

# CURRICULUM VITAE



## Part A. PERSONAL INFORMATION

PERSONAL INFORMATION			
First and Family Name	SOUMYA MUKHERJEE	Permanent Address	113/A, Bangur Park, Rishra, Hooghly West Bengal 712248, India
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## Part B. CURRENT POSITION

Affiliation	Department of Botany, Jangipur College, University of Kalyani, West Bengal 742213, India ( <a href="https://www.jangipurcollege.in/">https://www.jangipurcollege.in/</a> )
Designation	Assistant Professor (from 6.12.2016-present)
College Website url	<a href="http://www.jangipurcollege.in/department/staffnotes.php?x=151">http://www.jangipurcollege.in/department/staffnotes.php?x=151</a>
Current Research Area	Physiological and biochemical mechanisms of salinity tolerance during seed germination and seedling growth associated with ouabain-sensitive ATPase activity, serotonin, melatonin, nitric oxide and hydrogen sulfide signaling

## Part C. WORK EXPERIENCES

Designation	Affiliation	Year
Assistant Professor (Permanent)	Department of Botany, Jangipur College, University of Kalyani, West Bengal 742213, India	6.12.2016-present
Assistant Professor (Adhoc)	Department of Botany, Ramjas College, University of Delhi, Delhi, India	2015 (July)-2016 (December)
Assistant Professor (Adhoc)	Department of Botany, Shivaji College, University of Delhi, Delhi, India	2015 (April-June)
Assistant Professor (Guest)	Department of Botany, Shivaji College, University of Delhi, Delhi, India	2015 (January-March)

**Part D. EDUCATIONAL QUALIFICATIONS**

Level of Education	Institute and Board Affiliation	Year of Passing	Percentage Marks obtained
Ph.D in Botany	Department of Botany, University of Delhi (Mentor: Prof. Satish C Bhatla Laboratory of Plant Physiology and Biochemistry)	2015 Thesis title: <i>Salt-stress induced biochemical changes associated with seed germination and seedling growth in sunflower</i>	
Master of Science (Botany)	Department of Botany, University of Delhi, India	2010	74.6%
Bachelor of Science (Botany honours)	Asutosh College, University of Calcutta, West Bengal, India	2008	69.62%
Higher Secondary (12 <sup>th</sup> ) level	West Bengal Board of Higher Secondary Education (WBHSE) Bidhan Chandra Institution, Durgapur, West Bengal, India	2005	71.8%
Secondary (10 <sup>th</sup> level)	Indian Certificate of Secondary Education, St. Xavier's School Durgapur, West Bengal, India	2003	82.16%

**Part E. AWARDS AND FELLOWSHIPS**

Council of Scientific and Industrial Research (CSIR) National Eligibility Test- 2009	Qualified for NET-JRF All India Rank – 49 Junior and Senior Research Fellow- 2010-2015
GATE 2010 (IIT Guwahati)	Qualified All India Rank -617

**Part F. EVALUATION TASKS**

Reviewer for Project Proposal in Plant Physiology- October 2019	Executive Government Agency of National Science Centre (Narodowe Centrum Nauki – NCN), Poland
Subject Reviewer in Journals	Journal names- Plant signaling and Behaviour, Acta physiologia plantarum, Plant Cell Reports, Physiologia Plantarum, Journal of Plant Growth Regulation, Plant Physiology and Biochemistry, BMC plant biology, Plant biology, Scientific Reports, and PlosOne
Associate Editor	Plant Signaling and Behaviour, Taylor and Francis, online

**Part G. CONFERENCE, SYMPOSIUM & WORKSHOP PARTICIPATION**

Title of Conference/Symposium	Participation
2 <sup>nd</sup> <u>International</u> Symposium on Plant Signaling and Behaviour, New Delhi, India, March -2014	Member of Organizing committee & Participant in poster presentation
4 <sup>th</sup> <u>International</u> Symposium on Plant Signaling and Behaviour, St. Petersburg, Russia, June-2016	Participant in poster presentation

<u>National</u> workshop “Ankuran” on development of herbal garden , Shivaji College, New Delhi, India, January-2015	Member of Organizing committee
2 <sup>nd</sup> regional <u>National</u> Science and Technology Congress, University of Kalyani and Department of Higher Education, Science and Technology, December 2017	Participant in Oral presentation
<u>National</u> workshop on Intellectual Property Rights, Ramjas College, University of Delhi, August, 2016	Member of Organizing committee
The Academic Congress, University of Delhi, September, 2012	Participation

#### **Part H. TRAINING AND FACULTY DEVELOPMENT PROGRAMME**

<b>Name of the programme</b>	<b>Organization</b>	<b>Date</b>
Faculty Development Programme on ‘Entrepreneurship Development’	Enterprise Development Institute, Salt Lake, Kolkata	27 <sup>th</sup> March to 7 April, 2017
Orientation Programme	Human Resource Development Centre, Baba Saheb Ambedkar Marathwada University, Auranagbad, India	2 <sup>nd</sup> February to 1 <sup>st</sup> March, 2018
Refresher Course in Life Sciences	Human Resource Development Centre, University of Delhi, India	17 <sup>th</sup> June-11 <sup>th</sup> July, 2019
Short term general course on Intellectual Property Rights	World Intellectual Property Organization (WIPO), Geneva, Switzerland, India	June, 2019
Short term course on ‘Patent Cooperation Treaty’	World Intellectual Property Organization (WIPO), Geneva, Switzerland, India	November, 2019
Faculty Development Programme on ‘ICT Tools for Online Teaching’	Sri Guru Govind Singh College of Commerce, University of Delhi, India	9 <sup>th</sup> June-13 <sup>th</sup> June, 2020

### Recent Publications

Google scholar citations- 563    H-index- 11    i10 index- 12 cumulative impact factor- 104.69
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### Research Articles

1. Mukherjee, S., Bhatla, S.C. Exogenous Melatonin Modulates Endogenous H<sub>2</sub>S Homeostasis and L-Cysteine Desulfhydrase Activity in Salt-Stressed Tomato (*Solanum lycopersicum* L. var. cherry) Seedling Cotyledons. *J Plant Growth Regul* (2020). <https://doi.org/10.1007/s00344-020-10261-7> (IF 4.1)
2. Siddiqui MH, Khan MN, Mukherjee S, Alamri S, Basahi RA, Al-Amri AA, Alsubaie QD, Al-Munqedhi BMA, Ali HM, Almohisen IAA. Hydrogen sulfide (H<sub>2</sub>S) and potassium (K<sup>+</sup>) synergistically induce drought stress tolerance through regulation of H<sup>+</sup>-ATPase activity, sugar metabolism, and antioxidative defense in tomato seedlings. *Plant Cell Rep*. 2021 Aug;40(8):1543-1564. doi: 10.1007/s00299-021-02731-3 (IF 4.5)
3. Siddiqui MH, Alamri S, Mukherjee S, Al-Amri AA, Alsubaie QD, Al-Munqedhi BMA, Ali HM, Kalaji HM, Fahad S, Rajput VD, Narayan OP. Molybdenum and hydrogen sulfide synergistically mitigate arsenic toxicity by modulating defense system, nitrogen and cysteine assimilation in faba bean (*Vicia faba* L.) seedlings. *Environ Pollut*. 2021 Aug 12;290:117953. doi: 10.1016/j.envpol.2021.117953. (IF 8.0)
4. Khan MN, Siddiqui MH, Mukherjee S, Alamri S, Al-Amri AA, Alsubaie QD, Al-Munqedhi BMA, Ali HM. Calcium-hydrogen sulfide crosstalk during K<sup>+</sup>-deficient NaCl stress operates through regulation of Na<sup>+</sup>/H<sup>+</sup> antiport and antioxidative defense system in mung bean roots. *Plant Physiol Biochem*. 2021 Feb;159:211-225. doi: 10.1016/j.plaphy.2020.11.055. (IF 4.2)
5. Khan MN, Mukherjee S, Al-Huqail AA, Basahi RA, Ali HM, Al-Munqedhi BMA, Siddiqui MH, Kalaji HM. Exogenous Potassium (K<sup>+</sup>) Positively Regulates Na<sup>+</sup>/H<sup>+</sup> Antiport System, Carbohydrate Metabolism, and Ascorbate-Glutathione Cycle in H<sub>2</sub>S-Dependent Manner in NaCl-Stressed Tomato Seedling Roots. *Plants (Basel)*. 2021 May 10;10(5):948. doi: 10.3390/plants10050948. (IF 3.9)
6. Siddiqui MH, Khan MN, Mukherjee S, Basahi RA, Alamri S, Al-Amri AA, Alsubaie QD, Ali HM, Al-Munqedhi BMA, Almohisen IAA. Exogenous melatonin-mediated regulation of K<sup>+</sup> /Na<sup>+</sup> transport, H<sup>+</sup> -ATPase activity and enzymatic antioxidative defence operate through endogenous hydrogen sulphide signalling in NaCl-stressed

tomato seedling roots. Plant Biol (Stuttg). 2021 Sep;23(5):797-805. doi: 10.1111/plb.13296 (IF 3.0)

7. SA Abd Elhady, HGA El-Gawad, MFM Ibrahim, S Mukherjee, A Elkelish, et al Hydrogen peroxide supplementation in irrigation water alleviates drought stress and boosts growth and productivity of potato plants. Sustainability 2021 13(2), pp. 1–16, 899.(IF 3.2)

8. Ola H Abd Elbar, Amr Adel Elkelish, Reham Farag, Mukherjee S, Ayman F Abou-Hadid, Hussien M El-Hennawy. Protective Effect of  $\gamma$ -aminobutyric acid Against Chilling Stress During Reproductive Stage in Tomato Through Modulation of Sugar Metabolism, Chloroplast Integrity and Antioxidative Defense Systems. *Frontiers in Plant Science* doi: 10.3389/fpls.2021.663750 (IF 5.7)
9. Alamri S, Hu Y, Mukherjee S, Aftab T, Fahad S, Raza A, Ahmad M, Siddiqui MH. Silicon-induced postponement of leaf senescence is accompanied by modulation of antioxidative defense and ion homeostasis in mustard (*Brassica juncea*) seedlings exposed to salinity and drought stress. *Plant Physiol Biochem.* 2020 Dec; 157:47-59. doi: 10.1016/j.plaphy.2020.09.038. (IF 4.2)
10. Elkelish A, Ibrahim MFM, Ashour H, Bondok A, Mukherjee S, Aftab T, Hikal M, El-Yazied AA, Azab E, Gobouri AA, Moustafa-Farag M, Metwally AA, El-Gawad HGA. Exogenous Application of Nitric Oxide Mitigates Water Stress and Reduces Natural Viral Disease Incidence of Tomato Plants Subjected to Deficit Irrigation. *Agronomy.* 2021; 11(1):87. <https://doi.org/10.3390/agronomy11010087> (IF 2.2)
11. Abd El-Gawad HG, Mukherjee S, Farag R, Abd Elbar OH, Hikal M, Abou El-Yazied A, Abd Elhady SA, Helal N, ElKelish A, El Nahhas N, Azab E, Ismail IA, Mbarki S, Ibrahim MFM. Exogenous  $\gamma$ -aminobutyric acid (GABA)-induced signaling events and field performance associated with mitigation of drought stress in *Phaseolus vulgaris* L. *Plant Signal Behav.* 2021 Feb 1;16(2):1853384. doi: 10.1080/15592324.2020.1853384. (IF 2.2)
12. Mukherjee S, Bhatla SC. A novel fluorescence imaging approach to monitor salt stress-induced modulation of ouabain-sensitive ATPase activity in sunflower seedling roots. *Physiol Plant.* 2014 Apr;150(4):540-9. doi: 10.1111/ppl.12101. (IF- 4.1)
13. Mukherjee S, David A, Yadav S, Baluška F, Bhatla SC. Salt stress-induced seedling growth inhibition coincides with differential distribution of serotonin and melatonin in sunflower seedling roots and cotyledons. *Physiol Plant.* 2014 Dec;152(4):714-28. doi: 10.1111/ppl.12218. (IF- 4.1)
14. Saud Alamri, Manzer H. Siddiqui, Soumya Mukherjee, Ritesh Kumar, Hazem M. Kalaji, Mohammad Irfan, Tatiana Minkina, Vishnu D. Rajput. Molybdenum-induced endogenous nitric oxide (NO) signaling coordinately enhances resilience through chlorophyll metabolism, osmolyte accumulation and antioxidant system in arsenate stressed-wheat (*Triticum aestivum* L.) seedlings. *Environmental Pollution.* 2022, 292, 118268. (IF- 8.0)
15. Siddiqui MH, Mukherjee S, Kumar R, et al. Potassium and melatonin-mediated regulation of fructose-1,6-bisphosphatase (FBPase) and sedoheptulose-1,7-

bisphosphatase (SBPase) activity improve photosynthetic efficiency, carbon assimilation and modulate glyoxalase system accompanying tolerance to cadmium stress in tomato seedlings. *Plant Physiology and Biochemistry* 2021 Dec;171:49-65. DOI: 10.1016/j.plaphy.2021.12.018. PMID: 34971955. (IF 4.2)

### **Review Articles**

1. Bhatla SC, Gogna M, Jain P, Singh N, Mukherjee S, Kalra G. Signaling mechanisms and biochemical pathways regulating pollen-stigma interaction, seed development and seedling growth in sunflower under salt stress. *Plant Signal Behav.* 2021 Aug 25:1958129. doi: 10.1080/15592324.2021.1958129 (IF 2.2)
2. Akula R, Mukherjee S. New insights on neurotransmitters signaling mechanisms in plants. *Plant Signal Behav.* 2020 Jun 2;15(6):1737450. doi: 10.1080/15592324.2020.1737450. (IF 2.2)

3. Kaur H, Mukherjee S, Baluska F, Bhatla SC. Regulatory roles of serotonin and melatonin in abiotic stress tolerance in plants. *Plant Signal Behav.* 2015;10(11):e1049788. doi: 10.1080/15592324.2015.1049788. **(IF 2.2)**
  
4. Mukherjee S, Corpas FJ. Crosstalk among hydrogen sulfide (H<sub>2</sub>S), nitric oxide (NO) and carbon monoxide (CO) in root-system development and its rhizosphere interactions: A gaseous interactome. *Plant Physiol Biochem.* 2020 Oct;155:800-814. doi: 10.1016/j.plaphy.2020.08.020. **(IF 4.2)**
  
5. Mukherjee S. Insights into nitric oxide-melatonin crosstalk and N-nitrosomelatonin functioning in plants. *J Exp Bot.* 2019 Nov 18;70(21):6035-6047. doi: 10.1093/jxb/erz375 **(IF 6.9)**
  
6. Mukherjee S. Novel perspectives on the molecular crosstalk mechanisms of serotonin and melatonin in plants. *Plant Physiol Biochem.* 2018 Nov;132:33-45. doi: 10.1016/j.plaphy.2018.08.031 **(IF 4.2)**
  
7. Mukherjee S. Recent advancements in the mechanism of nitric oxide signaling associated with hydrogen sulfide and melatonin crosstalk during ethylene-induced fruit ripening in plants. *Nitric Oxide.* 2019 Jan 1;82:25-34. doi: 10.1016/j.niox.2018.11.003. **(IF 4.4)**
  
8. Keisham M, Mukherjee S, Bhatla SC. Mechanisms of Sodium Transport in Plants- Progresses and Challenges. *Int J Mol Sci.* 2018 Feb 25;19(3):647. doi: 10.3390/ijms19030647. **(IF 5.91)**
  
9. Mukherjee S Cysteine modifications (oxPTM) and protein sulphenylation-mediated sulfenome expression in plants: evolutionary conserved signaling networks? *Plant Signaling and Behavior*, 2021, 16(1), 1831792. **(IF 2.2)**
  
10. Morteza Soleimani Aghdam, Soumya Mukherjee, Francisco Borja Flores, Marino B Arnao, Zisheng Luo, Francisco J Corpas, Functions of Melatonin during Postharvest of Horticultural Crops, *Plant and Cell Physiology*, 2021;, pcab175, <https://doi.org/10.1093/pcp/pcab175> **(IF 4.9)**





# Exogenous Melatonin Modulates Endogenous H<sub>2</sub>S Homeostasis and L-Cysteine Desulphydrase Activity in Salt-Stressed Tomato (*Solanum lycopersicum* L. var. cherry) Seedling Cotyledons

Soumya Mukherjee<sup>1</sup> · Satish C. Bhatla<sup>2</sup>

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## Abstract

Although melatonin has been reported to function as a stress signaling molecule, not much information is available on the biochemical and molecular events associated with probable melatonin-hydrogen sulfide crosstalk in plants. Present work provides evidence on the role of melatonin in the modulation of H<sub>2</sub>S homeostasis during NaCl stress in dark-grown tomato (*Solanum lycopersicum* L. var. cherry) seedlings. NaCl stress (120 mM) inhibits hypocotyl elongation, promotes primary root growth and enhances electrolytic leakage from tomato seedlings. Treatment with H<sub>2</sub>S donor (100 μM; NaHS) tends to reverse these effects, all the more so (additive effect) in the presence of melatonin. NaCl stress and exogenous melatonin (30 μM) treatments modulate endogenous H<sub>2</sub>S accumulation and positively upregulate the activity of L-cysteine desulphydrase (L-DES; EC 4.4.1.15; cytosolic). Melatonin has been observed to temporally modulate the activity of specific isoforms of H<sub>2</sub>S biosynthesizing enzyme, L-DES in seedling cotyledons. Zymographic analysis of L-DES isoforms in tomato seedling cotyledons has provided novel findings in plant system. Melatonin treatment decreases H<sub>2</sub>S accumulation in NaCl-stressed seedling cotyledons which is accompanied by a contrasting increase in L-DES activity. Melatonin, therefore, regulates endogenous H<sub>2</sub>S concentration in seedling cotyledons (NaCl treated), thus indicating the role of H<sub>2</sub>S catabolism pathways in H<sub>2</sub>S homeostasis. Present findings thus reveal that exogenous melatonin modulates early H<sub>2</sub>S signaling in cotyledons of tomato seedlings subjected to NaCl stress. Furthermore, exogenous melatonin and H<sub>2</sub>S in combination (additive effect) ameliorate NaCl stress-induced growth changes in tomato seedlings.

**Keywords** H<sub>2</sub>S homeostasis · Melatonin · Salt stress · Tomato seedlings · L-cysteine desulphydrase · Long distance salt stress signaling

## Abbreviations

DMPD N, N-dimethyl-p-phenylenediamine

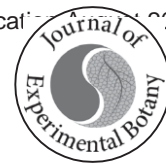
dihydrochloride  
DTT Dithiothreitol  
EC Electrical conductivity  
EDTA Ethylenediaminetetraacetic acid L-

DES L-cysteine desulphydrase  
 MB Methylene blue  
 NaHS Sodium hydrogen sulfide

## Introduction

Although melatonin has been reported to function as a stress signaling molecule, not much information is available on the biochemical and molecular events associated with probable melatonin-hydrogen sulfide crosstalk in plants. Kaya and Ashraf (2019b) have suggested the roles of melatonin and hydrogen sulfide in combating iron deficiency in pepper plants. However, melatonin-mediated H<sub>2</sub>S homeostasis, modulation of L-DES activity and long distance signaling in plant organs subjected to NaCl stress still

remain to



REVIEW PAPER

# Insights into nitric oxide–melatonin crosstalk and *N*-nitrosomelatonin functioning in plants

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Received 25 June 2019; Editorial decision 5 August 2019; Accepted 6 August 2019

Editor: Peter Bozhkov, Swedish University of Agricultural Sciences, Sweden

## Abstract

Similar to animal systems, plants have been suggested to possess both positive and antagonistic interactions between nitric oxide (NO) and melatonin. This review summarizes the current understanding of NO–melatonin crosstalk in plants with regard to redox homeostasis, regulation of gene expression, and developmental changes. It also addresses the possible role of *N*-nitrosomelatonin (NOMela), which is likely to be associated with redox signaling and long-distance communication. Localization and quantification of NOMela are expected to add new insights into its precise role in plants. Methodological advances in imaging, isolation, and quantification of such a transient molecule require further attention. The quest for the biological role of NOMela in plants should lure physiologists to pursue investigations to obtain solid experimental evidence.

**Keywords:** Abiotic stress, melatonin, nitric oxide, *N*-nitrosomelatonin (NOMela), reactive nitrogen species, redox signaling.



Contents lists available at ScienceDirect

Environmental Pollution

journal homepage:



# Molybdenum-induced endogenous nitric oxide (NO) signaling coordinately enhances resilience through chlorophyll metabolism, osmolyte accumulation and antioxidant system in arsenate stressed-wheat (*Triticum aestivum* L.) seedlings

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## ARTICLE INFO

### Keywords:

Arsenate  
Soluble carbohydrates  
Molybdenum  
Nitric oxide Nitrogen  
metabolism  
Photosynthesis  
Chlorophyll  
Wheat

## ABSTRACT

There is little information available to decipher the interaction between molybdenum (Mo) and nitric oxide (NO) in mitigating arsenic (As<sup>V</sup>) stress in plants. The present work highlights the associative role of exogenous Mo and endogenous NO signaling in regulating As<sup>V</sup> tolerance in wheat seedlings. Application of Mo (1 μM) on 25-day-old wheat seedlings grown in the presence (5 μM) or absence of As<sup>V</sup> stress caused improvement of photosynthetic pigment metabolism, reduction of electrolytic leakage and reactive oxygen species (ROS), and higher accumulation of osmolytes (proline and total soluble sugars). The molybdenum treatment upregulated antioxidative enzymes, such as superoxide dismutase, ascorbate peroxidase and glutathione reductase. In addition, the accumulation of nonenzymatic antioxidants (ascorbate and glutathione) was correlated with an increase in ascorbate peroxidase and glutathione reductase activity. The application of cPTIO (endogenous NO scavenger; 100 μM) reversed the Mo-mediated effects, thus indicating that endogenous NO may accompany Mo-induced mitigation of As<sup>V</sup> stress. Mo treatment stimulated the accumulation of endogenous NO in the presence of As<sup>V</sup> stress. Thus, it is evident that Mo and NO-mediated As<sup>V</sup> stress tolerance in wheat seedlings are primarily operative through chlorophyll restoration, osmolytes accumulation, reduced electrolytic leakage, and ROS homeostasis.



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## Molybdenum and hydrogen sulfide synergistically mitigate arsenic toxicity by modulating defense system, nitrogen and cysteine assimilation in faba bean (*Vicia faba* L.) seedlings<sup>☆</sup>

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### ABSTRACT

Hydrogen sulfide (H<sub>2</sub>S) has emerged as a potential gasotransmitter in plants with a beneficial role in stress amelioration. Despite the various known functions of H<sub>2</sub>S in plants, not much information is available to explain the associative role of molybdenum (Mo) and hydrogen sulfide (H<sub>2</sub>S) signaling in plants under arsenic toxicity. In view to address such lacunae in our understanding of the integrative roles of these biomolecules, the present work attempts to decipher the roles of Mo and H<sub>2</sub>S in mitigation of arsenate (AsV) toxicity in faba bean (*Vicia faba* L.) seedlings. AsV-stressed seedlings supplemented with exogenous Mo and/or NaHS treatments (H<sub>2</sub>S donor) showed resilience to AsV toxicity manifested by reduction of apoptosis, reactive oxygen species (ROS) content, down-regulation of NADPH oxidase and GOase activity followed by upregulation of antioxidative enzymes in leaves. Fluorescent localization of ROS in roots reveals changes in its intensity and spatial distribution in response to MO and NaHS supplementation during AsV stress. Under AsV toxicity conditions, seedlings subjected to Mo + NaHS showed an increased rate of nitrogen metabolism evident by elevation in nitrate reductase, nitrite reductase and glutamine synthetase activity. Furthermore, the application of Mo and NaHS in combination positively upregulates cysteine and hydrogen sulfide biosynthesis in the absence and presence of AsV stress. Mo plus NaHS-supplemented seedlings exposed to AsV toxicity showed a substantial reduction in oxidative stress manifested by reduced ELKG, lowered MDA content and higher accumulation of proline in leaves. Taken together, the present findings provide substantial evidence on the synergetic role of Mo and H<sub>2</sub>S in mitigating AsV stress in faba bean seedlings. Thus, the application of Mo and NaHS reveals their agronomic importance to encounter heavy metal stress for management of various food crops.



## Article

# Exogenous Potassium ( $K^+$ ) Positively Regulates $Na^+/H^+$ Antiport System, Carbohydrate Metabolism, and Ascorbate–Glutathione Cycle in $H_2S$ -Dependent Manner in NaCl-Stressed Tomato Seedling Roots

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**Abstract:** Potassium ( $K^+$ ) is one of the vital macronutrients required by plants for proper growth and blossoming harvest. In addition,  $K^+$  also plays a decisive role in promoting tolerance to various stresses. Under stressful conditions, plants deploy their defense system through various signaling molecules, including hydrogen sulfide ( $H_2S$ ). The present investigation was carried out to unravel the role of  $K^+$  and  $H_2S$  in plants under NaCl stress. The results of the study show that NaCl stress caused a reduction in  $K^+$  and an increase in  $Na^+$  content in the tomato seedling roots which coincided with a lower  $H^+$ -ATPase activity and  $K^+/Na^+$  ratio. However, application of 5 mM  $K^+$ , in association with endogenous  $H_2S$ , positively regulated the  $Na^+/H^+$  antiport system that accelerated  $K^+$  influx and  $Na^+$  efflux, resulting in the maintenance of a higher  $K^+/Na^+$  ratio. The role of  $K^+$  and  $H_2S$  in the regulation of the  $Na^+/H^+$  antiport system was validated by applying sodium orthovanadate (plasma membrane  $H^+$ -ATPase inhibitor), tetraethylammonium chloride ( $K^+$  channel blocker), amiloride ( $Na^+/H^+$  antiporter inhibitor), and hypotaurine (HT,  $H_2S$  scavenger). Application of 5 mM  $K^+$  positively regulated the ascorbate–glutathione cycle and activity of antioxidant enzymes that resulted in a reduction in reactive oxygen species generation and associated damage. Under NaCl stress,  $K^+$  also activated carbohydrate metabolism and proline accumulation that caused improvement in osmotic tolerance and enhanced the hydration level of the stressed seedlings. However, inclusion of the  $H_2S$  scavenger HT reversed the effect of  $K^+$ , suggesting  $H_2S$ -dependent functioning of  $K^+$  under NaCl stress. Therefore, the present findings report that  $K^+$ , in association with  $H_2S$ , alleviates NaCl-induced impairments by regulating the  $Na^+/H^+$  antiport system, carbohydrate metabolism, and antioxidative defense system.

**Keywords:** hydrogen sulfide; ionic homeostasis;  $Na^+/H^+$  antiport; oxidative stress; potassium; salinity

## 1. Introduction

Soil salinity is one of the menaces that limits crop production worldwide. Excessive accumulation of salts in the soil occurs due to poor irrigation and fertilizer management practices combined with high temperature and drought [1]. Salinity causes degradation of the soil structure and function that results in the loss of 1.5 million ha of arable land

every year, which culminates in an annual loss of USD 31 million [\[2\]](#). Salinity





