₂S 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	H ₂ S	NO+ H ₂ S
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

196

197 3.4 Ion Homeostasis and Na^+/K^+ Balance

198 The most severe nutrient imbalance was observed at 100 μM Cd. Our results confirm that Cd
 199 stress significantly reduced K^+ , Ca^{2+} , Fe, and Mg levels while increasing Na^+ and Cl^-
 200 accumulation. Fig. 2 depicts that Cd stress led to significant ion imbalances, with Na^+ and
 201 Cl^- levels increasing by 27.6% and 20.4% respectively, whereas K^+ , Ca^{2+} , Fe and Mg levels
 202 decreasing by 19.8%, 14.23%, 9.41% and 21.2% respectively at 100 μM Cd, resulting in an
 203 elevated Na^+/K^+ ratio (1.41 compared to 0.89 in control) in tomato plants. The severity of
 204 ionic imbalance was dose-dependent, with 100 μM Cd causing the most drastic reductions in
 205 essential nutrients. H_2S and NO treatments restored ion homeostasis, lowering Na^+/K^+ ratio to
 206 0.91 under NO + H_2S treatment. Application of NO and H_2S partially restored K^+ , Ca^{2+} , Fe
 207 and Mg levels while reducing Na^+ and Cl^- accumulation. The combined NO + H_2S treatment
 208 exhibited the strongest protective effects compared to individual applications, maintaining
 209 ionic balance similar to control plants and suggesting a synergistic interaction between these
 210 signalling molecules. This restoration suggests NO and H_2S modulate ion transporters,
 211 maintaining cellular ionic balance under Cd stress (Song et al., 2023). Cd stress disrupts ion
 212 uptake mechanisms by interfering with transport proteins and root membrane integrity. The
 213 observed decline in K^+ and Ca^{2+} levels align with previous findings, indicating Cd-induced
 214 competition with essential cations (Hasanuzzaman et al., 2022). Increased Na^+ accumulation
 215 suggests Cd-mediated impairment of ion selectivity, leading to osmotic stress and toxicity.
 216 NO + H_2S treatments restored K^+ and Ca^{2+} levels and reduced Na^+ accumulation. The
 217 restoration of nutrient balance by NO and H_2S suggests their role in enhancing ion transport
 218 and root integrity (Ali et al., 2023). The protective role of NO and H_2S in maintaining mineral
 219 balance is likely due to their ability to (i) enhance root ion transporters, (ii) regulate
 220 antioxidant systems, and (iii) reduce Cd accumulation in plant tissues (Zhang et al., 2021).
 221 The combined NO + H_2S treatment proved most effective, highlighting a potential crosstalk
 222 mechanism that strengthens Cd tolerance.

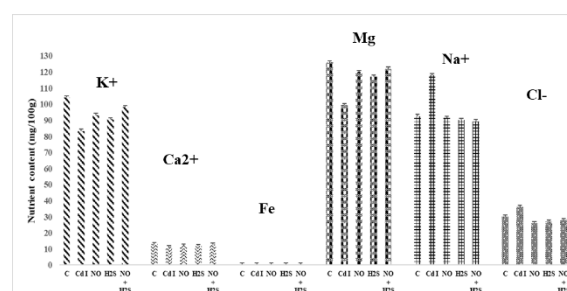


Fig. 2 Ion Homeostasis in Tomato plants

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228 3.5 Expression of Cd-Transport and Stress-Response Genes

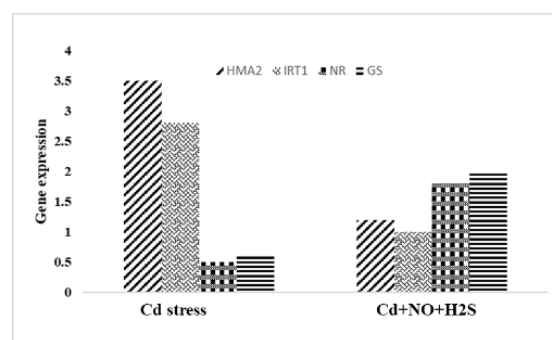
229 qRT-PCR analysis showed that Cd transporter genes (*HMA2*, *IRT1*) were significantly
230 upregulated in Cd-treated plants, while NO and H₂S treatments downregulated their
231 expression, reducing Cd uptake (Fig.3). Conversely, stress-related genes (*NR*, *GS*) showed
232 higher expression under NO+H₂S treatment, suggesting enhanced nitrogen metabolism
233 efficiency under Cd stress (Zhou et al., 2023).

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238

Fig. 3 Cd Transporter gene expression in Tomato plants

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240 4. Conclusion

241 Cd stress significantly reduced growth, disrupted nitrogen metabolism, and altered ion
242 homeostasis in *Solanum lycopersicum*. It disrupts nutrient homeostasis by reducing essential
243 mineral concentrations while increasing toxic ion accumulation. The application of NO and
244 H₂S effectively mitigates these effects, with the combined treatment showing the highest
245 protective potential by modulating Cd uptake, enhancing enzymatic activity, and improving
246 stress tolerance. These findings provide new insights into the role of NO and H₂S in
247 enhancing heavy metal tolerance and improving nutrient balance in tomato plants. Future
248 research should explore the molecular mechanisms underlying their interactions.

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 258 authors read and approved the final manuscript.

259 **Ethical approval-** Not applicable

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

12 261 **Consent to Publish-** All authors approved the final manuscript and consent to its publication.

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

2 263 **Data availability-** All the data are present in the manuscript.

264 **Ethical Statement-** Not Applicable.

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