REVIEW PAPER



Beneficial elements: New Players in improving nutrient use efficiency and abiotic stress tolerance

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Abstract

Plant requires seventeen essential mineral elements for proper growth and functioning classified as macro and micronutrients. Apart from these, cerium (Ce), cobalt (Co), iodine (I), aluminum (Al), selenium (Se), sodium (Na), lanthanum (La), silicon (Si), titanium (Ti), and vanadium (V) are evolving as pivotal bio-stimulants in plant growth and providing stress tolerance. Although, they are not mandatory for all plants directly but when they are supplemented, promote the plant growth positively and simulate multiple abiotic and biotic stresses tolerance. Though, these elements have crucial role in plant growth, still obscure the uptake, transport and molecular understanding as much of macro and micronutrients. However, in recent years scientists are giving more emphasis to explore their mechanisms associated with enhancing antioxidant defense, stress responsive proteins accumulation, and transcription factors under variety of stresses. Likely, they are also crosstalk with other essential elements and plant growth regulators (PGRs) (salicylic acid, SA; jasmonic acid, JA), which is crucial for signaling network perception and regulate plant growth. Recent technologies developed in the field of nanotechnology assist in the further understanding of their uptake, transport and functions at cellular level andoptimizing their concentrations for better plant growth. Bio-fortification of crops with beneficial elements provides some cues regarding their importance in plant growth and also in human balance nutrition. To considering the importance of these compound, this review aimed to explore the uptake and transport mechanisms of beneficial elements and their function in plant development. Consequently, we pinpoint the crosstalk's between PGRs and other mineral elements, which advance their crucial role during plant mineral nutrition and growth signaling. At the end, this review focused on the crucial role and mechanisms associated with these elements under multiple abiotic stresses that open exciting avanues in several directions related to crop stress breeding program.

Keywords Abiotic stress tolerance \cdot Antioxidant defense \cdot Biofortification \cdot Nutrient transporters \cdot Nutrients crosstalk \cdot Plant growth regulators

Introduction

The plant requires the supply of 17 elements' indispensable for their growth and survival, known as essential/necessary elements. Based upon the required quantity; they are classified further into macro and micronutrients having > 1000 and <100 mg kg⁻¹ dry weight respectively (Arnon and Stout 1939). However, few other elements also deploy an

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auspicious consequence to specific plant taxa and defined as beneficial elements. They do not fall under classical essentiality criteria for mineral nutrients by Arnon and Stout (1939); however, they are present ubiquitously (Pilon-Smits et al. 2009). Beneficial elements are not vital for survival but boost the plant biomass and yield (Marschner 2012). These beneficial elements (BEs) Al, Ce, Co, I, La, Na, Se, Si, Ti, and V have an indispensable role but still unexplored as macro and micronutrients. (Vatansever et al. 2017). Also, various essential elements can be substituted by beneficial elements for different non-specific metabolic processes, such as Si and C, Se and S, and Co and Ni (Ramirez et al.

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2018). They stimulate various growth-promoting pathways and help to alleviate abiotic and biotic stresses (Gómez-Merino and Trejo-Téllez 2018; Val-Torregrosa et al. 2021). Their functions can be predicted based on their localization in specific tissues; for example, higher tissue concentration suggests a structural or osmotic role or low tissue concentration suggests a potential role as enzyme co-factor (Pavlovic et al. 2021).

Recently, awareness about these elements has kept rising as scientists are trying to decipher novel aspects of plant nutrition to optimize plant yield. There are several novel strategies/methologies to mitigate the abiotic and biotic stress such as enhance expression of stress responsive genes through biotechnological tools, development of stress tolerant transgenics, engineering of mineran nutrient transporter, transcription factors and metabolite biosynthesis pathway genes and use of biostimulant such as beneficil elements (Nguyen et al. 2018; Yoon et al. 2020). These compounds had found to effectively minimize reactive oxygen species (ROS), enhance antioxidant defense, stress proteins accumulation, expression of stress responsive transcripts, and transcription factors under unfavourable situations (Imtiaz et al. 2018; Tripathi et al. 2021a; Huang et al. 2021). Likely, they also crosstalk with other essential elements and PGRs for optimizing signaling network and regulate plant processes under diverse environments (Iqbal et al. 2021a; Tripathi et al. 2021a). For instance, recent study on Si uptake and transportation revealed that it activates the *IPT7* (isopentenyl transferase), S-adenosyl-L-methionine dependent methyltransferase, 1-aminocyclopropane-1-carboxylate-oxidase genes associated with cytokinin, and ethylene (Khan et al. 2021). This study also reviewved the effect of Si on the expression of diverse PGRs in response to multiple stress conditions and suggested that Si crosstalk with signaling molecules is central mechanism to tolerance plant under unfavorable conditions. Recently, bio-fortification of crops with beneficial elements provides some cues regarding their importance in plant nutrition (Lara et al. 2017; Li et al. 2017). These elements can also be proved instrumental against variety of biotic and abiotic stresses. For example, selenium improves oxidative stress tolerance, Si counters salinity, drought, and induced resistance against pests and pathogens, and Ti reduces the injuries against Xanthomonas (Tripathi et al. 2021a; Wu et al. 2021). Also, some of these elements could modulate plant growth and development and photosynthesis (Piccolo et al. 2021). These elements have crucial importance in reduce chloroplast damage, improve electron transport rate, mesophyll conductance, carboxylation of rubisco, and rubiso activase activity, which ultimately boost the overall photosynthesis rate (Piccolo et al. 2021). Aluminium regulates the flower color and root development and triggers the antioxidative pathways; cerium helps grow shoots in certain species and is involved with catalase as a cofactor (Bojórquez-Quintal et al. 2017). These are also important for agriculture, especially in legume crops for mineralization, solubilization, and nitrogen fixation. For example, cobalt acts in atmospheric nitrogen fixation; similarly, iodine can improve nitrogen use in plants (Farooq et al. 2012; Medrano-Macías et al. 2016).

Further, BEs also involved in different signaling networking, for intance the La modulating Ca-calmodulin pathway (Aldon et al. 2018). Calcium mediated proteins such as Cadependent protein kinase (CPK), calcineurin- B like protein (CBL), and CPK-related protein kinase (CRK) initiate the downstream phosphorylation signaling, which liked to activation of stress responsive genes and ion channels activity (Saito and Uozumi 2020). Apart from that, some beneficial elements such as V improve plant secondary metabolism (Hanus-Fajerska et al.2021). A recent report summarized the integration of Si and secondary metabolites and concluded that Si amolierate the abiotic and biotic stress condition through the accumulation of secondary metabolites such as polyphenol oxidase (PPO), terpense, polyamines etc. (Ahanger et al. 2020). For example, in Camellia sinensis addition of 0.006 ppm Co ion act as elicators and promote the production of cinnamic acid up to 11.9% (Sutini et al. 2019). Moreover, other elements like chromium (Cr), silver (Ag), Tungsten (W), and fluorine (Fl) are little explored in plant nutrition and stress biology. Considering the emerging importance of these elements, scientists have investigated their uptake and transport in the plant. Their transport is primarily active co-dependent upon the specific transporter for essential elements (Fricke 2015; Adebayo et al. 2020). However, some of the beneficial elements transported through specific transporter, for example, Lsil and Lsi2 efflux transporter, actively transport the silicon (Ma et al. 2007; Yamaji et al. 2008). Further, the similarity between cation elements makes them replaceable for some metabolic pathways and often modulates signaling pathways with their cross-talk through PGRs and other signaling components (Kim et al. 2016; Hosseini et al. 2019).

Therefore, studying the cellular mechanisms of beneficial elements under different abiotic stresses will be of more interest. In the present time researcher primarily concentrated on the finding the uptake and transport mechanism of these element, which are stll less known. Also, the regulatory mechanism of benefical elements are poorly known and nanotechnology and biotechnology approaches help a lot in finding the deep understanding regarding these elements. Morover, the biofortication and transgenic approachesalso used to prepare super food for human health. This review explores the effects of beneficial factors in some model or cultivated plants where considerable modifications as well as their potential use as novel components for agricultural production has been noted. We will further cover their transport and absorption mechanism and cross-talk with plant growth regulators and other essential mineral nutrients inside the plant to understand their signaling network. An effort was made to highlight significant synergistic interactions of individual nutrients at the physiological, molecular, and biochemical levels. Therefore, this review will outline the beneficial elements crucial for global agrifood innovation.

Uptake and transport mechanism of beneficial elements

Silicon uptake and transport

Si is rarely present in free form and combinedly present as silicate and oxides. Silicon exists in soil solution mainly as $Si(OH)_4$. It is primarily deposited in the cell walls, endoplasmic reticulum, and intercellular spaces as hydrated,

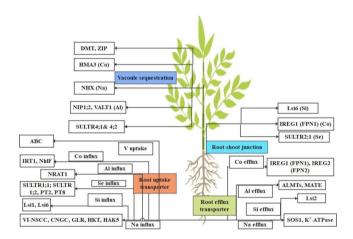


Fig. 1 Highlights the mechanism of beneficial elements transport in plants. The transport system of plants are includes the influx and uptake of ion through the selective ion channels such as HKT, HAK etc. which present of root membrnaes. The second categories of transporters involve the efflux of toxic ion through the efflux transporters such as IREG, MATE etc. These channels help in reducing the toxic concentration of these ions. Third categories of transporters involve the transporter which help in loading of ion in xylem tissue and present at root-shhot junction. After the ion transport in xylem ions reached to cell and target tissues where they transported through the specific channels and finally excess ions sequester in vacoular tissue to maintain ion homeostasis. *DMT; divalent metal transporter, ZIP; zinc regulated transporter, HMA; heavy metal transporting P-type ATPase, NHX; Na⁺/H⁺ antiporter, NIP; nodulin 26-like intrinsic proteins, VALT; vacoular Al transporter; IREG and IRT; iron regulted transporter, FPN; ferroprotein, SULTR; sulfate transporter, MATE; multidrug and toxic compound extrusion transporter, ALMT; Al activated malate transporter, SOS; salt overly sensitive transporter, ABC; ATP binding cassette transporter, PT; phosphate transporter; NRAT; nitrate transporter, HKT and HAK; high affinity K transporter, GLR; glutamate receptor transporter, CNGC; cyclic nucleotied gated channel, NSCC; non selective cation channels.

amorphous silica (SiO₂.nH₂O) (Gunes et al. 2007). Based on the Si accumulation capacity, plants are divided as Si accumulator, non-accumulator and intermediate (Ma et al. 2001). Since the apoplastic pathway is hindered by the Casparian strips in rice roots, the symplastic pathway therefore, facilitates the Si translocation (Hodson and Evans 2020). First Si transporter gene identified in rice was Lsil (low silicon 1) (Ma et al. 2004). *Lsi1* is a major Si influx passive transporter that belongs to group III Nodulin 26- like intrinsic protein (NIP3), an aquaporin subfamily at distal side of exodermis and endodermis of root cells (Deshmukh et al. 2020). Lsi2 is an anion efflux transporter and involved in the active transport of Si out of the cell to vascular tissues through the generating proton gradient (Mitani-Ueno and Ma 2021). Lsi6 is also a Si influx transporter and unloads Si from xylem into shoot parenchyma cells and different aerial plant parts (Pontigo et al. 2015). In nutshell, the Lsil, uptakes monosilicic acid (Si) from solution to root exodermis cells which enters into the root cortical cells through active transport of Lsi2 and then through apoplastic movements, reaches to endodermis through aerenchyma. Thus, Lsi1 and Lsi2 load the Si into root xylem and Lsi6 facilitates the transport of Si to the shoot portion (Yamaji et al. 2015).

Selenium uptake and transport

Selenium exits as selenide (Se²⁻), selenite (SeO₃²⁻) and selenate (SeO₄²⁻). Selenium is essential for animals and humans because of its role as cofactor in glutathione peroxidase. Many species of genera Astragalus, Xylorrhiza and Stanteyea are typical selenium- accumulators. Se uptake primarily depends upon the availability of Se (Chauhan et al. 2019). Plants prefer to uptake Se as Selenate (SeO^{2- $_4$}) or Selenite (SeO $^{2-}$ ₃). The transporter proteins for Se uptake in plants are present in root cell membranes. The highaffinity sulfate transporters AtSULTR1;1 and AtSULTR1;2, involved in Se uptake in A. thaliana (El Mehdawi et al. 2018). Once selenite influx into root cells by AtSULTR1;2, it further gets transported to leaves via xylem using lowaffinity SULTR2;1 transporter at roots and leaf vascular tissues (Hawkesford 2003). At this stage, selenate enters into the reductive sulfur assimilation pathway and is assimilated into selenocysteine and selenomethionine (Schiavon et al. 2015). The uptake mechanism of selenite involved phosphate transporters such as Oryza sativa phosphate transporter 2(OsPT2); OsPT8 (Song et al. 2017). Zhao et al. (2010) reported that apart from phosphate transporters, silicon influx transporter (OsNIP2;1) was also involved in selenite uptake in rice.

 Table 1 Important beneficial transporters and their functions

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Name of transporter	Element	Location	Function	References
<i>LSi1</i> (Low silicon 1)	Silicon	Root	Si transport from soil solution to root cell (Si influx)	Yan et al. 2018; Deshmukh et al. 2020
<i>LSi2</i> (Low silicon 2)	Silicon	Root	Si transport from root cell to apoplast (Si efflux)	Ma et al. 2007; Mitani-Ueno and Ma, 2021
LSi3	Silicon	Leaf paren- chyma tissue	Distribution of Si in leaf	Yamaji et al. 2015
Lsi 6	Silicon	Xylem paren- chyma of leaf sheath and leaf blade	Si transport from xylem to above ground and distribution in leaf	Pontigo et al. 2015
ALMT	Aluminium	Root	Al uptake, translocation, and tolerance	Kochian et al. 2015
NIP1;2	Aluminium	Root	Root-to-shoot Al translocation	Wang et al. 2017
ABC	Aluminium	Root	Modify the cell wall under stress	Huang et al. 2009
NRAT1	Aluminium	Root	Al uptake and tolerance	Xia et al. 2010
ATP bind- ing cassette (<i>ABC</i>)	Vanadium	Root	Upregulation on V and metal tolerance	Kim et al. 2007
DMT	Vanadium	Root	Cellular homeostasis of metals	Lin et al. 2013;
ZIP	Vanadium	Root	Cellular homeostasis of metals	Jenkitkasemwong et al. 2010
SULTR1;1	Selenium	Root	Root influx	El Mehdawi et al. 2018
SULTR1;2	Selenium	Root	Root influx	El Mehdawi et al. 2018
SULTR2;1	Selenium	Root	Translocation	El Mehdawi et al. 2018
SULTR3;1	Selenium	Root	Movement of selenate over plastid	Cao et al. 2013
SULTR4;1, SULTR4;2	Selenium	Root	Movement of selenate over vacuolar membrane	Cao et al. 2013
SULTR2;2, SULTR3;5	Selenium	Root	Translocation	Kataoka et al. 2004
Phosphate transporters	Selenium	Root	Uptake and transportation in cell membrane	Adebayo et al. 2020
Na:K/Cl	Iodine	Root	Regulate the concentration of ions in the xylem	Fricke 2015
NhlF	Cobalt	Root	Co uptake and transportation	Komeda et al. 1997
NiCoTs	Cobalt	Root	Co uptake and transportation	Eitinger et al. 2005
Ferropor- tins (FPNs)	Cobalt	Root	uploading of the xylem	Morrissey et al. 2009
ZIP	Cobalt	Root	Co uptake and transportation	Pedas and Husted 2009
CbiMNQO	Cobalt	Root	Co uptake and transportation	Bao et al. 2017
HKTs	Sodium	Root	Na ⁺ influx and transportation	Hanin et al. 2016
HAKs	Sodium	Root	Na ⁺ influx and transportation	Hanin et al. 2016
NHX	Sodium	Root	transporting Na ⁺ across cellular membranes	Apse and Blum- wald 2007
SOS1-3	Sodium	Root	Transporting Na ⁺ across cellular membranes	Apse and Blumwald 2007

Sodium uptake and transport

Brownell (1965) established the fact that sodium is an essential element for the halophyte Artriplex vesicaria.and some of the C4 species e.g. Chenopodiaceae, Amaranthaceae, and Cyperaceae. In these species, Na is vital for regenerating phosphoenol pyruvate, the substrate for the first carboxylation in the C₄ pathway. A high K⁺/ Na⁺ ratio maintained across the plasma membrane (PM) for K⁺ influx in the cells. However, under saline conditions, the passive influx of Na⁺ into the plant cells is more favoured (Gupta et al. 2002). Na⁺ efflux is facilitated by a Na⁺/H⁺ antiporter (SOS1). Na⁺ influx mostly occurs through ion channels such as nonselective cation channels (NSCC) in the roots for Na⁺ entry and another one is high affinity K⁺ transporter HKT (Apse and Blumwald 2007). Salt overly sensitive (SOS1) is Na^{+/} H⁺ antiporter upregulated under salt stress in which Na⁺ is export from cytosol to apolpast against import of H⁺ (Quan et al. 2017). The SOS1 is regulated by protein phosphorylation SOS2-SOS3 kinase complex, facilitated by high concentration of Ca²⁺ in cell (Quintero et al. 2002). SOS2 also regulates NHX activity (Fig. 1). SOS2 is a serine/threonine protein kinase (CIPK24) of the family SnRK3/CIPK. SOS3 is a myristoylated calcium-binding protein (CBL4) belonging to the recovering like SCaBPs/CBLs family (Sanchez-Barrena et al. 2007).

Aluminium uptake and transport

Under normal soil conditions, Aluminium (Al) exists in the form of Aluminium phosphate, silicate, oxides, and sulfide. Under acidic pH conditions (below 5.5), aluminium salt dissociates and converted into free aluminium ion (Al^{3+}) in the soil (Kochian et al. 2004). Xia et al. (2010) identified a PM-localized Al³⁺ transporter, OsNRAT1 (NRAMP Al transporter 1) in rice. The uptake of Al³⁺ in the cytoplasm activates the organic anion permease on the PM, which releases organic acids like citrate, oxalate, and malate. These organic anions chelate with the soil Al³⁺ and provide tolerance to Al toxicity. Aluminium activated transporters (ALMTs) and multidrug and toxic compound extrusion (MATE) transporters are specifically involved in the release of malate and citrate respectively in the soil which is involved in Al³⁺ extrusion process (Kochian et al. 2015). NIP1;2 (NOD26-like intrinsic protein 1-2) and VALT1 (Vacuolar Al transporter 1) transporter genes are involved in the Al³⁺ tolerance mechanism through sequestration into the vacuole (Negishi et al. 2012; Wang et al. 2017).

Other beneficial uptake and transport

Other than the above beneficial elements Co, I, La, Ti and Ce are also uptake and transported to shoot and leaves. For example, Co is not very abundant in plants, and taken up either as Co²⁺ or as an organic complex. Organic-bound fraction is the important source of Co in soils. Roots absorb Co through cortical cells in the xylem and operated by both active and passive diffusion (Kaur et al. 2016). Co uptake and transported through the transporters Nhif, NiCoTs, ZIP, CbiMnOO, and FPN (Komeda et al. 1997; Morrisev et al. 2009; Bao et al. 2017). The important beneficial elements transporters and their functions are highlighted in Table 1. However, there are limited study on I, La, Ti, V and Ce transporters from soil to stem and depth studies are going to trace their transporters and uptake mechanism. The important transporters involved in the beneficial elements influx, efflux, translocation and vacoular sequestration in plants are highlighted in Fig. 1.

Beneficial elements crosstalk with plant growth regulators and other nutrients

Silicon (Si) is a potent element interacted with number of phytohormones and plant nutrients (Chaiwong et al. 2020). Si increases auxin content and basipetal auxin translocation by improving PIN (PIN-FORMED) transporters (Moradtalab et al. 2018). Recent study conducted in poinsettia using the 75mgL^{-1} Si and showed that it alleviated the inhibitory effect of NPA (napthylpthamic acid; inhibitor of auxin transport) and promote root growth (Hu et al. 2020). Likewise, Tripathi et al. (2021b) found the involvement of Si in adventitious root formation under As stress associate with interaction of IAA (indole acetic acid) and nitric oxide (NO). Si mediated reduction of senescence and promotion of zeatinin meristematic regions under chilling stress (Moradtalab et al. 2018; Souri et al. 2020) and regulation of IPT (isopentyl transferase) genes under salinity stress in tomato (Gou et al. 2022). The deficiency of magnesium and its subsequent effect on plant morphology is alleviated by Si through cytokinin triggering (Hosseini et al. 2019). Silicon regulates the proline and cytokinin content in cucumber and confer salinity stress tolerance through the expression of CKX (cytokinin oxidase/ dehydrogenases) and IPT genes (Zhu et al. 2020). The secondary metabolites are accumulated at different vegetative and reproductive stages through Si mediated suppression of DELLA protein and thereby augmenting the effect of gibberellins along with synthesis of active form gibberellins (Moradtalab et al. 2018). Furthermore, reports of precursor GA (GA1, GA20) synthesis via Si mediated regulation of HSPs and antioxidant genes (for SOD, CAT,

GADPH etc.) under drought and/or salinity are evident (Al Murad et al. 2020; Khan et al. 2020a; Kim et al. 2016; Souri et al. 2020). Preliminary ABA assay in different horticultural crops showed temporal increase in ABA content with respect to exogenous Si application through Si mediated up-regulation of ABA biosynthetic genes under salinity condition (Al Murad et al. 2020). Conversely, Si helps in decreasing the ABA content by regulating transcription factors (for genes viz. PYL1, PYL4 and PYR8) under drought stress by by maintaining stomatal conductance and gaseous exchange in plants (Moradtalab et al. 2018; Khan et al. 2019a, 2020b). Synergistic effect of Si and brassinosteroids helps the plants in maintaining high proline and antioxidant content which ensures plants' resistance to abiotic stresses (viz. salt, HM stress) through intact membrane system (Siddiqui et al. 2018; Hussain et al. 2019; Maghsoudi et al. 2019). Such synergistic effect (between ABA and Si) is also reported by Gurmani et al. (2013) that produced better yield through improved photosynthesis along with a reduced ratio between Na⁺ and K⁺. Silicon application augments the

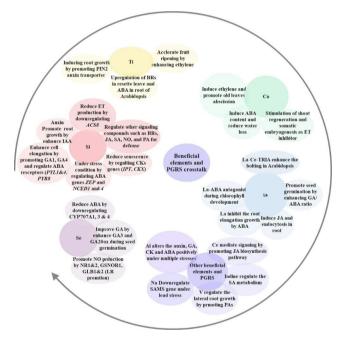


Fig. 2 Highlights the crosstalks between beneficial elements and plant growth regulators (PGRs) in regulation of different processes in plants. This figure highlights the crosstalk of different beneficial element such as La, Se, Si, Al, Na, Ce, Co, Ti, I and V with PAs, JAs, ABA, CK, GA, ET and auxin. This crostalk regulates the different processes and signaling network during different plant growth stages. *ABA; abscisic acid, GA; gibberellic acid, JA; jasmonic acid, NO; nitric oxide, CK; cytokinin, ET; ethylene, IPT; isopentenyl transferase, PAs; polyamines, CKX; cytokinin dehydrogenase, PGRs; plant growth regulators, SAMS; s-adenosyl methionine synthetase, SA; salicylic acid, NECD; 9- cis -epoxycarotenoid dioxygenase, CYP; cytochrome P450 monooxygenases, PYR; PYRABACTIN RESISTANCE1, PYL; PYR1-LIKE, ZEP; zeaxanthin epoxidase, GSNOR; S-nitrosoglutathione reductase, GLB; beta-galactosidase, PIN; PIN-FORMED, ACS; 1-Aminocyclopropane-1-carboxylic acid synthase.

endogenous SA production (through accumulation of PAL enzyme) under HM stress (Maghsoudi et al. 2019a; Souri et al. 2020). Another hormone JA reported to be more effective (imparting more genetic stability) during the onset of abiotic stress when applied along with silicon compared to their individual application (Nascimento et al. 2019). When exposed to environmental stress, both SA and Si elevated genes regulating antioxidant, rhizosphere acidification and Si absorption, and SA biosynthesis. ROS scavenging by ascorbate-glutathione pathway is possible through crosstalk of nitric oxide and silicon which further diminishes the effect of HM stress (Singh et al. 2020). Silicon takes part in reducing the competition between polyamines and ethylene biosynthesis through inhibition of ethylene precursor molecule (ACC) thus providing an additional support towards polyamine dominancy for salinity tolerance (Yin et al. 2019).

Interaction of Se with auxin hormone could be one of the reasons through which plant maintain high cellular water content through modified root architecture and Seethylene interplay a crucial role during post-harvest life of cut flowers (Costa et al. 2020). Experiment conducted using the Se and Zn nanoparticles (NPs) in B. napus under salinity showed improved in seed germination by reduction of ABA (CYP707A1, 3 and 4) and eleavation of GA related genes (GA20ox and GA3ox) (El-Badri et al. 2021). Titanium at higher concentration acts as stressor and the application of GA improves the wheat growth at all the doses of TiO₂ nanoparticles, showing the antagonistic interaction (Alharby et al. 2021). The study conducted using the 24-epibrassinolide and TiNPs in Pleioblastus pygmaeus provide improvemnts under Cu and Cd toxicity by enhancing antioxidant activity (85%), pigments (43%), and non-enzymatic antioxidant activities (47%) (Emamverdian et al. 2022). Similarly, application of TiNPs in Arabidopsis promted the root growth by inducing the PIN2 auxin transporter (Wei et al. 2020). Application of Co under unfavourable conditions increased ABA and ET hormones, which were linked to enhance plant resistance, promote abscission and reduce water losses in Phasoleus vulgaris (Schautmann and Wenzel 2002). A recent study conducted in switch grass reveals that application of La and ABA co-regulates the chlorophyll production and act as antagonist during seedling development (He et al. 2020). Similarly, the seed primed with La improve maize grain yield by improving photosynthetic attributes, reducing antioxidant defense and alter the level of ABA (Cui et al. 2019). There are also some evidences that showed that presence of Al induces the contents of chlorophyll, carotenoids, sugars, proline, PGRs such as ABA, auxin, CKs and secondary metabolites, which regulates the plant growth positively (Moreno-Alvarado et al. 2017). Study suggested that application of tricontanol (TRIA), Ce

and La induced the early bolting in Arabidopsis through the regulation of cytokinin levels (He and Loh 2002). Thus, the beneficial element crosstalk's with plant growth regulators and at low dose positively regulates the plant growth. The crostalks of beneficial element with important PGRs in regulation to plant growth and development are highlighted in Fig. 2.

Beneficial element Se act as antagonist of As toxicity through expression of As transporters and regulatory elements (Chauhan et al. 2020). Beneficial element Al increases P use efficiency and alleviates H⁺ and Fe toxicity under acidic condition and their interaction affect plant growth and development (Matsumoto and Yamaya 1986). Antagonistic reduction of Fe and Mn uptake by Al is strongly believed to be the mechanism that Al alleviates Fe and Mn toxicity (Ghasemi-Fasaeiet al. 2005). Ce along with being beneficial element, regulate the mechanism of other elements in plants such as decrease nitrogen assimilation and Mo absorption and interfere with Fe absorption in soil (Peralta-videa et al. 2014; Ramírez et al. 2018). For nitrogen fixation Co play vital role as constitute of cobalamin and alleviates N absorption (Chmielowska-Bak et al. 2014). Iodine Interfere in plant metabolism by showing synergistic effect with Cu, Fe, Mn. (Schlorke et al. 2016). Iodine also competes with Se for absorption site (Smolenet al. 2016). Lanthanum frequently has been found in conjunction with Ce and other elements from this family. At low dose of La, it promotes uptake of essential elements Fe, K, Ca, Mg and higher La concentration inhibits Ca, Cd and Fe absorption (Agathokleous et al. 2018). Ti helps in alleviating Cd toxicity in plants. Silicon alleviates As, B and Cd toxicity (Rizwan et al. 2019). Under stress conditions Si can be seen to enhance tolerance to multiple biotic and abiotic stresses (Kleiber 2018). Vanadium lower dose promotes P accumulation and vice-versa, also reduce Zn accumulation. Appropriately beneficial elements play major role to improve plant resistance to abiotic and biotic stresses at their low levels. But, the effective ranges for the beneficial elements is somewhat narrow and higher dose can be detrimental to plant metabolism. The crosstalks of beneficial elements with other important macro, micronutirents and heavy metals are highlighted in Table 2; Fig. 3.

Physiological, biochemical and molecular understanding of beneficial element for abiotic stress tolerance

Beneficial elements have dynamic role in regulating several crucial processes and biochemical reactions in plant during abiotic stresses, which are highlighted in Table 3; Fig. 4 and discussed thoroughly.

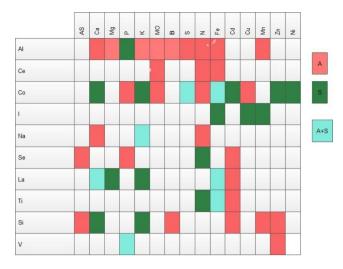


Fig. 3 highlights the crosstalks of beneficial elements with other elements (macro+micro+heavy metals). Different color indicates the relationship between them [red (antagonistic), Green (synergestic), Turquoise (dual effect)]. Some beneficial elements showed the dual effect means at low concentration acts as synergistic and opposite when the concentration is high. These figure can help in the use of beneficial elements in understanding the response of other metals and the effects on nutrient resource

Role of silicon in mitigating abiotic stress

In the last two decades, various researches have been accomplished in different crops and revealed the role of Si in managing unfavourable situations (Jinger et al. 2017; 2020c). However, meagre studies have been done so far in relation to modus of operandi of Si in abiotic stress mitigation (Jinger et al. 2018b; 2020d). Application of silicon fertilizer (soluble silicate or basic slag) in soil can enhance 10–25% yield of many crops including sugarcane, rice, sunflower and sugar beet. The role of Si in multiple abiotic stress tolerance are highlighted in Fig. 5.

Si in mitigating temperature stress

Elevated/high temperature (HT) leads to water losses from the plant due to increased transpiration. Thakral et al. (2021) reported that it might be due to breakdown of lipid and proteins of the cell membrane caused malfunctional changes in the cell membrane due to HT. Maghsoudi et al. (2016) showed that during HT, Si improved thermal stability and cell integrity of PM by reducing leakage of electrolytes in wheat. Application of Si in rice imparts its conglomeration in the vacant spaces within the cellulose micelle of epidermal cells, where it leads to formation of silica-cellulose membrane, that arrest the transpiration during HT stress. The combined foliar application of 24-epibrassinolide and Si improved the root length (37.25), shoot length (35%), leaf area (25.93%), photosynthetic rate (15.25%), stomatal conductance (10.32%), and antioxidant enzymes, which enhance HT tolerance abaility in wheat crop (Hussain et al. 2019). HT in wheat crop damage the ultrastructure of leaf such and cell organelle such as chloroplast and nucleus, which were restored whencrop are subjected to Si and SiNPs treatments They also reported the enhanced expression of aquaporins genes (*PIP1*; PM intrinsic protein and *NIP2*; noduline-26-like intrinsic protein), which maintain the cell water potential during heat stress (Younis et al. 2020). The similar kind of result was obtained in tomato crop, where the application of Si upregulated the expression of heat shock factors related genes (*HsfA1a-b*, *HsfA2-3*, and *HsfA7*), ABA (*NECD*) and SA related gene (*R1b1*, *PR-P2*, and *PAL*) under heat stress in tomato crop (Khan et al. 2020a&b).

Similarly, organo-silicon compounds protect the rice plants from frost injury (Loginov et al. 2011). Si fertilization protect the wheat plant from freezing stress by increasing antioxidant defence activity, membrane permeability, water retention in leaf tissues and by lowering lipid peroxidation (Liang et al. 2008). Current investigation reported that low temperature stress in aloevera and bamboo was suppressed by application of Si through increased antioxidant activities (Azarfam et al. 2020). In maize crop Si restored the micronutrient content (Zn and Mn), hormonal homeostasis and antioxidant defence activities as chilling stress subjected at early growth phase (Moradtalab et al. 2018). Transcriptomics analysis of grafted cucumber under low temperature stress Si improved the phenylpropanoid metabolism, MYB 44 (MYB domain protein), fatty acid metabolism, and antioxidant enzymes related transcript, which further related to chilling stress tolerance (Luan et al. 2022).

Role of Si in mitigating moisture stress

Physiological processes are hindered when plants face flooding and drought conditions owing to excess yield of ROS, which diminished the growth and development phenomenon in plants. Si application improves the oxidative defence system of the plants growing under flooded condition by increasing their resistance to flooding (Sayed and Gadallah 2014). Si fertilization minimised the oxidative damage in barley, when it was cultivated in the saturated soil. Recent studies reported that Si enhances antioxidant defence, root characters and plastid anatomy of rice when grown in waterlogged conditions (Pan et al. 2021). Si has potential role in mitigating drought stress (DS) conditions (Jinger et al. 2020a). In wheat, Si supplementation imparts drought resistance by alleviating the oxidative damage and improving the root architecture, biochemical and antioxidants defense such as expression of antioxidant enzymes, AsA-GSH pool and glyoxalase system (Hasanuzzamanet al. 2018; Zahoor et al. 2020). Drought stress mitigation in rice linked to Si application, which reduced theproline content. Similarly, Si application in maize improved and maintained the turgidity of the plant facing drought by decreasing transpiration (Mauad et al. 2016). Si application increased the root water uptake through the root endodermal silicification, suberization, and Casparian band development, which ultimately affect the root hydraulic conductance and water retention under DS (Fleck et al. 2015; Soukup et al. 2017). Moreover, the Si improved the expression of aquaporins transcripts (PIP1;6, PIP2;2, and PIP2;6) in sorghum crop in response to DS, which ultimately contributed in improvement of root hydraulic movement and uptake capacity (Chen et al. 2018; Wang et al. 2021). Likely, Si improved the light energy absorption and transformation through the stability of photosystem I (PS-I), PS-II, and chlorophyll protein complexes under DS (Wang et al. 2019).

Si application increased the lodging resistance and lignin deposition in rice crop (Dorairaj et al. 2020). Similarly, Jinger et al. (2020b) reported less than 1% lodging or practically no lodging in aerobic rice treated with calcium silicate at 120 kg Si/ha along with 90 kg P_2O_5 /ha and 100% lodging in untreated (control) field. A recent study conducted in rice under submergence stress reveals that the submergence reduced the root and shoot biomass, photosynthesis attributes, and damage the chlorophyll ultrastructure, which is restored when plants subjected to Si treatment (Pan et al. 2021). A sufficient supply of silicon permits rice plants to keep the leaves erect, uncurved and thus improves the assimilatory system, antioxidant defense, and osmolytes under submergence stress (Iqbal et al. 2021b).

Role of Si in mitigating salinity stress

Salinity is one of the major abiotic stresses causing ion toxicity (Na⁺ and Cl⁻) in the plant system. Si employs various processes for supressing salinity stress in the plant. Reduction in ion toxicity and improvement in water retention by decreasing transpiration, regulation of biosynthesis of phyto-hormones, depletion in osmotic stress, and modification of gene articulation are important Si-regulated tolerance mechanisms under salinity (Zargar et al. 2019).) Si improved the K⁺/Na⁺ ratio and increases relative water content, water use efficiency, photosynthetic efficiency by decreasing transpiration rate and ultimately provide salinity tolerance (Mateos-Naranjo et al. 2013). Si effect on the H⁺-ATPases and H⁺-PPase activity of PM and tonoplast, respectively, which eventually leads to compartmentalization of the salts in the vacuoles (Liang et al. 2006). Si supplementation minimizes the oxidative loss by improving antioxidant enzymes activity (superoxide dismutase, peroxidase, glutathione and ascorbate peroxidase) (Li et al. 2015). Si fertilization improves the salt resistance by

Table 2 Crosstalk of beneficial elements with other essential (macro and micro) and heavy metals

Beneficial element	Crosstalk with	Function	Mechanism	References
Se	As	Antagonist of As toxicity	Expression of As transporters and expression of regulatory elements such as WRKY	Chauhan et al. 2020
Al	Ca, Mg, P, K, Mo, and B	Antagonise essential elements	Restrict root growth and microbial mechanism essential for absorption of nutrients	Singh et al. 2017
Al	Ca, Mg	Antagonise each other absorption and uptake	Compete for the cation exchange sites on the plant roots	Liu and Xu 2015
Al	Р	Antagonise each other absorption and uptake	Formation of nontoxic Al-P complexes in soil	Hodson and Evans 2020
Al	Si	Antagonise each other absorption	formation of stable Al-Si complexes	Kopittke et al. 2017
Al	В	Antagonise each other absorption	Helps in enhancing root elongation, decreasing Al content in root apoplast	Zhu et al. 2019
Al	S	Antagonise each other absorption	Decreasing the transport of Al from roots to shoots and increasing the Al- induced secretion of citrate by roots.	Guo et al. 2017
Ce	Mo	Ce antagonise Mo absorption	Competition for binding site	Peralta-Videa et al. 2014
Ce	Ν	Decrease nitrogen assimilation	Mo is cofactor in nitrate reductase enzyme. Ce affect Mo absorption in turn decrease nitrogen assimilation.	Hille et al. 2011
Ce	Fe	Antagonise Fe absorption	Interfere with Fe absorption in soil	Ramírez et al. 2018
Co	Cd	Increases Cd toxicity in plants	Cobalt affects cell viability and expression of Cd-induced genes associated with plant signaling pathways.	Chmielowska- Bak et al. 2014
Co	P,S,Cu	Interfere with their metabolism	Reduces the translocation of P, S and Cu and drops the transpiration rate and water potential in the leaves of cauliflower	Nagajyoti et al. 2010
I	Cu,Fe,Mn	Synergistic effect	Ability of copper oxidases to oxidize $I - to I_2$ or HOI. It is possible that a greater amount of iodine present in plant tissues induces increased activity in the systems that dissipate the element, such as copper oxidases and possibly other oxidases with Fe and Mn	Schlorke et al. 2016
I	Se	Antagonistic effect	Competition for absorption site	Smolen ' et al. 2016
Na	K	Synergistic effect	Because in hydrated form Na and K both are chemically and structurally very similar	Maathuis 2009
Na	Ca, N,K	Antagonistic effect	Both at cellular and molecular level it interferes in absorption and assimilation	Maathuis 2014
Se	Cd	Inhibit Cd toxicity	Se treatments increase glutathione and phytochelatin levels and induce Cd- stress tolerance	Li et al. 2016
Se	Ν	Promotes N metabolism	Physiological process more strongly, because it prompts a stronger activa- tion of NR, GS and GOGAT, as well as producing a greater total reduced N concentration	Rios et al. 2010
Se	Р	Antagonistic effect	An increase in the P supply significantly inhibits Se accumulation in the root cell wall, but enhances the Se distribution in the organelles and soluble fractions of root cells	Liu et al. 2018
La	Ca	Antagonistic effect at higher La concentration	La inhibits Ca transport from the apoplast into the cytoplasm, blocks transport from the root to the straw and grain, replaces and competes for binding sites, and so results in the decrease of straw and grain Ca.	Xie et al. 2002
La	Fe, K, Ca, Mg	At low dose of La, it promotes uptake of essential elements	Entered into the leaf cells via the endocytosis activated by low-dose La(III), disrupting the homeostasis of essential elements in edible plant leave	Ben et al. 2021
La	Cd	Antagonistic effect	Reduces the cadmium accumulation by suppressing expression of transporter genes involved in cadmium uptake and translocation	Yang et al. 2019
Ti	Fe	Both synergistic and antagonistic effect	Under Fe deficiency, Ti helps induce the expression of genes related to Fe acquisition, thereby enhancing Fe uptake and utilization. At Ti concentration, and Ti competes with Fe for ligands or proteins	Lyu et al. 2017
Ti	Cd	Helps in alleviating Cd toxicity in plants	improved the chlorophyll and gas exchange parameters in leaves ultimately enhancing overall photosynthetic rate	Rizwan et al. 2019

Table 2 (continued)

Beneficial element	Crosstalk with	Function	Mechanism	References
Si	As	Silicon Alleviates Arsenic Toxicity	Si-enhanced antioxidant defense mechanism, improving the membrane stabil- ity (lower malondialdehyde), synthesis of chlorophyll pigments, antioxidant enzymatic activities (superoxide dismutase, peroxidase, catalase), and proline accumulation	Kashif et al. 2021
Si	В	Alleviates B toxicity	Si triggers endogenous H_2S accumulation that leads to up-regulation of anti- oxidant enzymes to protect pepper plants against boron toxicity	Kaya et al. 2020
Si	Cd	Alleviates Cd toxicity	Helps in decreasing Cd uptake and accumulation	Liu et al. 2020
Si	Ca	Synergistic effect	maintaining permeability of plasma membrane and enhancing shoot Ca under water stress	Kaya et al. 2006
V	Р	At high concentration causes low P in plants	Caused by the production of reactive oxygen species (ROS), consequent membrane lipid peroxidation and undermining of cell membrane integrity.	Imtiaz et al. 2017
V	Zn	Reduction of Zn accumulation	Attenuation of Zn accumulation in shoots and a lower bio-concentration factor (BCF) of Zn	Aihemaiti et al. 2019

*NR; nitrate reductase, GS and GOGAT; Glutamate synthase;

regulating the levels of JA, ABA, proline, GA, and glycine betaine (Koentjoro et al. 2021). Recently, Muneer and Jeong (2015) reported the application of Si in tomato plant grown under salt stress activated the genes controlling salinity stress (*DREB-1*, *DREB-2* and *DREB-3*). The transcriptomic analysis of si application under salinity stress revealed the upregulationof ABA biosynthesis genes (*NECD1*, &4), Na transporter (*SOS1*&2), and down regulate the *NHX1*, which ulmately regulate the oxidative stress and Na/K⁺ ratio (Kim et al. 2014; Bosnic et al. 2018). The protemics analysis under salinity stress in *Rosa hybrida* revealed the upregulation of proteins related to photosynthesis (22%), stress/ redox equilibrium (12%), ion binding (13%), transcription/ translation (20%), and ubiquitination (8%), when subjected to Si supplementation (Soundararajan et al. 2017).

Role of Si in mitigating heavy metal toxicity

Si ameliorated the toxicity of heavy metals (HMs) through the activation of numerous mechanisms like, immobilization, compartmentalization, co-precipitation, chelation, antioxidant stimulation, and alteration in gene expression (Zargar et al. 2019). Supplementation of Si decreases toxicity of Al, B, Cd, Mn, and Zn (Bhat et al. 2019). Immobilization of HMs through Si application in soil is the simplest and widely accepted mechanism. It occurs owing to changes in soil reaction and evolution of metal in soil by genesis of silicate nexus. Gu et al. (2011) observed that Si increased soil pH and decreased the phyto-availability of HMs to a great extent in rice. It also reduced the translocation of Zn from root to shoot and accelerated the attachment of Zn with cellulose of plant wall, thus reducing Zn content within above ground parts (Yamaji et al. 2008). Gu et al. (2011) reported co-precipitation mechanism, where Si and Cd make insoluble compounds in the culm of paddy which decreased HMs content in the shoot portion. Heavy metal detoxification by Si also involves the chelation of HMs with flavonoidphenolic or organic acids. Application of Si in maize led to chelation of Si with catechin and quercetin (phenolic compounds) which ultimately reduced the Al toxicity (Wang et al. 2004). HMs toxicity detoxification through Si also involved the activation of antioxidant defense. Application of Si in cucumber reduced Mn toxicity by reducing lipid peroxidation and increasing activity of antioxidants like SOD, APX, and GSH (enzymatic); and ascorbate and glutathione (non-enzymatic) (Shi et al. 2005). Recently, the role of Si in amelioration of HMs toxicity through the modulation of secondary metabolites production are well known. For instance, Si application modulated the expression of phenol and lignins in Barley (Vaga et al. 2019), flavonic and phenolic compounds in cucumber (Maksimavic et al. 2007), and tetrapreonoid and carotenoids in maize (Paula et al. 2015) under Al, Mn and Zn toxicity respectively. Consequently, Si allivated the toxicity of HMs through the downregulation of Nramp5 (natural resistance-associated macrophage protein 5), HMA2&3(The P1B-type heavy metal ATPase 2/3), NRT2 (nitrate transporter protein), AMT1 (ammonium transporter protein), PHT2 (phosphate transporter protein), and KAT 1 (potassium transporter protein), which help in sequestration of HMs and improve the transport of essential nutrients (vaculik et al. 2020).

Titanium (Ti)

Ti playes a pivotal role for improving the growth of plants due to promoting the uptake of nutrients, enhancing chlorophyll content and photosynthetic activity, and improving stress tolerance capacity (Buettner et al. 2012; Lyu et al. 2017). The seedlings of dust indicator plant named as *Tapertip hawksbeard* showed 11-fold increment in Ti while exposed to contaminated soil (Cook et al. 2009). Ti shows

Table 3 Abiotic stresses tolerance mechanism in plant through application of beneficial elements

Beneficial element	Crop	Stress	Mechanism	References
V	Arabidopsis thaliana	H ₂ O ₂ induced stress	Low concentration of V helps in increasing the level of ROS signalling molecule that is involved in organogenesis and also responsible for root hair formation (rhizogenesis) in stress condition.	Libik-Konieczny et al. 2015
	Oryza sativa Cicer arietinum Nicotiana tabacum	Drought and other abiotic stress	Enhances the activity of SOD, CAT, POD, and glutathione.	Imtiaz et al. 2018; Altaf et al. 2020; Wu et al. 2021
Si	Sorghum bicolour	Drought	Silicon is responsible for improving root growth system and helps in main- taining photosynthetic activity and stomatal conductance	Hattori et al. 2005
	Oryza sativa	Drought	Increase in photosynthetic activity, stomatal conductance ,water use effi- ciency and higher grain yield in rice	Crusciol et al. 2013
	Triticum astevium	Drought	Increase in chlorophyll content and relative water content on foliar applica- tion of Sillicon further grain biomass increased with reduced electrolyte leakage	Maghsoud et al. 2016
	Hordeum vulgare	Salinity	Increased activity of enzyme SOD, POD, CAT and glutathione reductase	Liang et al. 2003
	Gossypium hirsutum	Ni toxicity	Silicon reduces Nickel absorption and increases antioxidant defence mechanism	Khaliq et al. 2015
Ti	Triticum astevium Zea maize	Drought	Enhances the enzyme activity of catalase, peroxidise and nitrate reductase against drought	Bacilieri et al. 2017
La	Nicotiana tabacum	Drought	Activity of choline, ATPase and Mg ²⁺ were significantly increased	Chen et al. 2001
	Triticum astevium	Pb toxicity, Saline stress	Enhances antioxidant defence mechanism, Improved activity of SOD, CAT and POD antioxidant enzymes.	Pang et al. 2002; Yongsheng 2005
	Oryza sativa	Cu toxicity	La(III) amino acid chelaters chelates Cu ions and reduces toxicity in rice	Chen and Zhong, 2021
Se	Oryza sativa	As toxicity	Expression of As transporters and expression of regulatory elements such as WRKY	Chauhan et al. 2020
	Hordeum vulgare	Drought	Enhance the GSH-Px and CAT activity and decreases lipid peroxidation process	Habibi 2013
	Sorghum bicolor	Chilling stress	Enhances guaiacol and ascorbic acid peroxidise activity	Abbas 2012
	Sorghum bicolor	High temperature	Increases anti-oxidant activity	Djanaguiraman et al. 2010
	Triticum astevium	Chilling stress	Increases phenolics, anthocyanin and flavonoids and improves antioxidant defence mechanism	Akladious 2012
	Zea maize	Salinity	Improve ion transport and antioxidative properties	Jiang et al. 2017
	Lolium L	Saline and Heavy metal stress	Increases activity of SOD subsequently activating POD enzyme	Cartes et al. 2010
Со	Lycopersicon esculentum	drought	Increased activity of SOD, CAT, APX	Zhu et al. 2000
Al	Camellia sinensis	Drought	Enzymes like superoxide dismutase catalase increases	Ghanati et al. 2005
Na	Triticum astevium Oryza sativa	Salinity	Sodium transporters removes excess of sodium from roots and provide resistance against salinity	Subbarao et al. 2000
Ι	Solanum lycopersicum	Drought	Increases soluble solids fructose, glucose, ascorbic acid and phenols. Increased concentration of salicylic acid	Smolen et al. 2015
	Glycine max Lactuca sativa		Increased in concentration of enzymes SOD,APX and GR Increased in concentration of enzymes SOD,APX ,GSH and AA	Gupta et al. 2015 Leyva et al. 2011
Ce	cucumber	Chilling stress	Increased proline and chlorophyll content	Li Guo tai 2010
	Vigna unguiculata	Metal stress	In lower concentration Ce enhances proline and polyphenol oxidase activity in plants	Shyam and Aery 2012

* SOD; superoxide dismutase, CAT; catalase; POD; peroxidase, APX; ascorbate peroxidase, AA; amino acid, GR; glutathione reductase

both synergistic as well as antagonistic properties depending upon the amount of various elements present in the surroundings (Bacilieri et al. 2017). Tytanit or Mg-Titanit is used for commercial use and these were found to work as bio

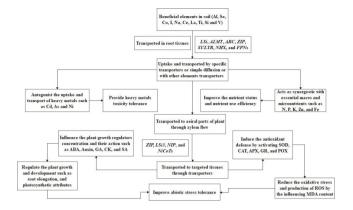


Fig. 4 Highlight the systematic way of response and mechanism of beneficial elements for abiotic stress tolerances. * ZIP; zinc regulated transporter, NHX; Na^+/H^+ antiporter, NIP; nodulin 26-like intrinsic proteins, FPN; ferroprotein, SULTR; sulfate transporter, ALMT; Al activated malate transporter, ABC; ATP binding cassette transporter, CNGC; cyclic nucleotied gated channel.

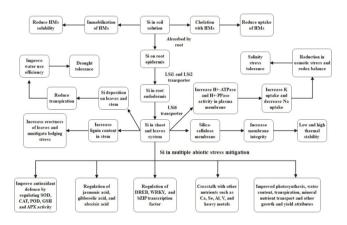


Fig. 5 Highlights the role of Si in multiple abiotic stress tolerance. Si is important beneficial elements which regulates the plant physiological, biochemical and molecular processes and improves the stress tolerance

stimulant. Hussain et al. (2021) reported that the phosphorous uptake in shade grown potato is enhanced with foliar application of Ti; significant improvement is also noticed in various plant growth and biomass attributes even in high and low phosphorus containing soils. They further indicated with 500 mg L^{-1} of Ti application was capable to enhance the rate of photosynthesis by 45% under shade grown and phosphorous stressed soybean crop. Its foliar application either alone or in combination with Mg to potato, winter wheat and spring barley enhanced the availability of nitrogen under N deficient condition (Tlustoš et al. 2005). Ti $@\ge$ 10 mg/kg concentrations was found toxic in oats (Avena sativa L. cv. Zlaťák) but addition of Mg was found to play an ameliorating role (Kužel et al.2007). It was further shown that when the soil is with nutritional optimum then Ti plays significant role in equalizing the plant nutrient content, particularly in Fluvisol, which are deficient in Mg, Fe, Zn, and Mn. Hence, Ti help to regulate plant growth during nutritional stress (Wadas and Kalinowski 2019). Further, tytanit application significantly increased hybrid alfalfa and red clover (Medicago x varia T. Martin and Trifoliumpratense L) yields, without improving the nutritional value of the plants (Sosnowski et al. 2020). TiO2-NP treatment in Zea mays L. moderates the H₂O₂ imposed stress effects by improving the proline content (1.23 fold), inducing the activity of SOD enzyme (1.42 fold) of antioxidative cascade, up regulating the activity of guaiacol peroxidase (91.07 fold) and down regulating CAT activity; this delineates how TiO₂-NP application modulates the oxidative stress in C₄ plants (Sarkar et al. 2021). Use of n-TiO₂ in combination with SNP enhanced SOD, CAT and APX activities with decreased MDA and H_2O_2 in barley under salinity; proposing it a promising approach for alleviating the salinity stress in barley (Karami and Sepheri 2018). Likewise, The Ti-NP showed the beneficial effect under cold stress in chickpea, heat stress in tomato, drought in wheat, and Cd toxicity in soybean (Qi et al. 2013; Jaberzadeh et al. 2013; Mohammadi et al. 2014; Singh and Lee 2016). In wheat crop application of TiNPs and calcium phosphate improved sedling root, and shoot length, fresh and dry biomass by 33, 53, 48 and 44% respectively under DS (Mustafa et al. 2021). They also found that the DS tolerance in wheat plant primarily through the enhanced activities of SOD, POX and CAT by 83, 74 and 81% respectively, which linked to reduce oxidative damage. The application of TiNPs under As toxicity upregulated the expression of GSH1 (glutathione), PCs (phytochelatins), and ABC1 genes in rice, which ameliotae the HMs toxicity symptom and reduce oxidative stress (Kiany et al. 2022).

Cobalt (Co)

The essentiality of cobaltin legume N₂ fixation and in root nodules of non-legumes (e.g. alder). Cobalt is known to play a pivotal role during overall plant growth, depending on its overall concentration in the root rhizosphere and in plants. Co is beneficial for plant growth at a low concentration; high concentration causes the detrimental effects (Gad 2012). Co is necessary for the outward appearance of plants like development of plant buds-leaf discs, plant stem coleoptiles etc. Beside this, cobalt is also important for various chemical and biological reactions essential in plants. In legumes Co, participated in pigments formation, activate enzymes needed for symbiotic N fixation (Farooq et al. 2012). Now it's been well well-known that Rhizobium and several other N2 fixing microorganism have a necessary necessity of cobalt. The coenzyme cobalamine (Vitamin B₁₂ and its derivatives) maily has Co (III) as the metal component. Propionate also serves as the energy source for plant growth (Gupta and Gupta 2018). Cobalt has a positive effect under DS in higher plants (Pilon-Smits et al. 2009; Gad et al. 2018; Akeel and Jahan 2020; Brengi et al. 2021). Co improves leaf resiatance to dehydration and cytoplasmic pressure, decreases the wilting coefficient hence increasing drought resistance (Schautmann, and Wenzel 2002). Priming of soybean seeds with cobalt solutions reduce the drastic effects of DS during seedling growth (Blaylock et al. 2000). Cobalt level has a positive effect on plant growth, leaf water status, ABA as well as xylem and phloem tissues being increased especially under water deficit conditions. Treatment of 7.5ppm Co had a major effect on tomato growth, yield, and fruit quality (Gad 2005). Application of Co @ 3 mg/kg soil improved leaf water content in tomato and potato leaves. Further it is also seen that application of Co improved water absorption capacity and increased water use efficiency hence saving 20% of irrigation water in beans. Co application also reduced transpiration rate, increased water absorption capacity, promotive effect on improved water potential and abscisic acid, auxin and gibberellin as well as xylem and phloem under water-limited conditions (Anter and Gad 2001; Gad et al. 2018).

Sodium (na)

Globally, sodium (Na⁺) salt is dominant in the saline soils and sixth most plentiful element found on earth (Rodríguez-Rosales et al. 2009). Na⁺ toxicity not only causes physiological drought by lowering soil solution osmotic potential but also makes nutritional disorder (Khan et al. 2019). Na⁺ can be a beneficial nutrient for those plants where potassium is deficient. Under salt stress, osmatic adjustment can be achieved by accumulation of various osmolytes i.e. organic solutes (proline, sugar, glycine betaine etc.) and inorganic ions (Na⁺, K⁺, Ca⁺ and Cl⁻). Partitioning of sodium in the vacuole is considered as a phenomenon of osmotic adjustment which reduces water potential and thus increases drought resistance (Cui et al. 2019). Na⁺ require less energy for osmotic regulation in plants so the use of Na⁺ as osmolyte is more economic and efficient (Chen et al. 2009). Sodium efflux protect the plants against salinity stress, under salt stress accumulation of Na⁺ in plant cell is determined by the ion exchange action of Na⁺ efflux and influx. Under adverse conditions, excess light energy is generated which decreases the activities of PSII & PSI resulting in decreases rate of photosynthetic and accumulation of large amount ROS (Hui-Hui et al. 2020). Na⁺ accumulation can be utilized not only for osmotic adjustment but also to reduce the photosynthesis inhibition via increased non-photochemical quenching caused by excess light energy (Xu et al. 2018). The higher concentration of Na⁺ in leaf increased leaf succulence, decreased cell solute potential, swelled leaf organ, enhanced water uptake and down-regulated stomatal density and stomatal aperture (Xi et al. 2018).

Lanthanum (La)

Lanthanum (La), a metal element which is a part of the rare earth element (REE) family. La has been commonly used in agriculture, where it showed beneficial effects on physio-biochemical attributes of plants at lowered concentrations (Hu et al. 2002). La is known to cause hormesis, a dose-dependent actions characterised by low-dose beneficial and high-dose inhibitory. In wheat, treated with La at 0.5-25 mg/L resulted in reduction of primary root elongation, and shoot biomass, which were associated to impaired nutrient homeostatus (Hu et al. 2002). At doses greater than 0.2 mM in solution. La inhibited maize and mungbean growth, root function, and nutritional status (Diatloff et al. 2008). In horseradish, La promoted cell growth and expansion at 30-35mM LaCl₃, but at 80mM caused damage to cell growth (Wang et al. 2014). In soybean 5-10mM La improved overall plant performance through improved nutrient homeostatis, whereas at 20-160mM concentration significantly affected photosynthetic rate and biomass attributes (de Oliveira et al. 2015). Application of lanthanum nitrate (1 mM) in tomato was non-responsive under drought stress and seems to be the result of unbalanced cell metabolism due to high dose of lanthanum which cause hormensis (Ippolito et al. 2011).

La has been studied at the seedling stage in few crops to find out its ability to alleviate heavy metal stress. For example, La amolierated the Cd toxicity in Phaseolus vulgaris and maize, which were due to increase in photosynthetic improvement, decrease MDA content, and induced antioxidant potential (Huang and Zhou 2006). Also, LaCl₃ application in maize crop improved tolerance to Cr stress through the upregulation of antioxidant activities, regulation of AsA- GSH cycle and improved chloroplast functions (Dai et al. 2017; Dai and Shan 2019). Furthermore, Exogenous application of La (III) of 20 mg/L in rice ameliorated Cu toxicity stress in rice through reduction in oxidative stress, improved chlorophyll content and promoted overall growth. Also, the concentrations of Cu (II) in rice leaves, stem and roots tissue were reduced with the use of La (III) via improving the ultrastructure of mesophyll cells (Zhong and Cheng 2020). Under salt stress, La³⁺ application (0.1mM) alleviate salinity induced osmotic stress in Saussurea involucrata as evident with the increase in leaf water potential, increased soluble proteins and proline content, improved total chlorophyll and carotenoids and decreased MDA content with elevated antioxidant machinery such as SOD, APX, CAT,

and GR (Xu et al. 2007). Also, tomato plants treated with LaCl₃ regulates AsA-GSH cycle in chloroplast and alleviates salt induced damages (Huang and Shan 2018). A recent study revealed that the crosstalk of La and Ca reduced the accumulation of Cd in plant and ameliorate the Cd toxicity through the downregulation of *Nramp5* transporter gene (Yang et al. 2021).

Aluminum (Al)

Aluminum is the 3rd prevalent element accounting for around 8.1% of its mass (Bojorquez-Quintalet al. 2017). A growing body of research supports involvement of Al roles in enhancing enhancing phosphorus efficiency, amelioration of Mn and Fe toxicity under acidic environments and managing plant growth (Muhammad, et al. 2019). Al also gives abiotic stress tolerance to plants by activating stress-related genes, as well as drawing PGPRs to roots through producing root exudates (Wang et al. 2015).

Al has been shown to affect a variety of intercellular functions by altering the cell wall properties and affecting transport of molecules across the PM (Singh et al. 2017). In M. malabathricum, Q. serrata and tea increased the P uptake and also root growth by higher P availability (Tomioka et al. 2005). Furthermore, the presence of Al affects nitrate, potassium, and magnesium absorption and transport, as well as root growth. Phosphorus tolerant genotypes exuded more malate from the root tips, implying that the increased phosphorus is due to increased organic acid secretion in the roots, which was aided by Al treatment. Citrate secretion was enhanced by Al and substantially reduced by P deficit, according to several publications. SbMATE expressioncontrolled citrate secretion, improved P nutrition, and raised Al toxicity tolerance, according to several reports (Richardson et al. 2011).

In acidic soil, Al decreases expansion of leaf, stomatal movement, and photosynthetic rate, by reducing P availability (Lyu et al. 2020). Similarly, Al stress reduces the ability of hyper accumulators to extract phytochemicals from contaminated soils (Zhou et al. 2020). Al stress disrupt soil rhizobia by reducing the efficacy of nodulation and N-fixation in legume species, by altering hormone levels and impair root growth (Kopittke et al. 2016; Jaiswal et al. 2018). The maintenance of DNA integrity, higher uptake of critical nutritional elements, and restricted uptake of HMs in root cells linked to Al-induced growth in tea plants (Sun et al. 2020). Following that, flavin monooxygenase-like proteins (YUCCA) were discovered to function downstream of TAA1 and regulate auxin concentrations in the trasition zone of the root apex in response to Al stress (Lvet al. 2019). Furthermore, under Al stress modulating auxin signalling in barley, miR393 plays a critical role in root growth suppression (Bai et al. 2017). Transcription factor (TF) sensitive to proton rhizotoxicity 1 (STOP1) involved in Al tolerance, and have crucial role in the Al signaling pathway. AtSTOP1, a zinc finger TF regulates the expression of downstream-STOP1 Al-resistance genes and its SUMOylation control Al resistance (Fanget al. 2020). To summarise, Al increases plant growth at low concentrations, enhances nutrient uptake, has a favourable influence on metabolism, and protects plants from abiotic and biotic stressors.

lodine (I)

Iodine is neither macro nor micro nutrient, however, it has critical role in production of antioxidants adaption for new environment and improvement of plant performance (Medrano et al. 2021). Further, the exogenous application of iodine in plants shows the beneficial effects like promotion of growth, enhancement in the production of antioxidants and increase in the tolerance to abiotic stress (Gonzaliet al. 2017). Several studies confirmed that iodine can act as pro oxidant which induces the antioxidant synthesis in tomato, lettuce and pepper etc. after application of iodate and iodide. These chemicals were found to increase both enzymatic (SOD and APX) and non-enzymatic (glutathione, and anthocyanins) antioxidants to impart tolerance to abiotic stresses (Medrano et al. 2021). Use of iodine or its products to promote plant growth and tolerance to stresses in plants has not been well explored. Thus, there is need to enhanceuse these products in agriculture which can contribute towards bio-fortification of crops (Gonzaliet al. 2017). KI used as a desiccant for screening of DS tolerance rice varieties at flowering stage (Kumar et al. (2012). Furthermore, at grain filling stage, it induces the effect of terminal drought by chemical desiccant (Kordenaeej et al. 2013).

Leyva et al. (2011) demonstrated the occurrence of salinity tolerance (100 mM of NaCl) with application of iodate (20-80 µm) in lettuce which results in increment in biomass and level of soluble sugars and decline in the Na⁺ and Cl⁻ ions along with enhanced antioxidant activity. Soybean seed treated with of IO₃ (20-80 μ m) showed the tolerance against 100 mM of cadmium chloride and heat stress. This study also confirms the finding that the exogenous application of iodine can be beneficial for stress tolerance in plants (Gupta and Rita 2016). Seed treatment with dry dressing of iodine and calcium carbonate in soybean and sunflower resulted in better germination, seedling growth and low level of membrane damage under high temperature and humidity (Deynéeand Mukherjee 1984). Application of iodine based product (KIO₃) in strawberry did not interfere under normal situations but under salt stress it improved the yield and fruit

quality due to increased activities of antioxidants in both leaves and fruits (Medranoet al.2021). The bioinformatics study shown that the iodinated protein in shoots were associated with chloroplast and involves in photosynthesis but in roots associated with various peroxidases. These reportes confirm the iodine as a potent nutrient involves in photosynthesis (Kiferle et al. 2021).

Selenium

Selenium is another beneficial element that is necessary for the health of humans and animal. Meanwhile, a recent study discovered that it is also necessary for plant growth and development. Hamilton (2004) asserts that Se small concentrations essential for normal functioning; moderate for maintaining homeostatic functions and large causing harmful effects. Numerous publications have been published in recent years describing Se as a powerful phytoprotectant capable of mitigating the harmful impacts of a variety of stresses (Hasanuzzaman et al. 2010; Sieprawska et al. 2015). Species of plants cultivated in medium supplemented with selenium have demonstrated increased tolerance to abiotic stress. According to earlier studies, Se can mitigate crop plants' abiotic stress by protecting chloroplasts, and increase chlorophyll content under stress circumstances (Sattar et al. 2019). Selenoproteins (Se) prevent oxidative stress-induced damage to plants by increasing metabolism, controlling redox reactions, enhancement in water and nutrient uptake under unfavourable situations (Sieprawska et al. 2015). When the production of ROS is out of balance in cells, stress is induced, and this leads to significant physiological disturbances (Lin et al. 2012). Under stress, Se enhances antioxidant enzyme activity and minimized oxidative stress through lipid peroxidation in terms of malondialdehyde concentration, either directly or indirectly (Sattar et al. 2019). Elevated proline is seen as a promising sign of cold (Cechin et al. 2008), metal stress (Zahedi et al. 2011), salinity (Chun et al. 2018), drought stress (Ahmed et al. 2021). As previously reported, Se boosted proline accumulation, improving photosynthetic efficiency, ATP synthesis, and water utilization (Desoky et al. 2021). Proline mitigates the detrimental effects of ROS and increases plant resistance by inhibiting ROS produced under salinity stress (Howlader et al. 2018). Se restored proline and soluble sugar levels while preventing photosynthetic damage by maintaining RWC and protecting Rubisco (Desoky et al. 2021). Se modulating ROS mechanisms under abiotic stress conditions indicates strengthening of antioxidant defense (Ahmed et al. 2018). Wang et al. (2012) demonstrated under salt stress condition, chloroplasts and mitochondria, as well as other cellular organelles, were favorably impacted by Se. When it comes to chlorophyll, chloroplasts, and leaf mesophyll cells, the mitochondrial cristae grew more visible and more abundant. Exogenous Se treatment improved chlorophyll and carotenoid pigments and improved stomatal conductance and photosynthesis (Elkelish et al. 2019). Salinity disturbs water status in the soil which reduce the water uptake from roots to shoots (Ahanger et al. 2017). The results suggest that Se treatment boosted RWC through the deposition of sugars under stress situations. It is possible that Se administration increases the Na⁺/H⁺ antiporter expression, hence diminishing its harmful effects (Desoky et al. 2021). In metal stress condition, Se ions can prevent such interaction by 'inactivating' metals prior they bind to proteins (MeSeO₃) and forming SeH groups in proteins (Sieprawska et al. 2015). Beneficial effects of Se on crucial processes under adverse conditions are associated with strengthening of antioxidative machinery and, improved tolerance to oxidative stress. Application of SeNPs with NO stimulated the expression of dehydration response element B1A (DREB1A), PAL (phenylalanine ammonia lyase), hydroxycinnamoyl-CoA quinate transferase (HCT1) increased 29.6, 36.4% and 30-fold respectively in chickory, which ultimately improved the antioxidant defense and secondary metabolism (Abedi et al. 2021).

Cerium (Ce)

Cerium is one of the rare earth element (REE) out of 17 element present (Ramos et al. 2016), accounting for 0.0043% of total mineral. It has role in improvement of germination, height of the plant, root development and biomass weight, productivity, content of the chlorophyll, total sugars, and the nutritional condition of numerous species are among the beneficial impacts (Chen et al. 2015). Aside from promoting N assimilation and PSII activity, the Ce can also stimulate plant functional processes. The effects of Ce on metabolic activities and physiology were dose- and time-dependent, species- and vegetative-stage specific, and dependent on management conditions (Zhao et al. 2012). Under various abiotic stresses, Cerium promotes plant growth by improving photosynthetic activity and antioxidant capacity. Consistent with alterations in antioxidant enzymes and antioxidants, the addition of Ce³⁺ lowered the elevated levels of H₂O₂ and MDA in leaves generated by stress treatments (Hong et al. 2017). Different findings revealed that Ce^{3+} might enhance antioxidant potential and protect the plant membrane system from oxidative stress-induced damage produced by a variety of stress. According to Liang et al. (2006) adding Ce^{3+} to rape seedlings (*Brassica juncea* L.) under UVB exposure increased growth, photosynthesis and the antioxidant defence. In plant science and agriculture,

CeO₂ nanoparticles (Ce-NP) are used to stimulate antioxidant enzyme activity and minimize membrane damage and leakage (Cao et al. 2018). Utilizing Ce-NPs aids in cell structure preservation by acting catalyst for chlorophyll formation and ROS minimizing, as well as preserving chloroplastic structure and PM integrity (Jahani et al. 2019; Jurkow et al. 2020). Under salt stress condition, Moldavian balm plants morphological, physiological and biochemical activity improved by the Ce-NPs exogenous application (Mohammadi et al. 2021). In rice crop poly acrylic acid CeNPs used under salt stress and showed increment in NO production (30.5%) by expression of nia2 (nitrate reductase) and redox signaling (Zhou et al. 2021). Therefore, more studies needs to be focused at molecular level to in-depth study in respect to their action in plant growth and stress tolerances.

Vanadium (V)

Vanadium along with being chemical hard malleable element, it is also an imperative beneficial element. Its mean concentration varies from 20 to 120 mg kg⁻¹ which is almost similar to Zn concentration in earth crust (Baken et al. 2012). As early mentioned that small amount of beneficial elements act as nutrient although only tetravalent form (V^{+4}) of vanadium is beneficial to plant growth and development due to its least toxicity, mobility and most dominant in the soil (Tripathi et al. 2018). Tetravalent form (V^{+4}) help chlorophyll biosynthesis, nitrogen fixation and also increase potassium uptake and accumulation in the plants (Barker and Pilbeam 2015). Higher level of V cause plant physiological balance disturbance, reduction in biomass growth and ultimately yield production and appropriate concentration of vanadium can enhance plant growth and development (Hanus-Fajerskaet al.2021). Different V solution containing 40 and 80 mg/l had vigorous stem, leaf and root growth, more stem length, higher number of leaves in Chinese green mustard plants. While in tomato plants chlorophyll concentration, leave and flowers number, and stem and root attributes were reduced under $0-20 \text{ mg/l NH}_4 \text{VO3}$. Tomato plants started wilting after 2-3 days nutrient solutions with 40 and 80 mg/l V concentration and showed negative response to root, stem and leaf growth (Badmaevet al. 1999; Vachirapatamaet al. 2011) Another experiment with application of different doses of V show positive effect in maize (Zea mays) production and kernel quality (Mukherjee et al. 2004). In basil (Ocimum basilicum), there is linear relationship in dry biomass increment and increasing V doses up to 0 to 40 mg L⁻¹ (Harland and Harland 1994). Arabidopsis thaliana can tolerate more oxidative stress with oxidovanadium (IV) penetration (Rojek et al. 2019).

In some plant species V facilitates electron transportation in light reaction through photosystems I and II and act like redox catalyzer.

It has also been confirmed that V cross talk with certain elements such as P, Zn, Mo and Cu and amolirated the Cu toxicity. Low (47 mg/L) concentration of V promotes P accumulation and enhanced chlorophyll and amino acid production, while higher V concentration cause decrement in P concentration and promote ROS production (García-Jiménez et al. 2018; Imtiaz et al. 2017). Some ionic form of V is structurally similar to phosphate (Pi), which interfering in the enzymatic reaction of like phosphatases, ATPases, and phosphortransferases (Martinet al.1996). Ultimately V used to decrease the harmful effects or prevent transport of toxic trace metals, such as Cu, Hg, and Pb (Akoumianaki-Ioannidouet al. 2016).

Role of beneficial elements against biotic stress

The beneficial elements do not seem to be essential for the vital functions of the plants, but may play ancrucial role during activation of plant defense, thereby protection of plants from different biotic stresses (plant pathogens), insect pests and herbivores (Gómez-Merino, and Trejo-Téllez 2018). Si has inevitable role in plant defense mechanisms against several plant pathogens. Si can activate plant defense by different ways like activating defense related enzymes, antimicrobial compounds (phytoalexins), pathogenesis related proteins (PRPs), and secondary metabolites, regulating different signaling pathways and activation of defense related genes (Ranjan et al. 2021).

The powdery mildew (Erysiphe cichoracearum) infected Arabidopsis plants when treated with Si showed increased production of JA, ET, and SA in leaves, leads to resistance (Bakhat et al. 2018). Similar activation of JA and ET biosynthesis pathway and induction of plant resistance was observed in Si treated rice crop infected with Magnaporthe oryzae (Brunings et al. 2009). A likewise result was observed on spot blotch (Bipolaris sorokiniana) infected wheat plants when treated with Si showed late pathogen entry into epidermal cells and reduced colonization in foliar tissues (Domiciano et al. 2013). Si treated rice plants showed less number of lesions of Pyricularia grisea and Rhizoctonia solani due to increased incubation period and restricted hyphal entry into epidermal cells (Rodrigues et al. 2001; Seebold et al. 2004). Si activated JA and ET induced resistance in response to bacterial disease like, Ralstonia solanacearum in tomato (Chen et al. 2009; Ghareeb et al. 2011).

Selenium treated *B. juncea* plants showed protection from a fungal pathogen *Alternaria brassicicola* causing Alternaria blight and the general stem/root pathogen Fusarium sp. by inhibiting the growth of the fungus. (Hanson et al. 2003). Similarly, the application of sodium selenite on tomato plants against Fusarium wilt caused by Fusariumoxysporum f. sp. lycopersici race 3, showed increased production of total protein contents, phenolic compounds and antioxidant potential in susceptible and resistant cultivars. (Companioniet al. 2012). The role of selenium has also been observed in sodium selenite treated tomato plants infected with the gray mold pathogen Botrytis cinerea. The gray mold in tomato caused by the B. cinerea, inhibited spore germination by the 24 mg/L Se linked to increased ROS production (Wu et al. 2016). Titanium (Ti) as a beneficial element against plant pathogens has also been observed. Lyu et al. (2017) showed that nanoparticles nTi increase tolerance to bacteria Xanthomonas perforans. The reduced disease intensification and incidence of leaf blight (Xanthomonas oryzae pv. oryzae) and curvularia leaf spot (Curvularia lunata) were observed with TiO₂ (Chao and Choi 2005). Similarly, TiO₂ application suppressed brown blotch disease caused by Mycosphaerellacruenta and Cercospora leaf spots caused by Cercosporarosicola in field grown cowpea crops (Owolade and Ogunleti 2008). The beneficial role of TiO₂ has been showed in case of Geranium bacterial leaf spot (Xanthomonas hortorum pv. pelargonii) and Poinsettia bacterial leaf spot (Xanthomonas axonopodis pv. poinsettiicola) (Norman and Chen 2011). Furthermore, TiO₂ importance was showed in recycled irrigation water for elimination of both fungal and bacterial pathogens (Yao et al. 2007). The concentration of 40 mg/L nTiO₂ effectively reduced the spot blotch in wheat caused by Bipolaris sorokiniana (Satti et al. 2021).

Till now, there are very limited research studies on effect of iodine against plant pathogen. However, the possible potential of iodine as an inductor of plant defense against plant pathogens cannot be ruled out. Iodine may activate plant defense through redox potential or changes in the chemical nature of the cuticle (Shaw et al. 2007), which is very essential for the activation of systemic acquired resistance (SAR) (Xia et al. 2009). The iodine induced modifications in the cuticle may alter the interaction of host and pathogens (Gniwotta et al. 2005; Silva-Moreno et al. 2016). Therefore, iodine could be used as beneficial tools against plant pathogens.

There are very little reports on the use of Lanthanum (La) and Cobalt (Co) against plant pathogens. Although, La increases plant biomass and possibly improves plant defense mechanisms against plant pathogens due to increased Si accumulation in stems. (Ilya Fastovets et al. 2017). Similarly, Co at 2 ppm can reduce disease incidence of Fusarium wilt diseases of lentil. (El-Hersh et al. 2011). The above studies on the role of beneficial elements against

plant pathogens indicated that it has immense potential to be used as novel tools for the activation of plant defense and controlling plant diseases (Fig. 6).

Conclusions

Presented review analysis complied the crucial role of beneficial elements in one frame and concluded that they have potential to improve plant health in sustainable ways. Although, earlier studies considered them as toxic materials as they showed toxicity symptoms on higher concentrations. These elements have stronger potential to crosstalk's with essential and heavy metals in plant tissues and need of more research focusing on increasing the nutrient use efficiency and alleviation of heavy metals toxicity. Consequently, their strong potential with plant growth regulators, modulates the crucial signaling network and processes. Moreover, their potential application in stress tolerance is excellent, as they are strong activator of antioxidant defense systems. Further, the bio-fortification of agricultural crop with beneficial elements is future need equally as micro-nutrients. Some of previous attempt for beneficial elements biofortification in crop plants are highlighted in Table 4, which showed the extraordinary results in plant growth and development. Therefore, future research program could be more focus on bio-fortification and the molecular studies which opens new avenue in stress physiology and mineral nutrition to secure global food security in near future.

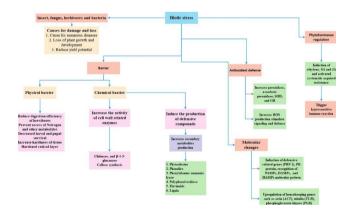


Fig. 6 Highlights the mechanism of biotic stresses through the beneficial elements. The beneficial elements acts as barrier for the pathogens which inhibit the entry into the plant system, secondly they also activated some cell wall related enzymes which also defense against biotic stresses. Beneficial elements also enhanced the secondary metabolites production, which activated the defense system. Moreover, they involved in the production of antioxidant enzymes which minimize the oxidative stress. With this the activation of JA, SA, and ET hormone activated systematic resistance against biotic stresses. Together, all of these changes enhance the plant defense system and provide immunity against biotic stresses

Element	Form	Method applied	Dose	Plant/Crop	Action/Role	References
Selenium (Se)	Selenate	Field/Soil applied	12 to 120 g ha ⁻¹	Rice (Oryza sativa L.)	Increase Se content in grains, change in antioxidant activities and gas exchanges	De Lima Lessa et al. 2019
Silicon	K ₂ SiO ₃	Nutrient solution (NS)	3.6 mM	Green bean (<i>Phaseolus</i> <i>vulgaris</i> L.)	Increase in Si contant in pod,	Monte- sano et al. 2016
Silicon	SiO2	Nutrient solution (NS)	50-100 mg L(-1)	leafy vegetables	more bioaccessible Si	D'Imperio et al. 2015
Selenium	Na ₂ SeO ₄	Nutrient Solution	100 μM Se	Fragaria × anan- assa cv. Elsanta	Shoots fresh weight increased by 20% and leaf area by 17%; and Se concentration in shoot and root by $125.08 \pm 13.89 \ \mu g \ g^{-1} \ DW$ and $174.42 \pm 14.35 \ \mu g \ g^{-1} \ DW$ respectively.	Mimmo et al. 2017
Iodine	KI	Hydroponic	0.25, 0.50, 1.00, 2.50,5.00 mg L-1	Capsicum annuum L.	Increase iodine uptake and accumulation, Higher ascorbic acid and soluble sugar contents and lower in total acidity content, increase chl-az content, lower MDA content and higher in CAT, POD and SOD activities	Li et al. 2017
Silicon	Na2SiO3	Hydroponic	50 mg L-1 and 100 mg L-1	(Fragaria × ananassa 'Elsanta	TSS did not affected by Si biofortification but reduced titratable acidity, Higher sweetness index, increase its accumulation in fruits	Valen- tinuzzi et al. 2017
Selenium	Selenate (Na_2SeO_4) and selenite (Na_2SeO_3)	Soil/field	0 to 60 µM	Butterhead let- tuce (<i>L. sativa</i> L. var. capitata)	Increase Se content, freash weight of root/shoot and leaf area at low concentration, increase photosyn- thetic pigments at low concentration	Haw- rylak- Nowak 2013
Selenium	Sodium sele- nate (Na ₂ SeO ₄)	Foliar application	0, 12, 21, 38, 68, and 120 g ha ⁻¹	Wheat	increase of 48% in wheat productivity and 30% in biomass production, increasing also the net pho- tosynthetic rate with 21 g ha ⁻¹ , positively affects APX and carbohydrates contents; total nitrogen content also increased with 21 and 38 g ha ⁻¹ , increase Se content	Lara et al. 2019
Selenium	g sodium selenate (Na2SeO4)	foliar spray	$40 \text{ mg Se } \mathrm{L}^{-1}$	Wheat under drought stress	Reduce osmotic potential and improved turgor by 63%, increase transpiration rate, improves TSS accumulation by 33%, free amino acid by 118%, increased antioxidant activity and grains yield by 24%. Its also increase Se accumulation and FE and Na uptake.	Nawaz et al. 2014
Selenium	Selenate (Na ₂ SeO ₄) and selenite (Na ₂ SeO ₃)	Growth media	2–80 µm	Cucumber (<i>Cucumis sati-</i> vus L.)	At low concentration fresh weight and leaf area Increase but decrease with increase in Se concen- tration, increase Se accumulation.	Haw- rylak- Nowak et al. 2015
Iodine	Iodide and iodate (IO ⁻ ₃)	Nutrient solution	I^- (20, 40, 80 μmol L^{-1} as KI) and IO ⁻ ₃ (20, 40, 80 μmol L^{-1} as KIO ₃)	Lettuce(Lactuca sativa)	Reduction in biomass with I ⁻ formbut no effects observed in IO_3^- application; increase in antioxi- dants such as ascorbic acid and glutathione (GSH); iodate (IO_3^-) application increased the activities of SOD, ascorbate peroxidase, and CAT	Blasco et al. 2011
Iodine	Iodate	Nutrient solution	0, 20, 40, 80 μM	Lettuce(<i>Lactuca</i> <i>sativa</i>) under salinity stress	Induced the activity of enzymes shikimate dehydro- genase and phenylalanine ammonia-lyase as well as the lower enzyme polyphenol oxidase, thus increase total phenols; and positively effects on biomass production	Blasco et al. 2013
Iodine	potassium iodide (KI) and potassium iodate (KIO ₃)	soil-applied	0, 0.1, 0.25, 1, 2.5, 5, 10 and 20 mg I kg ⁻¹ soil	Wheat (<i>Triticum</i> <i>aestivum</i>), Rice (<i>Oryza sativa</i>) an Maize (<i>Zea mays</i>)	Increase iodine concentration in shoot and grains.	Cakmak et al. 2017

Table 4 Bio-fortification of agricultural crops with beneficial elements and their role in plant growth

Author contributions Rajesh Kumar Singhal and Shah Fahad designed the study; Pawan Kumar., Prince Choyal., Talha Javed., Dinesh Jinger., Prabha Singh., Debanjana Saha. and Prathibha MD., wrote the manuscript; Bandana Bose., Akash H. and N.K. Gupta., help in diagrams. Rekha Sodani., Devanshu Dev., Dalpat Lal Suthar., Ke Liu., Matthew Tom Harrison., Adnan Noor Shah.,

Taufiq Nawaz and Shah Saud revised the manuscript; Supervision Rajesh Kumar Singhal. Ethics Approval: All authors have read and agreed to the published version of the manuscript.

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Declarations

Conflict of interest All authors declare that there is no conflict of interest.

Consent for publication Not applicable.

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