



Beneficial elements in plants: developing resilience under stressful environments

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Introduction

With urbanization, rapid industrialization, and uncontrolled anthropogenic activities, abiotic stresses have plagued the world—from more intense hurricanes to record-breaking temperatures, waterlogging, salinity, potentially toxic metals, mineral toxicity, and persistent droughts—threatening the stability of food-production systems. For example, increased salinization of arable land is predicted to have disastrous global implications, resulting in 30% land loss within the next 25 years, and up to 50% by the year 2050 (Yamaguchi and Blumwald 2005). Similarly, potentially toxic metals

contamination of urban lands and other natural habitats has become a major environmental concern. Rising CO₂ concentrations are one of the most hazardous gaseous environmental pollutants. According to the IPCC (2021), CO₂ levels could reach 500–1,000 μmol mol⁻¹ by 2100, causing global mean temperatures to rise 1.5 to 4 °C above pre-industrial levels by 2025 and 2100, respectively (Warren et al. 2021). These environmental changes will adversely affect the survival, biomass production, and yield stability of staple food crops up to 70%, hence threaten the global food security (Mantri et al. 2012). The global population may exceed nine billion by 2050, and crop yields will need to more than double to feed an expanding global population. As a result, there is a pressing need for groundbreaking solutions to tackle this problem, including developing abiotic stress-resistant/tolerant crop varieties to ensure food and nutritional security and safety in a globally equitable way. Maintaining optimum level of nutrients (macro- and micronutrients) is essential for increasing agricultural productivity and abiotic stress resistance (Kapoor et al. 2022; Nazir et al. 2022; Silva et al. 2022; Fig. 1). This editorial explores insights into the critical role of beneficial elements in plant defense during diverse abiotic stresses. Furthermore, the existing but less explored potential of genetic engineering to maintain beneficial nutritional content for ensuring sustainable agricultural growth and global food security under ambient and stressful environments has also been discussed.

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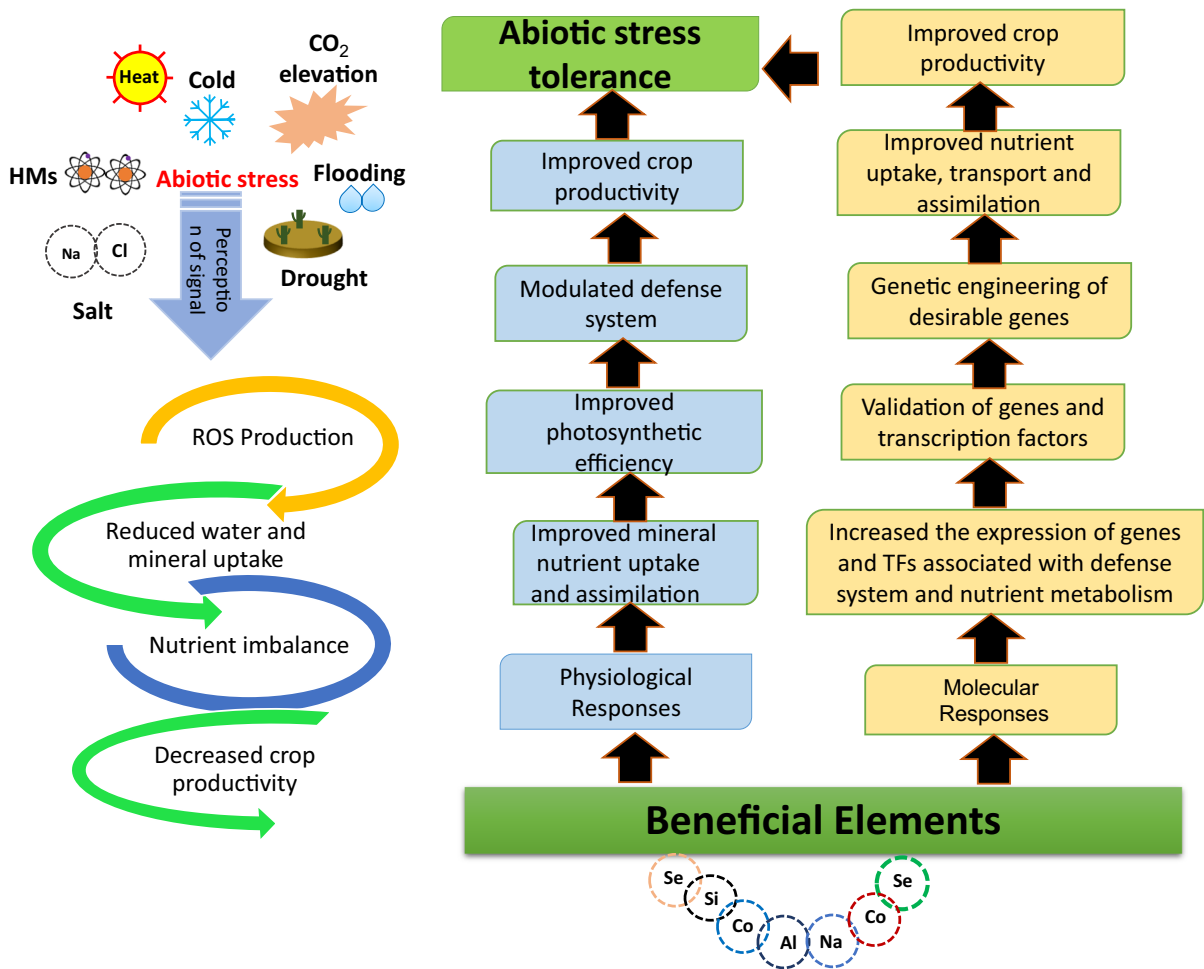


Fig. 1 Beneficial elements trigger physiological and molecular acclimations in plants to mitigate stress-induced adversities and readjust nutrient pools for sustaining plant growth and crop productivity under abiotic stress conditions. Generating engineered plants by modulating the expression of genes

associated with nutrient metabolism and the defense system can help maintain nutritional content and improve crop productivity under abiotic stress. Al, aluminium; Co, cobalt; Na, sodium; Se, selenium; Si, silicon

Critical role of beneficial elements in plants under stressful environments

Mineral elements play a critical role in ameliorating abiotic-stress-induced adversities in plants and ensuring their enhanced growth and survival under stressful environments (Bashir and John 2023; Riyazuddin et al. 2022; Bhardwaj et al. 2022; Khan et al. 2021). Recently, silicon-nanoparticles (SiNPs; 2.5 mM) reduced the effects of cadmium (Cd) toxicity on growth, antioxidant defense systems, Cd uptake and transport, and cell-wall adsorption in rice (*Oryza sativa*) seedlings (Riaz et al. 2022). Furthermore,

the application of selenium (Se) fertilizers [selenite (SeO_3^{2-}), fermented Se, and potassium selenoacetate (Se-AAF)] at 30 g ha^{-1} during different stages of rice growth significantly enhanced total biomass, yield, and total Se content (Yuan et al. 2022). Similarly, Se supplementation enhanced photosynthetic capacity, antioxidant defense systems, reproductive function, and yield traits of lentil (*Lens culinaris*) grown under combined heat and drought stress (Sita et al. 2022). Exogenous Se supplementation (30 and 60 mg/L) was recently found to ameliorate cold stress in maize seedlings, which may be related to improved photosynthetic capacity and increased activities

and expression of antioxidant enzymes (Cao et al. 2022). In another study, the application of potassium iodate (KIO_3) or an iodine-based biostimulant product improved the yield and quality (high potassium, K and phosphorous, P concentrations) of strawberry (*Fragaria ananassa*) fruit under salt stress (Medrano Macias et al. 2021). Under drought stress, seed priming treatment with cobalt (Co; 44.5 μM for 72 h) reversed drought-triggered oxidative damage in rice by influencing proline metabolism and secondary metabolites production which stabilized redox balance and the defense system (Tourky et al. 2023).

Molecular evidence on the contribution of Si in ameliorating drought-induced damage in wheat (*Triticum aestivum*) revealed that application of Si (204 mg kg^{-1}) enhanced ascorbate (AsA) and reduced glutathione (GSH) levels, total phenolic and flavonoid concentrations, AsA-GSH cycle genes (*TaMDHAR*, *TaDHAR*, *TaGS*, and *TaGR*), and genes encoding enzymes of the flavonoid biosynthesis pathway (*TaPAL*, *TaCHS*, *TaF3H*, *TaDFR*, and *TaANS*), indicating that Si plays a critical role in the synchronized transcriptional activation of myriad antioxidant defenses (Ma et al. 2016). Additionally, transcriptomic analyses showed increased expression of antioxidant-encoding enzymes including superoxide dismutase (*SOD*), ascorbate peroxidase (*APX*), glutathione S-transferases (*GST*) and peroxidase (*POX*), and transporters involved in Cd-chelation, which decreased Cd toxicity in Se-treated rice plants (Jiao et al. 2022). Furthermore, combined application of Si and Se to maize (*Zea mays*) plants caused differential expressions of transporter genes (*ZmNHX* and *ZmSOS2*) involved in the uptake, exclusion and sequestration of sodium (Na^+) in the vacuoles of the roots (Xu et al. 2021). Likewise, foliar application of Se and Si composite soils decreased Cd and lead (Pb) translocation and enhanced physiological and biochemical responses by downregulating the transcriptions of Cd transporter-related genes including *OsLCT1*, *OsCCX2*, *OsHMA2* and *OsPCRI* genes in leaves, and *OsLCT1*, *OsCCX2*, *TaCNR2* and *OSPCRI* in peduncles of rice plants exposed to combined Cd and Pb stress (Wang et al. 2021). In another study, combined application of Si and brassinosteroid (BR; 1 mM) improved the resilience of tomato (*Solanum lycopersicum*) seedlings under chilling stress by upregulating the expression of genes encoding enzymes involved in antioxidant defense, such as catalase (*CAT*), monodehydroascorbate reductase (*MDHAR*), dehydroascorbate

reductase (*DHAR*), and glutathione reductase (*GR*), and related mRNA gene expression patterns (Bashir and John 2023). Khattab et al. (2014) revealed that Si and Se increased the expression of two TFs—DREB2A (dehydration-responsive element-binding protein) and NAC5 gene—and some drought-specific genes (e.g., *OsCMO* encoding rice choline monooxygenase and dehydrin *OsRAB16b*). This activation produced important osmoprotectants (proline and glycine betaine) and increased rice tolerance to drought stress. These studies will aid in deciphering the beneficial elements-influenced molecular regulatory networks governing abiotic stress responses in plants, thereby providing novel opportunities for developing abiotic stress tolerant plants. With insufficient reports to elucidate the molecular mechanism of nutrient metabolism under abiotic stresses, investigating regulatory networks of nutrient metabolism could explain how nutrients are metabolized under stressful environments.

Deploying genetic engineering to maintain nutritional content under ambient and stressful environments

Modulating the expression of genes involved in nutrient uptake, transport, and distribution in engineered plants may help maintain nutritional levels and increase plant growth under normal and stressful conditions. For instance, overexpression of the H^+ -pyrophosphatase gene *AVPI* (from *Arabidopsis thaliana*; Arabidopsis) increases Na^+ and Ca^{2+} accumulation in the leaves and roots of transgenic alfalfa (*Medicago sativa*) under salinity stress, even though K^+ levels significantly decrease, more so in transgenic lines than the WT (wild type; Bao et al. 2009). However, under water stress, overexpression of *AVPI* in alfalfa leads to a significant accumulation of all three cations (Na^+ , K^+ , and Ca^{2+}) in transgenic lines. This study elucidated the role of *AVPI* in preserving intracellular K^+ and Na^+ levels, which is crucial for plant acclimation to drought and salinity stress (Niu et al. 1995). Overexpression of the phosphate transporter gene *OsPT8* improves the inorganic phosphate (Pi) and Se contents in *Nicotiana tabacum* (tobacco) under a high Pi concentration (Song et al. 2017), implying that *OsPT8* might be a potential candidate gene for breeding Se-enriched tobacco. In addition, activation of wheat Na^+/H^+ antiporter gene (*TaNHX2*) in

transgenic tomato lines increases mineral nutrient levels, elevates chlorophyll concentrations, enhances crop growth, and tolerance to salt stress (Yarra et al. 2012). Overexpression of the Si-uptake gene (*Lsi1-OX*) in cold-sensitive rice mediates transcriptional regulatory networks and enhances Si accumulation and translocation capacity and helped maintain Si levels, crucial for increasing plant resistance to chilling stress (Fang et al. 2017). Moreover, the overexpression of the sorghum (*Sorghum bicolor*) *MATE* gene (*SbMATE*; aluminium activated malate transporter gene), increases tolerance against aluminium (Al) in terms of enhanced photosynthetic and growth performance in transgenic sugarcane (*Saccharum officinarum*) plants (Ribeiro et al. 2021). Furthermore, overexpression of *NRT1.1B*, a member of rice peptide transporter (PTR) family significantly promoted selenomethionine (SeMet) translocation from roots to shoots in rice, resulting in increased Se concentrations in shoots and rice grains, indicating that *NRT1.1B* has great potential for improving Se concentrations in grains by facilitating SeMet translocation, and the findings provide new insight into breeding of Se-enriched rice varieties (Zhang et al. 2019). There are still insufficient reports to explicate the molecular mechanism of beneficial elements under abiotic stresses, therefore more exploration is required to understand the role of important genes in maintaining beneficial elements nutritional content to meet the requirements for abiotic stress tolerance and sustainable agriculture.

In conclusions, beneficial elements have garnered a lot of attention in recent years because of their pivotal contribution in abiotic stress resilience and crop production sustainability. The current special issue sheds light on the critical role and underlying mechanisms of beneficial elements in mitigating abiotic-stress-induced adversities in plants and maintaining their enhanced growth and survival under stressful environments. In the near future, it will be interesting to investigate the various roles of beneficial elements in the conflict between plants and environmental exposures. To understand this, the characterization and identification of key genes would be effective in exploring the intrinsic signaling mechanism of beneficial elements interaction, providing a new way to induce tolerance in plants with enhanced nutritional value that can effectively meet the requirements for abiotic stress tolerance and sustainable agriculture.

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