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Effects of PEG-simulated drought stress and selenite treatment on mineral nutrient homeostasis in wheat roots and shoots

Feiyan Yu[1,2,3], *Ying Wang*[1,2], *Xue Luo*[1,2], *Kaiwei Li*[1,2], *Jingwen Hou*[1,2], *Gaogao Dai*[1,2], *Huimin Yuan*[1,2], *Lianhe Zhang*[1,2,3]*

[1]*Agricultural College, Henan University of Science and Technology, Luoyang, Henan, P.R. China*
[2]*Luoyang Key Laboratory of Plant Nutrition and Environmental Ecology, Luoyang, Henan, P.R. China*
[3]*Henan Jinxiwang Agricultural Science and Technology Company Limited, Luoyang, Henan, P.R. China*
**Corresponding author: lhzhang2007@126.com*

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Abstract: Drought stress severely impairs seed germination and early seedling establishment, and disrupts the uptake and distribution of essential mineral nutrients in plants. This study investigated the effects of polyethylene glycol (PEG)-simulated drought and Na_2SeO_3 application on the accumulation and redistribution of phosphorus (P), potassium (K), calcium (Ca), sulphur (S), magnesium (Mg), iron (Fe), zinc (Zn), copper (Cu), and manganese (Mn) in wheat roots and shoots. Under PEG-simulated drought, increasing PEG concentrations resulted in a progressive decline in nutrient concentrations in both roots and shoots, with significant reductions in K, Ca, S, Zn, and Mn in roots, and K, Ca, Mg, and Mn in shoots. However, Na_2SeO_3 application mitigated these adverse effects by enhancing nutrient redistribution during early seedling growth. Specifically, under 15% PEG-simulated drought stress, Na_2SeO_3 treatments significantly increased shoot K, Mg, Fe, and Cu concentrations, highlighting selenium's role in facilitating the translocation of these key elements. These results demonstrate that Na_2SeO_3 effectively mitigates drought-related nutrient imbalances and promotes ion remobilisation from germinating seeds to developing roots and shoots under water-deficient conditions.

Keywords: osmotic stress; selenium supplementation; nutrient redistribution; abiotic stress mitigation; cereal crops

Drought stress is one of the most significant abiotic constraints limiting agricultural productivity worldwide, particularly in arid and semi-arid regions (PICC 2021). As a critical phase in the plant life cycle, seed germination is highly sensitive to water deficit, which can severely impair germination rates, seedling establishment, and subsequent crop yields (Farooq et al. 2012). Wheat (*Triticum aestivum* L.), a staple crop that feeds over 35% of the global population, is particularly vulnerable to drought stress during germination, often resulting in poor seedling vigour and reduced grain production (Shiferaw et al. 2013).

Seed germination is a complex process that involves the mobilisation of stored reserves, including carbohydrates, proteins, and minerals, to support the growth of the embryonic axis (Bewley et al. 2013). During germination, potassium (K), calcium (Ca), magnesium (Mg), sulphur (S), phosphorus (P), iron (Fe), zinc (Zn), copper (Cu), and manganese (Mn) are translocated from storage tissues to the growing

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embryo, where they play critical roles in cellular metabolism, enzyme activation, and osmotic regulation (Marschner 2013). However, drought stress disrupts ion homeostasis, leading to impaired nutrient uptake, translocation, and utilisation, which ultimately inhibits its seed germination and seedling growth (Saddam et al. 2016). For instance, drought stress has been shown to reduce the concentrations of K, Ca, and Mg in germinating seeds, thereby compromising root elongation and nutrient uptake (Fahim et al. 2014). Similarly, the decline in Zn or Mn concentration under drought stress can impair antioxidant enzyme activities, exacerbate oxidative damage, and further inhibit germination (Yao et al. 2009).

Selenium (Se), a beneficial micronutrient for plants, has gained attention for its potential to mitigate the adverse effects of abiotic stresses, including drought (Feng et al. 2013). Se exists in various chemical forms, with selenite (SeO_3^{2-}) and selenate (SeO_4^{2-}) being the most common inorganic forms available to plants. Among these, selenite has been increasingly studied due to its unique physiological effects, including its ability to enhance antioxidant capacity, regulate ion homeostasis, and improve water use efficiency under stress conditions (Djanaguiraman et al. 2010, Hasanuzzaman et al. 2020). Several studies have demonstrated that exogenous application of selenite can significantly improve seed germination and seedling growth under drought stress (Fahim et al. 2014, Saddam et al. 2016). For example, selenite treatment has been reported to improve ion homeostasis by enhancing the uptake and translocation of essential minerals, such as K, Ca, and Zn, thereby promoting root and shoot growth under stress conditions (Yao et al. 2009). Despite promising findings, how selenite regulates ion homeostasis in roots and shoots of germinating grains under drought remains unclear. This study, therefore, systematically investigates selenite-mediated ion homeostasis under PEG-simulated drought.

MATERIAL AND METHODS

Seed germination treatment. Surface-sterilised wheat seeds (*Triticum aestivum* L. cv. 9612) were immersed in 3% H_2O_2 (*v*/*v*) for 5 min, rinsed thoroughly, and assigned to two treatments: (1) drought simulation *via* imbibition in polyethylene glycol 6000 (PEG-6000) solutions (0, 5, 10, 15%); (2) combined treatment *via* imbibition in 15% PEG-6000 supplemented with 0, 0.25, 0.5, 1.0, 2.0 μmol/L Na_2SeO_3. After 12 h imbibition, seeds were rinsed, transferred to 9-cm Petri dishes lined with triple-layered moist filter paper, and arranged uniformly for germination.

Seed germination under PEG-simulated drought and Se treatments. After sowing, each dish was treated with 10 mL of either PEG-6000 (0, 5, 10, 15%) or 15% PEG-6000 supplemented with Na_2SeO_3 (0, 0.25, 0.5, 1.0, 2.0 μmol/L). Dishes were incubated at 25 °C under controlled conditions. Solutions were replenished periodically to maintain consistent osmotic stress and nutrient levels. After 8 days, seedlings were harvested; roots and shoots were separated for elemental analysis of P, K, Ca, S, Mg, Fe, Cu, Zn, and Mn. Solutions were replenished periodically throughout germination to maintain stable moisture and exact treatment concentrations.

Sample digestion. All glassware was pre-soaked in a 10% dilute HCl solution for 24 h. All reagents used were of superior grade purity. 0.1–0.2 g of samples were weighed into 100 mL digestion tubes. Then, 5 mL of mixed acid (HNO_3:$HClO_4$, 4:1, *v*/*v*) was added and left at room temperature overnight. Digestion was performed the following day using an AIM 600 fully automatic program digestion instrument under the following program: pre-digestion at 100 °C for 1 h; then 150 °C for 4 h. After cooling, the digestate was diluted to 25 mL with ultrapure water in a capped graduated test tube (Liu et al. 2025).

Determination of ion concentration. The concentration of P, K, Ca, S, Mg, Fe, Cu, Zn, and Mn was determined using a Malaysian-manufactured Agilent 5110 inductively coupled plasma optical emission spectrometer (ICP-OES, California, USA) with the following operational parameters: RF power maintained at 1200 W, peristaltic pump speed set to 12 rpm, plasma gas flow (high-purity argon) at 12.0 L/min, auxiliary gas flow (high-purity argon) at 1.2 L/min, nebuliser carrier gas flow at 0.7 L/min, and a 15 s stabilisation period before data acquisition.

Data processing. Figures were generated using Prism 10.1.2 (California, USA). Statistical analyses were performed using SPSS software (version 13.0, SPSS Inc., Chicago, USA). Different letters indicate significant differences between treatments and the control, as evaluated by one-way ANOVA with Tukey's test ($P < 0.005$).

RESULTS

Effects of PEG-simulated drought and selenite co-treatment on P concentrations in wheat roots and shoots. PEG-simulated drought exerted negligible effects on P homeostasis, with no significant

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alterations in root or shoot P concentrations across osmotic stress levels (Figure 1A). Under 15% PEG stress, Na_2SeO_3 application effectively prevented the decline of P levels, maintaining stable concentrations in shoots and roots compared to stressed controls (Figure 1B). This selenite-mediated stabilisation of P enhanced osmoregulatory capacity by promoting vacuolar compartmentalisation of P, which reduced cellular water loss and improved drought tolerance.

Effects of PEG-simulated drought and selenite co-treatment on K concentrations in wheat roots and shoots. PEG-simulated drought progressively reduced K concentrations in wheat roots and shoots (Figure 1C), with significant shoot depletion at 10–15% PEG and root decline at 5–15% PEG ($P < 0.005$), indicating disrupted K homeostasis. Critically, under 15% PEG stress, Na_2SeO_3 restored K allocation patterns: all concentrations increased shoot K, with 2.0 μmol/L resulting in a significant increase ($P < 0.005$), whereas root K was non-significantly reduced at concentrations of 0.75–2.0 μmol/L (Figure 1D). This selenite-mediated restoration of shoot K enhances cellular osmotic potential, reducing water loss and improving drought tolerance.

Effects of PEG-simulated drought and selenite co-treatment on Ca concentrations in wheat roots and shoots. PEG-simulated drought dose-dependently reduced Ca concentrations in wheat tissues (Figure 1E), with significant reductions in shoots at 15% PEG and in roots at 10–15% PEG ($P < 0.005$), indicating PEG disrupted Ca homeostasis. Crucially, under equivalent 15% PEG stress, Na_2SeO_3 co-treatment prevented the decline of Ca levels, maintaining root and shoot Ca concentrations at levels comparable to the controls with no significant differences (Figure 1F, $P < 0.005$). This preservation of Ca homeostasis highlights selenite's role in mitigating PEG-induced ion disruption, possibly through mechanisms such as membrane stabilisation or modulation of Ca transport under osmotic stress.

Effects of PEG-simulated drought and selenite co-treatment on S concentrations in wheat roots and shoots. PEG-simulated drought selectively impaired sulfur homeostasis in wheat, significantly reducing root S concentrations at 5–15% PEG ($P < 0.005$) while leaving shoot S unaffected (Figure 1G). Crucially, under 15% PEG stress, Na_2SeO_3 co-treatment effectively restored root S homeostasis. All concentrations maintained root S at control-equivalent levels without significant differences (Figure 1H, $P < 0.005$). Concurrently, 1.0–2.0 μmol/L selenite induced non-significant upward trends in shoot S, collectively demonstrating selenite's capacity to stabilise S allocation patterns compromised by osmotic stress.

Effects of PEG-simulated drought and selenite co-treatment on Mg concentrations in wheat roots and shoots. PEG-simulated drought drastically reduced shoot Mg concentrations at 15% ($P < 0.005$), while inducing non-significant declining trends in roots (Figure 1I). Critically, under equivalent 15% PEG stress, 1.0 μmol/L Na_2SeO_3 remarkably reversed shoot Mg reduction, increasing concentration significantly *versus* control ($P < 0.005$), and maintained root Mg at comparable levels despite osmotic stress (Figure 1J). This selenite-mediated Mg restoration in shoots enhances photosynthetic efficiency through chlorophyll synthesis and electron transport optimisation. At the same time, elevated Mg activates enzymes for osmotic potential maintenance and facilitates ribosomal protein synthesis, collectively improving drought resilience.

Effects of PEG-simulated drought and selenite co-treatment on Fe concentrations in wheat roots and shoots. Under PEG-simulated drought, root and shoot Fe concentrations showed non-significant declining trends (Figure 2A). Critically, 1.0 μmol/L Na_2SeO_3 under equivalent 15% PEG stress reversed this trend in shoots, significantly increasing Fe *versus* PEG control ($P < 0.005$), while higher concentrations (0.25–2.0 μmol/L) strategically reduced root Fe allocation (significantly at 2.0 μmol/L) (Figure 2B). This selenite-mediated Fe redistribution optimises physiological partitioning: elevated shoot Fe enhances antioxidant capacity, thereby mitigating oxidative damage, and indicates a strategic reallocation of resources toward stress defence mechanisms.

Effects of PEG-simulated drought and selenite co-treatment on Cu concentrations in wheat roots and shoots. PEG-simulated drought induced tissue-specific Cu dysregulation. Exposure to 5–15% PEG increased root Cu while marginally reducing shoot Cu at higher concentrations; however, these changes were not statistically significant (Figure 2C). Under 15% PEG stress, Na_2SeO_3 counterbalanced this dysregulation. 1.0–2.0 μmol/L significantly increased shoot Cu ($P < 0.005$) and progressively decreased root Cu (significant reduction at 2.0 μmol/L, $P < 0.005$) (Figure 2D). This selenite-mediated Cu redistribution enhances photosynthetic electron transport *via* plastocyanin activation and bolsters superoxide dismutase (SOD) activity, collectively mitigating drought-induced oxidative damage.

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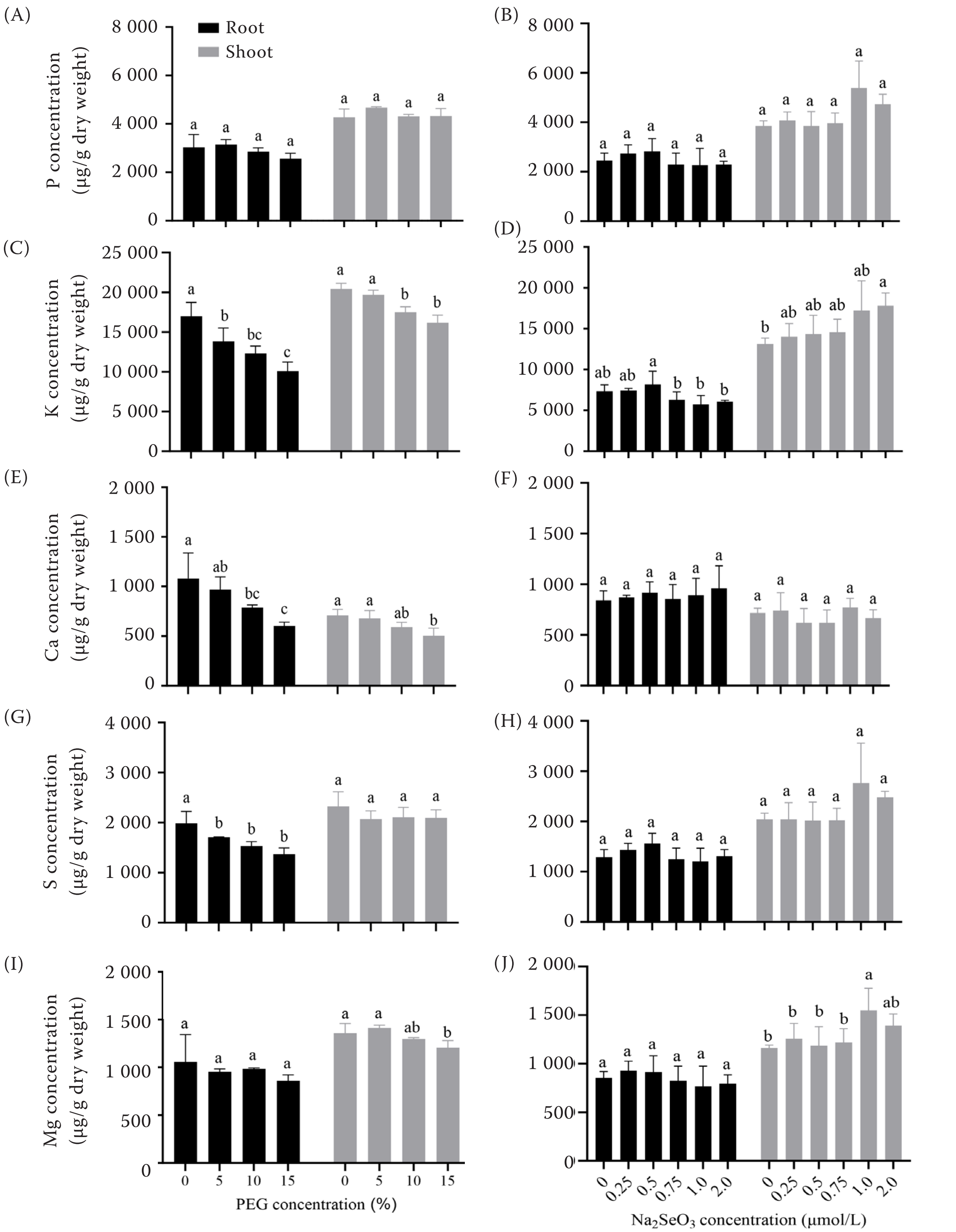

Figure 1. Effects of polyethylene glycol (PEG) and Na_2SeO_3 concentration gradients on (A) P levels; (B) K levels; (C) Ca levels; (D) S levels and (E) Mg levels in wheat roots and shoots. The Na_2SeO_3 treatments were applied under 15% PEG-induced drought stress. Data represent mean ± standard deviation (*n* = 3). Different lowercase letters indicate statistically significant differences among different treatments ($P < 0.05$)

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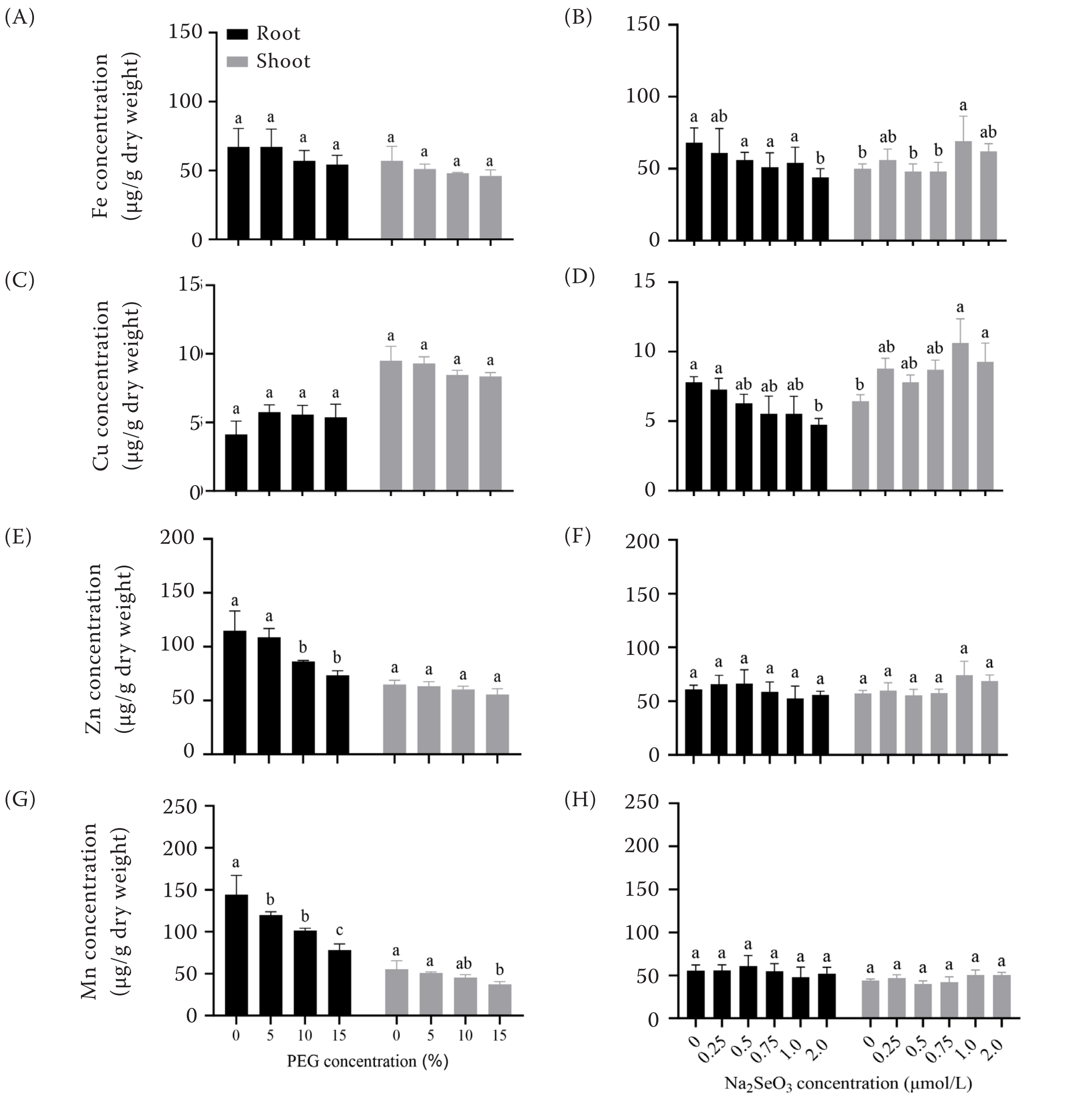

Figure 2. Effects of polyethylene glycol (PEG) and Na_2SeO_3 concentration gradients on (A) Fe levels; (B) Cu levels; (C) Zn levels, and (D) Mn levels in wheat roots and shoots. The Na_2SeO_3 treatments were applied under 15% PEG-induced drought stress. Data represent mean ± standard deviation (*n* = 3). Different lowercase letters indicate statistically significant differences among different treatments ($P < 0.05$)

Effects of PEG-simulated drought and selenite co-treatment on Zn concentrations in wheat roots and shoots. PEG-simulated drought severely reduced Zn concentrations, with 10–15% PEG causing significant root Zn reductions ($P < 0.005$) (Figure 2E). Critically, under 15% PEG stress, Na_2SeO_3 prevented shoot Zn decline, maintaining shoot Zn at stable levels compared to PEG-stressed control ($P < 0.005$), while root Zn also remained stable under osmotic stress (Figure 2F). This selenite-mediated maintenance of Zn homeostasis supports the activation of metalloenzymes involved in carbon metabolism and antioxidant defence, thereby mitigating drought-induced physiological impairments.

Effects of PEG-simulated drought and selenite co-treatment on Mn concentrations in wheat roots and shoots. PEG-simulated drought significantly reduced Mn concentrations in both tissues: shoots at 15% PEG

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($P < 0.005$) and roots at all concentrations ($P < 0.005$), indicating systemic Mn dysregulation (Figure 2G). Under 15% PEG stress, Na_2SeO_3 effectively mitigated this impairment. 1.0–2.0 µmol/L treatments non-significantly increased shoot Mn *versus* PEG control, restoring levels to near-normal ranges, while maintaining root Mn at concentrations comparable to non-stressed plants despite osmotic challenge (Figure 2H). This selenite-mediated Mn stabilisation preserves critical physiological functions: shoot Mn sustains photosystem II integrity and superoxide dismutase activation, collectively enhancing drought resilience.

DISCUSSION

Mineral ions play a critical role in seed germination and early seedling growth, serving as essential nutrients, cofactors for numerous enzymes, and signalling molecules that regulate cellular processes (Marschner 2013). During seed development, ions such as K, Ca, Mg, S, Fe, Zn, and Mn are transported from roots and leaves to the grains, where they are subsequently used during germination (White and Broadley 2009). Upon germination, these ions are mobilised from seeds and translocated to the growing embryo to support root and shoot development (White and Broadley 2009). However, environmental stresses such as drought, often simulated using PEG, can disrupt ion homeostasis. This disruption leads to impaired nutrient uptake, translocation, and utilisation, as well as compromised seed germination and seedling growth (Farooq et al. 2012). In the present study, PEG-simulated osmotic stress significantly reduced K, Ca, S, Zn, and Mn in roots, and K, Ca, Mg, and Mn in shoots of early wheat seedlings. This aligns with previous studies demonstrating that drought stress inhibits ion uptake and translocation, thereby compromising seedling establishment (Fahim et al. 2014). Furthermore, the reductions in Mg and Mn concentration in shoots may exacerbate the effects of drought stress, as these ions are involved in chlorophyll synthesis, photosynthesis, and electron transport, respectively (Marschner 2013). The overall declines in ion concentrations under PEG stress underscore the importance of ion homeostasis for seed germination and early seedling growth.

Interestingly, the application of Na_2SeO_3 significantly increased the concentrations of K, Mg, Fe, and Cu in the shoots of early seedlings under PEG-simulated drought. This suggests that selenite enhances ion uptake, translocation, or utilisation, thereby mitigating the adverse effects of drought stress on seed germination. The mechanisms underlying selenite's effects on ion homeostasis may involve the upregulation of ion transporters, the stabilisation of cellular membranes, or the enhancement of antioxidant defence systems (Feng et al. 2013, Hasanuzzaman et al. 2020). For example, Se has been shown to enhance the expression of genes encoding potassium transporters, such as HAK5 and AKT1, which facilitate K uptake under stress conditions (Djanaguiraman et al. 2010). Additionally, Se may improve membrane integrity and function, thereby enhancing the efficiency of ion transport and utilisation (Yao et al. 2009). These effects likely contribute to the observed improvement in seedling growth under PEG stress.

The increases in K, Mg, Fe, and Cu concentrations in the shoot under selenite treatments during PEG-simulated drought are important, as these ions play a critical role in shoot development and stress tolerance. K is a key osmolyte involved in stomatal regulation and osmotic adjustment, thereby contributing to water homeostasis under drought stress. As a central component of chlorophyll, Mg is essential for photosynthetic efficiency and energy metabolism. Fe is indispensable for chlorophyll synthesis and electron transport in photosynthesis, and it acts as a cofactor for enzymes involved in antioxidant defence. Cu is a cofactor for numerous oxidoreductases, including superoxide dismutase, which plays a vital role in reactive oxygen species scavenging and lignin formation in cell walls (Marschner 2013). The increase in these ions in the shoot may enhance shoot growth and photosynthetic efficiency, further supporting seedling development. These findings align with previous studies demonstrating that Se improves drought tolerance by enhancing ion homeostasis and nutrient utilisation (Saddam et al. 2016).

The ability of selenite to enhance ion concentration under PEG stress may be closely linked to its effects on antioxidant defence systems and membrane integrity. Drought stress often leads to the overproduction of reactive oxygen species (ROS), which can damage cellular membranes and disrupt ion transport (Gill and Tuteja 2010). Se has been shown to enhance the activities of antioxidant enzymes, such as SOD and peroxidase (POD), which mitigate oxidative damage and maintain membrane integrity (Wang et al. 2024). By reducing oxidative stress, selenite may enhance the efficiency of ion transporters and channels, thereby improving ion uptake and translocation under stress conditions. Additionally, Se may stabilise cellular

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membranes, preventing ion leakage and maintaining ion homeostasis (Yao et al. 2009). These effects likely contribute to the improvement in seedling growth under PEG stress. Notably, selenite treatments significantly enhanced the accumulation of Fe and Cu in shoots, which may substantially improve the plant's antioxidant capacity and stress resilience. Fe serves as a cofactor for antioxidant enzymes, while Cu is essential for copper/zinc superoxide dismutase (Cu/Zn-SOD) (Marschner 2013). The elevated levels of these metals enhance metabolic functionality and reinforce antioxidant capacity under drought conditions. This selenite-induced increase in Fe and Cu is likely mediated through a shift in SOD isoform expression or metal cofactor preference. Superoxide dismutase exists as multiple isoforms – Cu/Zn-SOD, Fe-SOD, and Mn-SOD – each utilising specific metal cofactors for detoxifying reactive oxygen species (Grene et al. 2002). The concurrent rise in both Fe and Cu implies a coordinated enhancement of SOD-mediated antioxidant defence, possibly through sustained activation of both Fe-SOD and Cu/Zn-SOD pathways. By bolstering the availability of these essential metal cofactors, selenite not only facilitates more efficient ROS scavenging but also supports essential physiological processes such as photosynthesis and mitochondrial respiration. Consequently, the increased Fe and Cu concentrations contribute to a stronger systemic antioxidant response, improved membrane integrity, and enhanced overall drought tolerance.

In conclusion, this study demonstrates that selenite significantly enhances the accumulation of K, Mg, Fe, and Cu in the shoots under PEG-simulated drought stress. These effects are likely mediated through the enhancement of antioxidant enzyme activities, the stabilisation of cellular membranes, and the improvement of ion transport and utilisation. The findings highlight the potential of Se as a protective agent against drought stress and provide valuable insights into the mechanisms underlying its beneficial effects. Future research should explore the molecular pathways through which Se regulates ion homeostasis, as well as the long-term implications of Se application for crop resilience under field conditions.

REFERENCES

Bewley J.D., Bradford K.J., Hilhorst H.W.M., Nonogaki H. (2013): Seeds: Physiology of Development, Germination and Dormancy. 3rd Edition. New York, Heidelberg, Springer.

Djanaguiraman M., Prasad P.V.V., Seppanen M. (2010): Selenium protects sorghum leaves from oxidative damage under high temperature stress by enhancing antioxidant defense system. Plant Physiology and Biochemistry, 48: 999–1007.

Fahim N., Yasin A.M., Rashid A., Ahmad W.E., Nauman S.R. (2014): Selenium regulates seedling growth in wheat under drought stress. Advances in Chemistry, 1: 143567.

Farooq M., Hussain M., Wahid A., Siddique K.H.M. (2012): Drought Stress in Plant: An Overview. Berlin, Springer.

Feng R.W., Wei C.Y., Tu S.X. (2013): The roles of selenium in protecting plants against abiotic stresses. Environmental and Experimental Botany, 87: 58–68.

Gill S.S., Tuteja N. (2010): Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. Plant Physiology and Biochemistry, 48: 909–930.

Grene A.R., Neval E., Heath L.S. (2002): Role of superoxide dismutases (SODs) in controlling oxidative stress in plants. Journal of Experimental Botany, 372: 1331–1341.

Hasanuzzaman M., Bhuyan M.H.M.B., Raza A., Hawrylak-Nowak B., Fujita M. (2020): Selenium in plants: boon or bane? Environmental and Experimental Botany, 2020: 104170.

Liu Y.H., Wang Y., Yuan H.M., Gao X.K., Luo X., Liu R., Lei S.C., Hao M.H., Wang Z.W., Feiyan Y., Wang X.G., Hu B., Chu C.C., Zhang L.H. (2025): Boosting selenium accumulation in rice grains by enhancing NRT1.1B-mediated MeSeCys translocation. Plant Communications, 2025: 101412.

Marschner P. (2013): Mineral Nutrition of Higher Plants. Academic Press.

PICC (2021): Climate Change 2021 – The Physical Science Basis: Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change.

Saddam H., Fahad K., Hafiz A., Nie L.X. (2016): Physiological and biochemical mechanisms of seed priming-induced chilling tolerance in rice cultivars. Frontiers in Plant Science, 7: 116.

Shiferaw B., Smale M., Braun H.J., Duveiller E., Muricho G. (2013): Crops that feed the world 10. Past successes and future challenges to the role played by wheat in global food security. Food Security, 5: 291–317.

Wang Y., Zhu Q., Wang Z., Wang J.P., Wang Z., Feiyan Y., Zhang L.H. (2024): Effects of foliar application of amino acid-chelated selenite on photosynthetic characteristics of peanut (*Arachis hypogaea* L.) leaves at the podding stage. Plant, Soil and Environment, 70: 17–25.

White P.J., Broadley M.R. (2009): Biofortification of crops with seven mineral elements often lacking in human diets-iron, zinc, copper, calcium, magnesium, selenium and iodine. New Phytologist, 182: 49–84.

Yao X., Chu J., Wang G. (2009): Effects of selenium on wheat seedlings under drought stress. Biological Trace Element Research, 130: 283–290.

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