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REVIEW

Where is plant beneficial element research heading?

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Highlights

- This review summarizes the mechanisms of action of plant-beneficial elements.
- It recommends products, application methods, and the optimal concentration ranges.
- It proposes five breakthrough directions for future research on beneficial elements.

Abstract

Maintaining optimal crop nutritional levels is crucial for maximizing yield and enhancing stress resistance. In addition to the 17 essential nutrients, there are many plant-beneficial elements: silicon, aluminum, selenium, titanium, iodine, vanadium, cobalt, sodium, and rare earth elements. They are not essential for all plants, but some are crucial for specific plant species. However, the mechanisms of action of many beneficial elements are still unclear, and products containing beneficial elements have not been widely accepted and used by the public. This review systematically summarizes the current knowledge of plant-beneficial elements. Most importantly, we offer suggestions for future research on beneficial elements, which include integrating cross-disciplinary and innovative technologies, expanding the scope of application and elemental spies, broadening the spatial and temporal scales of research, incorporating beneficial elements into the soil health evaluation system, and shifting from single to multi-element applications. In the future, research on beneficial elements should be closely centered around “mechanism+application” to meet the ever-increasing demands driven by population growth, improve human health, tackle environmental challenges, and promote rural economic development.

Keywords: plant nutrients, beneficial elements, fertilizer, soil health

1. Introduction

According to the “mineral element theory” proposed by German scientists Carl Sprengel and Justus von Liebig, certain mineral elements have been identified as essential for plant growth and development (Kirkby 2023). Research over the course of nearly two centuries has consistently revealed the roles of various elements in sustaining plant growth and development, increasing yield, and enhancing plant stress tolerance (Bai 2019; Kirkby *et al.* 2023). In addition, fertilizer production based on these studies is crucial for meeting the food demands of the rapidly growing global population and for promoting rural economic development (Vitousek *et al.* 2009; Yang W *et al*. 2024). To date, 17 essential elements have been identified, including nitrogen, phosphorus, potassium, and others, which play irreplaceable roles in plant growth and development (Table 1) (Arnon and Stout 1939; Epstein 1965; Kumar *et al.* 2021; Brown *et al.* 2022; Houmani and Corpas 2024). However, as environmental issues are becoming more complex and our needs for agricultural products more diverse, exploring more elements is essential.

Certain elements, known as beneficial elements, are important for plant growth and development, but they are not necessarily essential for every plant taxon (Mittal *et al.* 2023). Beneficial elements reported to date include silicon (Si), aluminum (Al), selenium (Se), titanium (Ti), iodine (I), vanadium (V), cobalt (Co), sodium (Na), and rare earth elements (REE; a total of 17 elements, including the

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Table 1 Classification schemes of plant elements

Classification I (proposed by Arnon and Stout 1939; Epstein 1965)	Classification II (proposed by Arnon and Stout 1939; Epstein 1965)	Classification III (proposed by Brown *et al.* 2022)	Elements
Essential elements	Macroelements	Plant nutrients	C, H, O, N, P, K, Ca, Mg, S
	Microelements		Fe, Mn, Zn, Cu, Mo, B, Cl, Ni
Nonessential elements	Beneficial elements		Si, Al, Se, Ti, I, V, Co, Na, La, Ce
	Toxic elements	Non-nutrients	Cd, Pb, As, Hg, Cr(VI), some others
	Undefined elements		Cr(III), Ag, some others

lanthanide elements, scandium, and yttrium; Table 1) (Singhal *et al.* 2023). Ample evidence suggests that some of them are crucial for maintaining the growth and yield of specific plants, e.g., Si can increase rice yield and biomass by 36 and 39%, respectively (Yang X *et al.* 2024). Although the number of articles on beneficial elements in plants has been increasing year by year, research on these elements still faces several challenges.

First, other reviews on beneficial elements (Pilon-Smits *et al.* 2009; Piccolo *et al.* 2021; Khan *et al.* 2023a; Mittal *et al.* 2023; Singhal *et al.* 2023) showed that although numerous studies have consistently highlighted the roles of beneficial elements in mitigating various stresses — such as toxic metals, salinity, microplastics, organic pollutants, diseases, and pests — the underlying mechanisms often involve factors like antioxidant enzymes, photosynthesis, water and nutrient uptake, ion balance, membrane integrity, root growth, root exudates, and hormones. Many of the observed effects of beneficial elements have not yet been definitively linked to specific molecular pathways and thus may be only secondary effects resulting from changes in other plant processes (Coskun *et al.* 2019; Pang *et al.* 2024b). Second, it is essential not only to develop innovative products and application methods for beneficial elements but also to assess their feasibility, cost-effectiveness, and safety. Researchers also bear the responsibility of transforming their findings into advanced productive forces and should strive to promote the acceptance and adoption of beneficial elements by farmers and governments. Finally, we can no longer cling to traditional research methods. Achieving significant breakthroughs will require integrating innovative techniques and research concepts from other disciplines into the study of beneficial elements. Given these challenges, this review summarizes the existing knowledge and research on beneficial elements in plants, and it addresses how they benefit plants, what their mechanisms of action and associated controversies and future research directions are, and how they can be better utilized to support agricultural production, expand economic benefits, and promote human health in the future.

Table 2 provides a detailed introduction to the basic knowledge of various beneficial elements, including their abundance ranking and content in the Earth's crust, the main forms and minerals, plant transport proteins, distribution sites at the tissue and subcellular levels, materials frequently used in research, general tolerance concentrations in plants, examples of accumulating species, and the maximal concentrations in accumulating species. This information can give readers a preliminary understanding of the overall context before delving into the discussion.

2. Panacea: Evidence for the beneficial effects of diverse elements on plants

Many of the beneficial elements have impacts on physiological processes such as photosynthesis, antioxidant enzyme activities, and hormone synthesis (Pilon-Smits *et al.* 2009; Piccolo *et al.* 2021; Khan *et al.* 2023a; Mittal *et al.* 2023; Singhal *et al.* 2023). However, these general effects do not constitute a specific mechanism of action for some beneficial elements in plants and are more likely the indirect results of improved plant growth (Lyu *et al.* 2017; Piccolo *et al.* 2021). This review focuses on highlighting the direct impacts of beneficial elements identified to date (Fig. 1), rather than listing their effects on a wide range of physiological processes as in previous reviews.

2.1. Silicon (Si)

Silicon deposited in the cell wall can serve as a defensive barrier, with functions including opening the angle of leaves and keeping the leaf erect to improve photosynthetic efficiency, stabilizing cell membranes to suppress dehydration and electrolyte leakage, reducing cell heat load by mid-infrared thermal emission, resisting damage from wind, insects, and herbivores, preventing toxic metals and pathogens from entering cells, and hindering host recognition by pathogens (Wang *et al.* 2005; Coskun *et al.* 2019; Thorne *et al.* 2020; Vaculík *et al.* 2020; Pang *et al.* 2024b). Moreover, Si increases the remobilization of essential elements such as P and Fe in plants (Pavlovic *et al.* 2016; Pang *et al.* 2023b). Si partially replaces the role of lignin and reduces energy costs for plant defense (Hodson and Guppy 2022; de Tombeur *et al.* 2023). While many studies have documented changes in antioxidant enzymes and hormone levels in plants following Si application, recent evidence indicates that these effects are more likely downstream responses triggered by the defensive barrier function of Si (Coskun *et al.* 2019; Pang *et al.* 2024d).

2.2. Aluminum (Al)

Aluminum is beneficial for tea and some native tropical shrubs, which are adapted to acidic soils with low availability of macronutrients such as Ca, N, P, K, and Mg (Bojórquez-Quintal *et al.* 2017). For example, 1 mmol L^{-1} Al can promote the growth of tea roots by maintaining DNA integrity in meristematic cells, thereby enhancing the absorption of macronutrients, whereas 60 μmol L^{-1} causes stress in tomatoes (Sun *et al.* 2020; Dong *et al.* 2024). Aluminum can promote the secretion of organic acids such as malate

Table 2 Basic knowledge of beneficial elements

Elements[1)]	Abundance ranking in Earth's crust	Content in the Earth's crust	Main forms	Main minerals	Transport proteins[2)]	Distribution sites at the tissue level[3)]	Distribution sites at the subcellular level	Materials frequently used in research	Tolerance concentration of general plants	Examples of accumulating species	Maximal concentrations in accumulating species (mg kg^{-1} dry weight)	References
Si	2	28%	SiO_2, silicates, H_4SiO_4	Quartz, most rock	Lsi1, 2, 3, 6	Shoots, roots	Cell wall	H_4SiO_4, silicates, SiO_2 nanoparticles	Unreported	Rice (*Oryza sativa* L.), sorghum (*Sorghum bicolor* L.), bamboo (*Phyllostachys heterocycla* Mitf.)	100,000	Exley (2015); Zellner *et al.* (2021); Pang *et al.* (2024a)
Al	3	8%	Al^{3+}, $AlOH^{2+}$, $Al(OH)_2^+$, $Al(OH)_3$, $Al(OH)_4^-$	Aluminosilicate ore, bauxite	ALMT, MATE, AtALS3, Nrat1, NIP1;2	Roots	Cell wall	$AlCl_3$	500	Tea (*Camellia sinensis*)	13,500	Bojórquez-Quintal *et al.* (2017); Shetty *et al.* (2021)
Se	69	0.000005%	Se^{2-}, SeO_3^{2-}, SeO_4^{2-}, SeCys, SeMet	Sulfide ores	SULTR1;1, SULTR1;2, OsPT2, OsPT8, amino acid transporters	Shoots	Vacuole	Na_2SeO_4, Na_2SeO_3	2	*Stanleya pinnata*, *Cardamine hupingshanesis*, *Astragalus bisulcatus*	1,000	Quinn *et al.* (2011); Hasanuzzaman *et al.* (2020)
Ti	9	0.57%	Ti(II), Ti(III), Ti(IV)	Anatase, rutile, brookite	IRT1/FRO2 system, YS1	Roots	Cell wall	$TiCl_3$, Ti-ascorbate, TiO_2 nanoparticles	50	Horsetail (*Equisetum* spp.), Beach morning glory (*Ipomoea pescaprae* (L.) R. Br.)	578	Lyu *et al.* (2017)
I	63	0.00005%	Organic iodine, IO_3^-, I^-, I_2, CH_3I	IO_3^-, I^- (ocean)	CCC, CLC, HOL, stomata, cuticular waxes	Roots	Organelles	KI, KIO_3, organic iodine	200	Marine algae	5,939	Kato *et al.* (2013); Medrano-Macías *et al.* (2016); Zhang *et al.* (2023)
V	20	0.01%	V(II), V(III), V(IV), V(V)	Vanadium titano-magnetite	P uptake system	Roots	Cell wall	NH_4VO_3, $NaVO_3$	25	Dog's tail grass (*Setaria viridis*)	1,100	Chen *et al.* (2021); Yuan *et al.* (2022)
Co	30	0.003%	Co^{2+}, Co^{3+}	Cobaltite, smaltite, erythrite	Nramp, ZIP, HMA, FPN, IRT1, ARG1	Roots	Vacuole, cell wall	$CoCl_2$, $Co(NO_3)_2$	30	*Rinorea* cf. *bengalensis*	1,200	Lwalaba *et al.* (2017); Hu *et al.* (2021); Huang *et al.* (2024)
Na	6	2.4%	Na^+	Sodium salt	CNGCs, HKT, KUP/HAK/KT, NHX, SOS1	Shoots	Vacuole	NaCl	1,000	Sugar beet (*Beta vulgaris* L.)	30,000	Møller and Tester (2007); Kronzucker *et al.* (2013); Deinlein *et al.* (2014)

[1)] Si, Al, Na, and Ti are all among the top ten most abundant elements in the Earth's crust, whereas others such as Se and rare earth elements (REE) are relatively rare (Anjum *et al.* 2015). Iodine is mainly found in the ocean (Zhang *et al.* 2023). Many elements display multiple forms and valence states. For instance, at different pH values, the forms of Al include Al^{3+}, $AlOH^{2+}$, $Al(OH)_2^+$, $Al(OH)_3$, and $Al(OH)_4^-$ (Bojórquez-Quintal *et al.* 2017). The valencies of Ti and V range from +2 to +4, and +2 to +5, respectively (Lyu *et al.* 2017; Aihemaiti *et al.* 2020). REE typically exists as trivalent cations (RE^{3+}); however, cerium (Ce) exists with valence states of +3 and +4, and europium (Eu) with valence states of +2 and +3 (Tao *et al.* 2022).

[2)] The processes involved in the uptake of beneficial elements are divided into passive and active transport. The contribution of passive transport is influenced by element concentration in the environment, plant types, and growth conditions (Sattelmacher 2001; Exley 2015; Robe and Barberon 2023). In early research, the active transport of Si and Se by plants was discovered through metabolic inhibitors or low temperatures (Liang *et al.* 2006; Li *et al.* 2008). The chemical similarities between beneficial elements and essential elements also helps in finding transporters for beneficial elements (e.g., Se and S, Ti and Fe, and Na and K share similar transporters) (Lyu *et al.* 2017).

[3)] There are significant differences in the concentrations of beneficial elements among different species. For instance, the shoot Si concentration ranges from 0.1 to 10% in the plant kingdom (Hodson *et al.* 2005). The shoot Co concentration can reach over 1,000 mg kg^{-1} in accumulators, whereas for most plants, a concentration between 30 and 40 mg kg^{-1} is considered the threshold of toxicity (Hu *et al.* 2021). At the tissue level, Se and Na are usually accumulated in shoots, whereas Al, Ti, I, V, and Co are usually deposited in roots (Lyu *et al.* 2017; Hasanuzzaman *et al.* 2020). In rice and bamboo, the Si concentration in shoots is higher than that in roots, whereas in tomato and cucumber, the Si concentration in shoots is equivalent to or slightly lower than that in roots (Lux *et al.* 1999; 2003; Zhou J *et al.* 2022). At the subcellular level, Se, I, and Na are mainly distributed in cells, whereas Si, Al, Ti, and V are basically deposited in the cell wall.

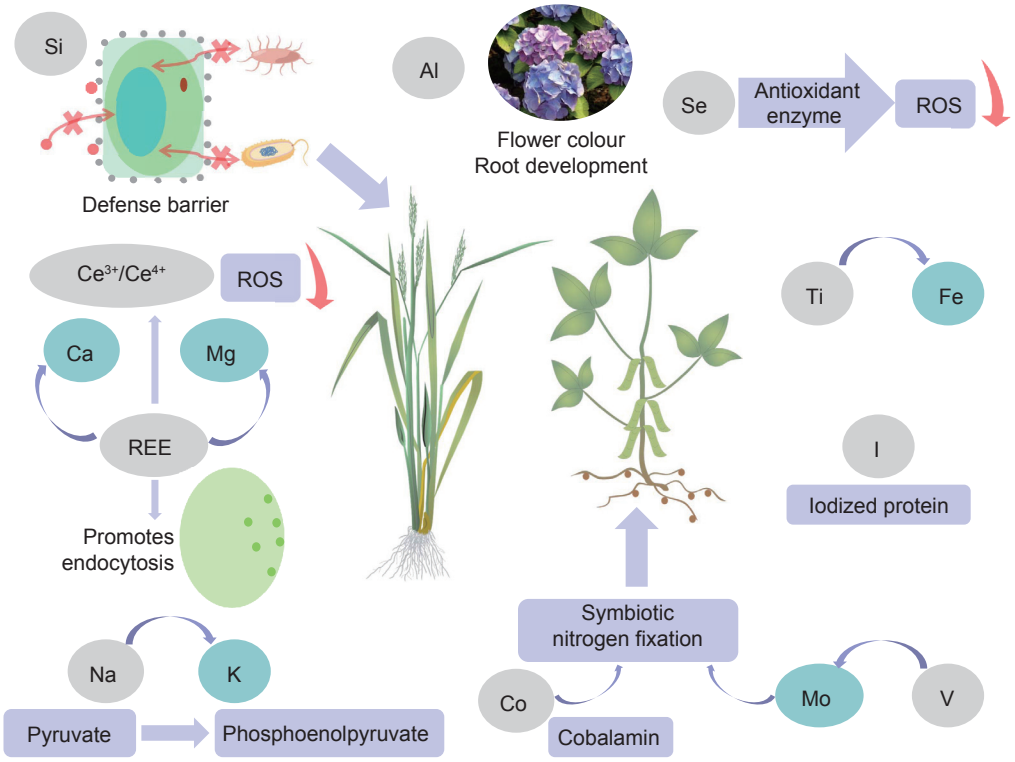


Fig. 1 Mechanism of action of beneficial elements. Beneficial elements and essential elements are represented by silver and green circles, respectively. Specifically, silicon forms a defensive barrier against biotic and abiotic stresses (Pang *et al.* 2024b); aluminum affects flower color and root growth (Bojórquez-Quintal *et al.* 2017); selenium promotes the clearance of reactive oxygen species (Hasanuzzaman *et al.* 2020); titanium alleviates iron-deficiency stress (Lyu *et al.* 2017); iodine leads to the formation of protein–iodide complexes (Riyazuddin *et al.* 2023); vanadium and cobalt enhance microbial nitrogen fixation (Harwood 2020; Hu *et al.* 2021); sodium partially replaces potassium (Kronzucker *et al.* 2013); and some rare earth elements can replace calcium and magnesium, eliminate reactive oxygen species, and promote endocytosis (Ozturk *et al.* 2023). ROS, reactive oxygen species; REE, rare earth elements.

and citrate, as well as mucilage. These substances not only increase P availability in the soil and reduce the toxicity of Fe and Mn, but also act as signaling molecules and carbon sources, which stimulate the colonization of plant growth-promoting rhizobacteria and promote biofilm formation on root surfaces (Muhammad *et al.* 2019; Ofoe *et al.* 2023). Aluminum can help control biotic stress by inhibiting the germination of pathogen hyphae and sporangia through its accumulation in leaves. Aluminum triggers localized reactive oxygen species accumulation and systemically induces the nitric oxide and salicylic acid-dependent pathways, thereby increasing gene expression and protein activity related to disease resistance (Ofoe *et al.* 2023). Al also modulates flower color. For example, in *Hydrangea macrophylla*, Al and pH are important factors that affect the color of sepals, which range from red to blue (Schreiber *et al.* 2011).

2.3. Selenium (Se)

Selenium is the active center of glutathione peroxidase in mammals, but not in plants (Do Carmo Santos *et al.* 2024). Nevertheless, the role of Se in reducing reactive oxygen species (ROS) levels has also been widely reported, which involves the antioxidant activity of Se itself and the activation of antioxidant enzymes by Se (Feng *et al.* 2013; Hasanuzzaman *et al.* 2020). In addition, Se can reduce the toxicity of toxic metals by complexing with them and promoting the production of phytochelatins (Lai *et al.* 2022). Therefore, Se has beneficial effects on cell structure and function under toxic metal stress, such as rebuilding chloroplast ultrastructure and stabilizing cell membranes (Lai *et al.* 2022). The uptake and transport of selenite and selenate in plants involves phosphate and sulfate transporters, respectively, and allows Se to regulate the absorption and utilization of P and S in plants (Ikram *et al.* 2024). Selenium also influences plant hormones such as auxins, gibberellins, ethylene, abscisic acid, cytokinins, jasmonic acid, and salicylic acid, with the specific effects varying depending on the dose (Ikram *et al.* 2024). Although Se binding proteins have been found in plants, their beneficial roles in specific physiological processes remain unclear.

2.4. Titanium (Ti)

Since Ti and Fe are transition metals with similar physical and chemical properties, the most plausible mechanism to explain the role of Ti in promoting plant growth is through its interaction with Fe. When plants experience Fe deficiency, Ti induces the expression of iron transporters, such as *IRT*, and *YS1*, to increase Fe absorption (Lyu *et al.* 2017). Iron plays crucial roles in electron transport and chlorophyll formation (Therby-Vale *et al.* 2022), and iron transporters can also transport other elements such as Zn and Mn (Guerinot 2000), which explains the beneficial effects of Ti on photosynthesis

and nutrient absorption. In addition, Ti enhances the N utilization efficiency by promoting photosynthesis, while also improving P absorption through modifications of root morphology, root exudates, and rhizosphere pH (Qi *et al.* 2024). In the future, identifying Ti-binding proteins in plants will provide a breakthrough in understanding the mechanisms of Ti's effects. In addition, TiO_2 nanoparticles exhibit photocatalytic properties and generate reactive oxygen species under light to inhibit pathogen growth and degrade organic pesticides and herbicides in the soil (Lyu *et al.* 2017).

2.5. Iodine (I)

Experiments on *Arabidopsis* showed that iodine increases biomass and leads to early flowering (Kiferle *et al.* 2021). Although numerous studies have found that I increases both enzymatic (e.g., SOD and APX) and non-enzymatic (e.g., glutathione and anthocyanins) antioxidants in plants, thereby enhancing tolerance to abiotic stress, the mechanism of its action is unknown at present (Riyazuddin *et al.* 2023). The discovery of iodinated proteins provides a potential mechanistic explanation. Given that I can bind to tyrosine and histidine, iodination has been reported in several proteins involved in the maintenance and stability of photosynthetic protein complexes, the key enzyme of glycolysis (GAPC1), several cell-wall-related proteins, and many class III peroxidases involved in redox regulation (Riyazuddin *et al.* 2023). Iodinated proteins have been identified in *Arabidopsis*, corn, tomato, and wheat. The iodinated proteins in shoots are primarily associated with chloroplasts, whereas those in roots are mainly linked to peroxidases (Kiferle *et al.* 2021).

2.6. Vanadium (V)

The tetravalent form of V is beneficial for plants by aiding in chlorophyll biosynthesis, nitrogen fixation, enhancing the uptake and accumulation of essential elements, and improving the antioxidant defense systems (Rojek *et al.* 2019; Kaur *et al.* 2023). Vanadium can act as a redox catalyst in the electron transport chains of photosystems I and II (García-Jiménez *et al.* 2018). The similarity between V and Mo allows V to function as a coenzyme factor for nitrogenase, thereby promoting microbial nitrogen fixation (Harwood 2020). In addition, V is structurally and electronically similar to P, which allows it to participate in the inhibition and activation of enzymes that interact with phosphorylated substrates like phosphatases, ATPases, and phosphotransferases (Akabayov and Akabayov 2014; García-Jiménez *et al.* 2018). Lower doses of V can also promote P uptake (Imtiaz *et al.* 2017). Moreover, there are also V-dependent haloperoxidases in algae which are responsible for the oxidation of halides and the absorption of iodine (Leblanc *et al.* 2006). However, the claim that V imparts greater tissue elasticity and positively influences cell and organelle structures lacks robust experimental evidence (García-Jiménez *et al.* 2018; Kaur *et al.* 2023).

2.7. Cobalt (Co)

Cobalt is a component of cobalamin, or vitamin B12, which is required in several N_2-fixing enzymes (methionine synthase, methyl malonyl-CoA mutase, and ribonucleotide reductase) in N_2-fixing microorganisms and some algae. Therefore, cobalt plays a vital role in Fabaceae and algae (Hu *et al.* 2021). In addition, plants also contain Co-containing proteins, as Co shares similarities with Zn, Fe, Cu, and Ni, allowing Co to partially substitute for their functions when the availability of these nutrients is limited (Jensen *et al.* 2020). Some of the Co-containing enzymes contribute to plant growth and stress resistance. For example, carbonic anhydrase enhances photosynthesis, while Co-containing peroxidase activates the antioxidant system (Hu *et al.* 2021).

2.8. Sodium (Na)

Sodium and potassium (K) are alkali metals that have similar physical and chemical properties; thus, when K is deficient, Na can partially replace K in many of its roles (Maathuis 2014). Na can activate some enzymes with high specificity for K, such as sucrose synthase (Kronzucker *et al.* 2013). However, the ATPase activity in sugar beet and Avicennia roots is activated by a combination of K and Na, rather than by K or Na alone (Subbarao *et al.* 2003). Na can also partially substitute for K in regulating stomatal opening and closure, thereby influencing gas exchange and water-use efficiency (Subbarao *et al.* 2003). Salt-tolerant plants utilize Na as an osmoticum to balance high osmotic potential and promote rapid growth, thus gaining a competitive advantage. Even when the growth medium is not deficient in K, Chenopodiaceae species such as spinach and sugar beet can benefit from Na (Kronzucker *et al.* 2013). In addition, C_4 plants require Na to promote the conversion of pyruvate into phosphoenolpyruvate and rely on the Na^+-dependent pyruvate transport system to transport pyruvate into the chloroplasts (Furumoto *et al.* 2011). Na is also involved in chlorophyll synthesis and nitrate uptake and assimilation in C_4 plants (Subbarao *et al.* 2003).

2.9. Rare earth elements (REE)

RE^{3+} can undergo displacement reactions with Ca^{2+} and Mg^{2+}, thereby affecting Ca^{2+} channels in plants and replacing Mg^{2+} at the active site of RuBisCo to enhance photosynthetic efficiency (Ozturk *et al.* 2023). REE also promotes endocytosis in plants (Wang *et al.* 2014), which impacts the acquisition and transportation of mineral elements (Cheng *et al.* 2021; Zhang *et al.* 2024). REEs can promote the synthesis of secondary metabolites such as tanshinones, taxol, crocin, phenylethanoid glycosides, alkaloids, raubasine and flavonoids, possibly by activating related enzymes (Kaur *et al.* 2024). In addition, lanthanum (La) can act as a cell cycle inducer to interfere with mitosis, inducing the formation of polyploid cells to increase plant biomass (Kaur *et al.* 2024). Due to the strong ROS scavenging abilities of Ce^{3+}/Ce^{4+} redox reactions, CeO_2 nanoparticles enhance plant stress resistance (Celardo *et al.* 2011; Wang *et al.* 2024).

3. Dispute: Beneficial but not necessary

3.1. Accumulation or exclusion

Many hypotheses have been proposed to explain why specific beneficial elements are used only in specific plants.

One hypothesis is that plants may have developed the ability to accumulate specific elements over time to adapt to environments with high concentrations of these elements. For instance, Se-accumulating plants are mainly distributed in areas with high soil Se concentrations (Cappa *et al.* 2014). However, aluminum uptake by Al-accumulating plants is independent of available soil Al concentrations (Khairil and Burslem 2018). An alternative hypothesis is that plants may gain certain advantages through the accumulation of specific elements. For example, the accumulation of Al and Se protects plants from herbivorous insects, and the toxicity of these elements inhibits colonization by pathogenic bacteria (Freeman *et al.* 2007; Bojórquez-Quintal *et al.* 2017). In addition, plants that accumulate a certain element can concentrate that element in the topsoil through litter deposition and decomposition or leaf excretion, and that element can inhibit the growth of other plants (Morris *et al.* 2009; El Mehdawi and Pilon-Smits 2012). This phenomenon differs from biochemical allelopathy and is defined as elemental allelopathy, which is believed to drive the success of many invasive weeds, including *Acroptilon repens*, *Tamarix* spp., *Halogeton glomeratus*, *Salsola iberica*, and *Mesambryenthemum crystallinum* (Morris *et al.* 2009).

Plants that utilize beneficial elements typically exhibit rapid uptake of and tolerance to these elements, whereas plants that do not utilize these elements either lack their transporters or exhibit efflux mechanisms. For example, the Si transport activities of Lsi1 and Lsi2 have been mainly identified in Poaceae and Cucurbitaceae but are often weakly active or absent in low-Si plants (Ma and Yamaji 2015; Pang *et al.* 2024b). Another example is that rice can volatilize I in the form of CH_3I, thus preventing I toxicity (Zhang *et al.* 2023).

3.2. Toxicity and plant tolerance

While beneficial elements can support the growth of certain plants, the same concentrations of these elements may be harmful to others. For instance, Al in acidic soil will inhibit the growth of calcicole plants, as characterized by damaged roots (Shetty *et al.* 2021), and Na is the primary source of salt stress in most glycophytic plants (Kronzucker *et al.* 2013). Other plant beneficial elements, such as Se, Co, and I, are crucial for human health, so there is growing interest in increasing the accumulation of these elements in the plants and obtaining them through plant-based diets (Lee and Pearce 2015; Xia *et al.* 2021; Santos *et al.* 2023). However, Se induces stress in plants at higher concentrations, with selenite being more toxic than selenate and organic Se being the safest (Hawrylak-Nowak *et al.* 2015). Selenium toxicity in plants is attributed to Se-induced oxidative stress and the formation of nonspecific selenoproteins due to its similarity to S (Hasanuzzaman *et al.* 2020). High concentrations of Co lead to a pale leaf color, discoloration of leaf veins, leaf detachment, and Fe deficiency (Hu *et al.* 2021). Likewise, high I concentrations may inhibit plant growth (Medrano-Macías *et al.* 2016). Overall, the mechanisms by which these metals and metalloids cause stress in plants mainly include 1) excessive ROS production causing oxidative injury; 2) increased osmotic pressure and cell membrane damage causing osmotic stress; 3) disruption of enzyme synthesis and activity, which disrupts metabolism; and 4) effects on hormone metabolism (Anjum *et al.* 2015).

Here, we summarize the suitable concentration ranges of beneficial elements (Fig. 2) and classify the elements into two categories: those largely tolerated by plants (plant-tolerated beneficial elements) and those for which plants are rather sensitive (plant-sensitive beneficial elements). Beneficial concentrations of elements such as Si, Al, and Na are at millimolar levels (Epstein 1999; Fung *et al.* 2008; Exley 2015; Fang *et al.* 2017; Pang *et al.* 2023a), indicating that plants generally exhibit high tolerance to these elements. In contrast, the beneficial concentrations of Ti, V, Co, I, and Se are mostly at micromolar levels (Wallace *et al.* 1977; Tewari *et al.* 2002; Chatterjee *et al.* 2006; Hawrylak-Nowak *et al.* 2015; García-Jiménez *et al.* 2018; Incrocci *et al.* 2019), suggesting that plants are extremely sensitive to these elements and only a slight increase in the concentration may inhibit plant growth. However, there are currently two issues with the information in Fig. 2: First, the number of species investigated is rather limited; and second, only a hydroponic environment has been investigated. To better serve the needs of agricultural production, future studies need to determine the optimal ranges of beneficial elements in different soils and using different plants.

4. Application: Products and technologies serving agriculture

4.1. Product type

On one hand, the growing global population demands an adequate, nutritious, and safe food supply; on the other hand, crops are experiencing various forms of stress due to climate change and environmental pollution. Beneficial elements excel in promoting plant growth and enhancing stress resistance, and they can be transferred to the human body through the food chain (Khan *et al.* 2023a). However, over the past century, intensive farming practices, the excessive use of inorganic fertilizers, yield-driven dilution effects, and climate change have collectively caused a sharp decline in essential trace element concentrations in agricultural products (Marles 2017; Zhu *et al.* 2018). Some beneficial elements may also follow a similar trend. In addition, although some beneficial elements can be abundant in soil systems — such as silicon, which is the second most abundant element in the Earth's crust — their accessibility for plants is limited (Thakral *et al.* 2024). One study estimated that five consecutive rounds of rice cultivation will deplete most of the available Si in the soil (Liang *et al.* 2015). By 2030, the market for beneficial elements in agriculture is expected to grow to $8.21 billion, with an annual growth rate of approximately 11% (Trejo-Téllez and Gómez-Merino 2023).

Most beneficial elements are obtained from rocks and minerals by smelting (Pang *et al.* 2024b). Due to the growing scarcity of mineral resources, waste products from coal mining, metallurgy, and chemical industries are increasingly being repurposed as fertilizers. This approach is more economical and environmentally friendly, with steel slag-based Si fertilizer serving as a notable example (Das *et al.*

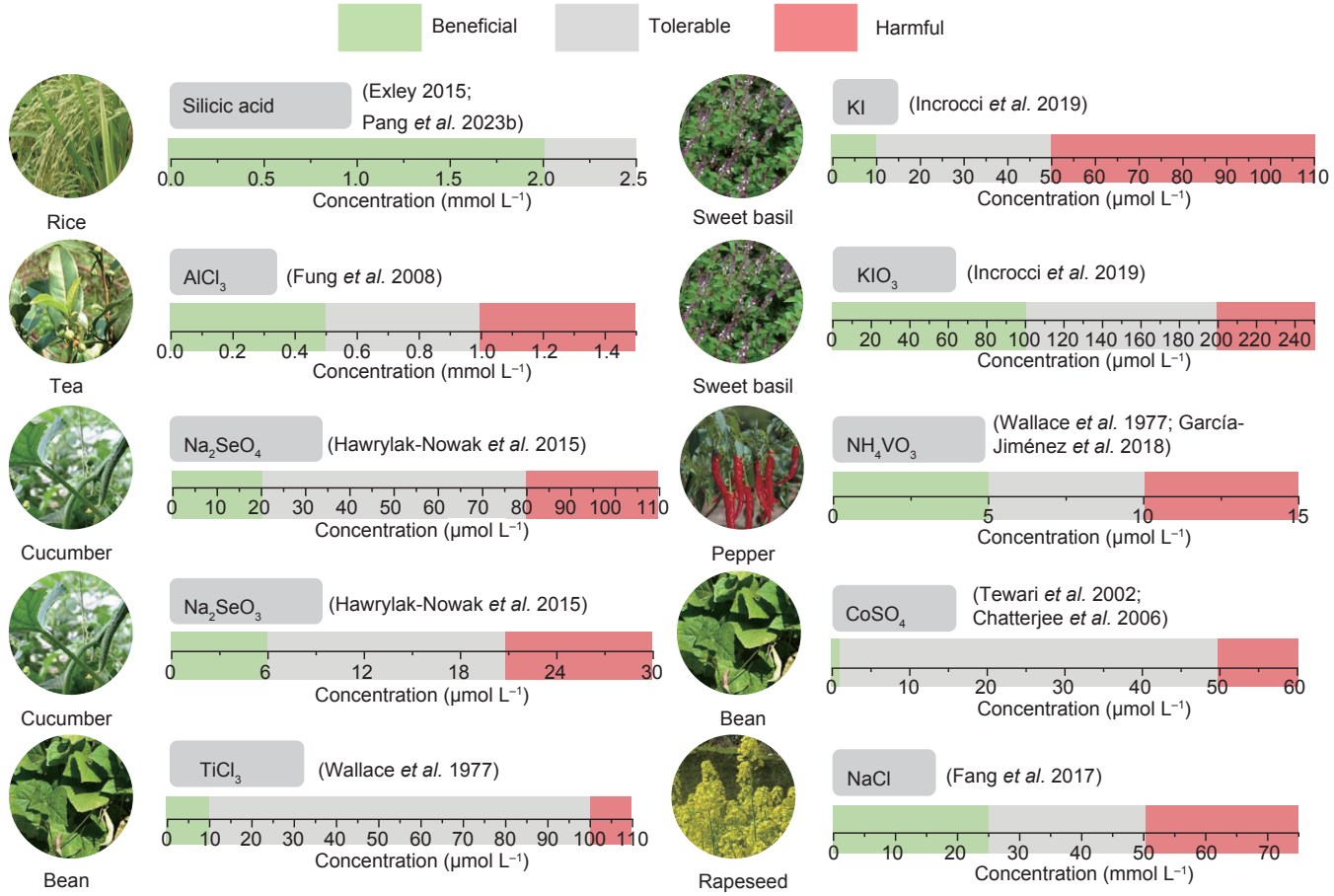


Fig. 2 Suitable range of beneficial elements (in nutrient solution). Green, gray, and red represent the beneficial, tolerated, and harmful concentration ranges, respectively. In addition, the figure shows the tested plant species, the elemental forms used, and the references. The beneficial concentrations of Si, Al, and Na are in the millimolar range, and they are defined as the plant-tolerated beneficial elements. The beneficial concentrations of Ti, V, Co, I, and Se are mostly at the micromolar level, and they are defined as the plant-sensitive beneficial elements.

2022). Given that Poaceae and diatoms accumulate Si, both can be used to produce plant-sourced Si fertilizers (Pang *et al.* 2024b). Similarly, algae can be applied as a source of I for plants (Medrano-Macías *et al.* 2016). Nanomaterials have received increasing attention because of their unique properties, such as high surface area, high adhesion ability, and ability to control release (Grillo *et al.* 2021). For example, Se, Si, and Ce nanoparticles exhibit more pronounced effects on plant growth and development than their bulk forms (Mukarram *et al.* 2022; Khan *et al.* 2023b; Wang *et al.* 2024). In addition, microbial fertilizers can be used to mobilize the beneficial elements in soil, while reducing the demand for chemical fertilizers and protecting the environment (Raza *et al.* 2023).

4.2. Application technology

The traditional application methods of beneficial element products have primarily included seed soaking, root dipping, soil application, and foliar spraying. In recent years, a novel technology known as phytoinjection has emerged (Cao *et al.* 2020, 2023). The advantages and disadvantages of these methods are detailed in Table 3. The application of beneficial elements should be closely related to their mechanisms of action and action locations. For example, Co primarily functions at the root level, making soilv application more effective compared with foliar spraying. Conversely, I is more readily utilized by leaves, making foliar spraying a more suitable method (Medrano-Macías *et al.* 2016). When Si is employed to counteract the effects of toxic metals in soil by inhibiting transfer to the shoot, its application through the soil gives better results (Pang *et al.* 2024b, 2025a). However, when Si is used to resist pathogens and insects on leaves or to minimize the transfer of toxins to seeds, foliar sprays are more effective (Guo *et al.* 2022). The application of beneficial elements also requires selecting the appropriate periods according to the crop's needs. In rice, approximately 66% of Si accumulates during the reproductive stage; therefore, a sufficient Si supply is crucial during this period (Pang *et al.* 2024b). Overall, the key to enhancing fertilizer efficiency is to comprehensively analyze the demand for beneficial elements at different growth stages of crops and achieve timely fertilization. In addition, it is important to ensure that new products and technologies are not limited to the laboratory but are promoted for use in agricultural practice. In addition to assessing their effects on yield enhancement and stress resistance, the following factors should also be considered:

Table 3 Application technologies of beneficial elements

Application technology	Advantages	Disadvantages
Seed soaking/ Root dipping	Easy to operate, no impact on soil	Effect is limited to the early stages of growth
Soil application	Convenient, does not require fertilizers to be fully soluble	Cause soil pollution; disrupt soil microbial communities; harm soil health
Foliar spraying	Direct absorption through stomata and cuticular channels; less soil disturbance; precise application of expensive elements	Cannot be sprayed onto all plants; easily washed away by rainwater; easily blocked by the cuticle and epidermis
Phytoinjection	Direct delivery to deep plant tissues	High cost; difficult operation

the feasibility of industrial-scale production and transport, potential ecological risks and health threats, and affordability and operability for farmers.

5. Future: Disciplined innovation and sustainable development

5.1. Embracing interdisciplinary and innovative technologies

Beneficial elements can be investigated from both the spatial (more precise observations and identification) and molecular (more specific genes and pathways) dimensions. Spatial dimensions involve studying the distribution and morphology of beneficial elements at the organ, tissue, and subcellular levels, whereas molecular dimensions involve identifying the molecular mechanisms of uptake, transport, complexation, metabolic regulation of beneficial elements, and interactions between beneficial elements, plants, and microorganisms. Interdisciplinary approaches that link research on beneficial elements with new technologies and methods are urgently needed.

Spatial dimension Beneficial elements can be visualized in plants using methods based on X-ray fluorescence or mass spectrometry (Fig. 3). These technologies differ in the range of analyzable elements, detection limits, quantitative capabilities, resolution, and sample pretreatment requirements (Table 4). In addition to focusing on observing element distribution at the organ and cellular levels in detail, we can also take a broader view in analyzing the element concentrations in crops across the entire field. The use of unmanned aerial vehicle multispectral remote sensing, combined with multiple linear regression, artificial neural networks, extreme learning machines, support vector machines, and random forests, can help to establish correlations between element concentrations and crop morphology, structure, and leaf color, thereby facilitating the rapid diagnosis of crop nutritional status (Peng *et al.* 2022). However, the current research effort on beneficial elements within this technology remains insufficient (Oivukkamäki *et al.* 2023).

Molecular dimension Technological innovation facilitates studies on the absorption and transport processes of beneficial elements, interactions among elements, mechanisms of action, and plant tolerance mechanisms. It also informs the development of breeding strategies to enhance the utilization efficiency of beneficial elements and reduce the accumulation of toxic elements.

The similarities in physical and chemical properties among different elements can be utilized in some areas of research (Fig. 4-A). For example, due to the similarity in structure between arsenite and silicate, arsenite may be unintentionally absorbed by the Si-uptake pathway in rice roots (Ma *et al.* 2008). Based on this, researchers constructed a knockout mutant of the rice silicon uptake gene (*Lsi2*) using CRISPR-Cas9 technology. The experimental results showed that As accumulation in the grains of this mutant rice was reduced, which strongly confirmed the above-mentioned absorption correlation (Xu *et al.* 2024). By integrating evidence from chemistry, soil science, mineralogy, and plant biology, researchers have made significant progress in understanding the interactions between beneficial elements and essential elements. For instance, Si has been found to enhance N uptake in plants under a suboptimal N supply through mechanisms such as promoting biological N fixation, increasing soil N availability, and upregulating the genes involved in N absorption and transport (Pavlovic *et al.* 2021). Si also helps plants cope with P deficiency by improving root P uptake and mobilizing internal P for reuse (Pavlovic *et al.* 2021; Pang *et al.* 2023b). In addition, Si regulates Fe homeostasis by influencing Fe availability in the rhizosphere and root apoplast, as well as modulating the expression of genes involved in Fe transport (Pavlovic *et al.* 2021). Furthermore, Ti, Co, and Na have been shown to aid N uptake, while Al, Ti, and V promote P absorption (see Section 2 for details).

In recent years, many studies have used synchrotron radiation to analyze the crystal structures of plant proteins. For example, the unique structure of Lsi1 was characterized by a hydrophilic selectivity filter composed of five residues, which provides a structural basis for its high selectivity in Si absorption (Fig. 4-B) (Saitoh *et al.* 2021). Similarly, the use of autoradiography to study the binding of elements and proteins provides direct evidence for the roles of various elements in plant physiological processes. For example, I is a structural component of several proteins, and conserved iodized proteins are synthesized in the roots and stems of phylogenetically distant species (Fig. 4-C) (Kiferle *et al.* 2021).

Two genetic approaches of forward genetics and reverse genetics have emerged as the most crucial means for studying the genes involved in plant element uptake or tolerance. In forward genetics approaches, researchers first induce mutations in genes (using methods such as chemical mutagenesis, radiation mutagenesis, or natural mutagenesis), and then identify the altered traits, locate the mutated genes,

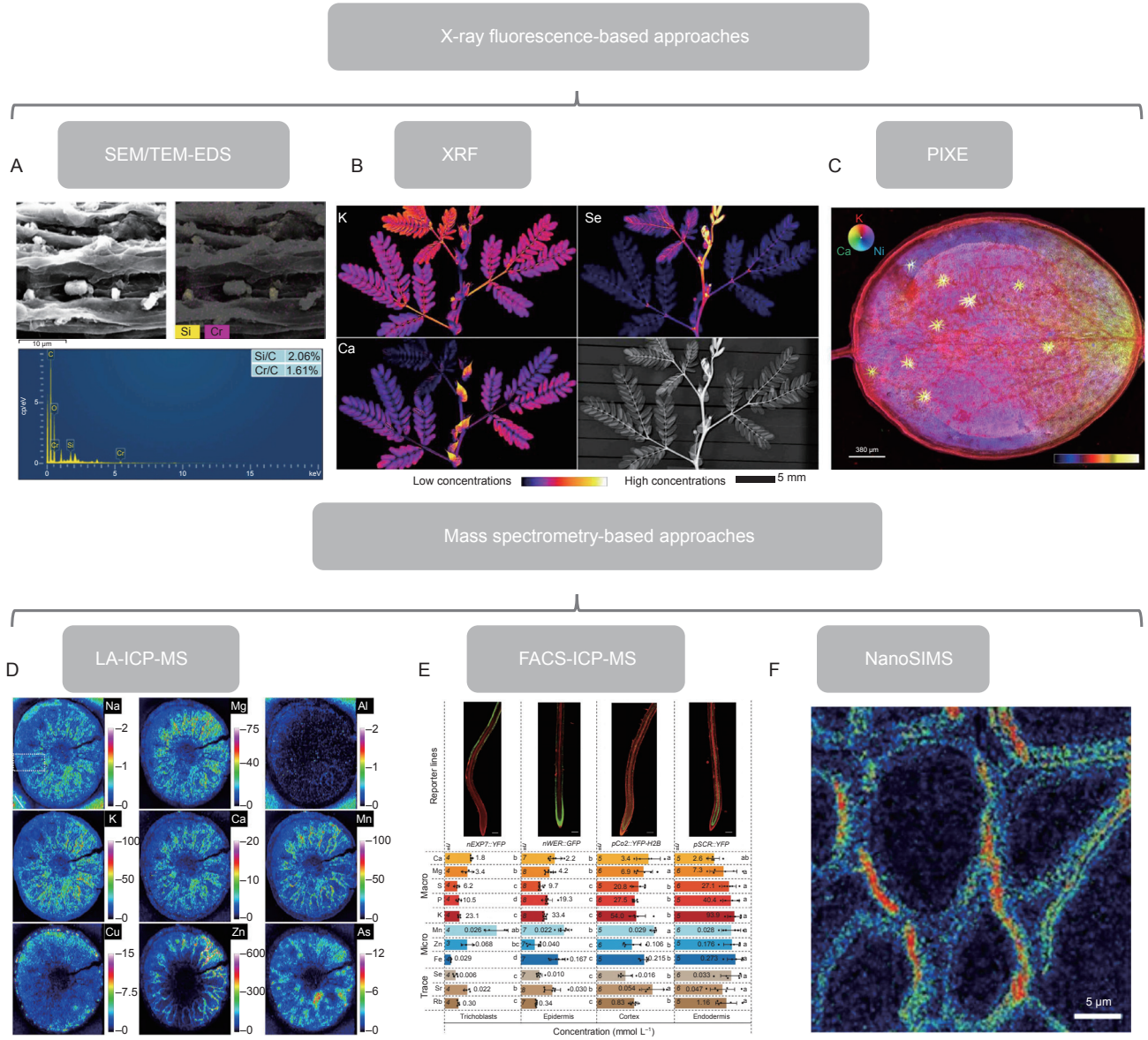


Fig. 3 Techniques for studying beneficial elements in spatial dimensions. A–C, case studies using X-ray fluorescence-based approaches, including using scanning electron microscopy-based energy-dispersive X-ray spectroscopy (SEM-EDS) to study the distribution and concentrations of silicon (Si) and chromium (Cr) in rice root tips (A) (Pang *et al.* 2024a), using X-ray fluorescence spectrometer (XRF) to observe the distributions of potassium (K), calcium (Ca), and selenium (Se) in a fresh hydrated shoot of the Se hyperaccumulator *Neptunia amplexicaulis* (B) (Kopittke *et al.* 2020), and using particle-induced X-ray emission (PIXE) to study the distributions of K, Ca, and nickel (Ni) of an *Alyssum murale* seed capsule (C) (Laird *et al.* 2019). D–F, case studies using mass spectrometry-based approaches, including using laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) to map multielement imaging in rice nodes (D) (Yamaji and Ma 2019), using fluorescence-activated cell sorting–inductively coupled plasma mass spectrometry (FACS-ICP-MS) to map the element distribution of different types of cells in *Arabidopsis thaliana* roots (E) (Giehl *et al.* 2023), and using nanoscale secondary ion mass spectroscopy (NanoSIMS) for studying Si distribution in blast fibers of textile hemp (*Cannabis sativa*) (F) (Guerriero *et al.* 2020).

and ultimately identify their functions (Peters *et al.* 2003; Aklilu 2021). Then, a genetic linkage map, bulk segregation analysis (BSA), or genome-wide association study (GWAS) can be used to identify the locations of the mutations (Zhou *et al.* 2018; Alqudah *et al.* 2020). For example, several rice mutants lacking Si absorption and transport functions in the plants were obtained through mutagenesis (Ma *et al.* 2002, 2007). Some studies have used GWAS to identify novel genes associated with plant Na and Al tolerance (Fig. 4-D) (Zhou J *et al.* 2022; Yu *et al.* 2023). In addition, plant materials with differential traits can also be derived from libraries constructed by T-DNA insertion and transposon or retrotransposon labeling (Wang *et al.* 2013). Because of the known tag sequences, the mutation locations are easily identified during this process. After target gene identification, a target gene mutant can be constructed using CRISPR-Cas9 technology to validate phenotypic differences, subcellular localization can be performed using laser confocal microscopy or fluorescence microscopy, the protein can be expressed and purified *in vitro* using *E. coli* or yeast, and protein interactions can be studied using immunoprecipitation and yeast hybridization techniques. The process of determining

Table 4 Element visualization technologies

Approach	Principle	Specific technology	Characteristics
X-ray fluorescence-based approaches	Using incident electrons, high-energy X-rays, or protons to scan the sample and excite a series of different elements, the concentration of elements is determined by measuring the characteristic fluorescent X-rays emitted from the sample (Kopittke *et al.* 2020; van der Ent *et al.* 2020)	SEM/TEM-EDS	Requires high vacuum, sample dehydration, and carbon coating; suitable for high-concentration elements (detection limit: 0.1–1.0%)
		XRF	Non-destructive, minimal sample preparation, and capable of analyzing entire plant tissues; synchrotron-based XRF offers sub-μm resolution (Blamey *et al.* 2018; Kopittke *et al.* 2020).
		PIXE	Provides 1–3 μm resolution and can analyze a wider range of elements than XRF (Laird *et al.* 2019)
Mass spectrometry-based approaches	By ionizing atoms or molecules in the sample, they are then separated and detected based on their mass-to-charge ratios (m/z)	LA-ICP-MS/ FACS-ICP-MS	Ideal for high-sensitivity studies, such as elemental distribution in different cell types (Giehl *et al.* 2023)
		NanoSIMS	Limited availability and accessibility. Provides exceptional spatial resolution (50 nm) and detection limits (<1 ppm), making it suitable for subcellular-level analysis of elements (Moore *et al.* 2011; Guerriero *et al.* 2020; Mandel *et al.* 2022)

plant Al tolerance genes is a good example of using a whole set of experiments to ensure the reliability of the results (Fig. 4-E) (Yamaji *et al.* 2009; Kochian *et al.* 2015; Zhou *et al.* 2023; Xu *et al.* 2025). In contrast, reverse genetics involves the use of known genomic sequence information from omics studies to knock out/interfere with/overexpress target genes through molecular biological methods and identify the corresponding phenotypic traits (Peters *et al.* 2003; Aklilu 2021). For example, researchers used RNA-seq to compare differentially expressed genes in Al-tolerant and -sensitive plants under Al stress to identify potential Al tolerance genes (Zhou H W *et al.* 2022).

Besides transporters, endocytosis is another way in which plants obtain nutrients (Cheng *et al.* 2021; Zhang *et al.* 2024). Using fluorescence labeling and confocal laser scanning microscopy, arabinogalactan proteins (AGPs) were found to act as extracellular cargo receptors that move across the plasma membrane to initiate endocytosis and REE promotes the cross-membrane translocation of AGPs to activate endocytosis (Fig. 4-F) (Wang *et al.* 2019).

The root-associated microbiome has been recognized as the “second genome” of plants, and it contributes to plant health (Berendsen *et al.* 2012). Many beneficial elements, such as Co and vanadium (V), promote plant growth by affecting the soil microorganisms that play a role in symbiotic N_2 fixation (see Section 2.2 for details). In addition, sequencing techniques such as 16S, Internal Transcribed Spacer (ITS), and metagenomic sequencing as well as data analysis techniques such as principal component analysis and structural equation modeling have helped reveal the correlations between essential trace elements and soil microorganisms (abundance, diversity, and function) (Dai *et al.* 2023). In addition, some *in situ* detection techniques can also be used to analyze the interactions between elements, plants, and microorganisms at the soil-root interface. A combination of the diffusive gradients in the thin films technique (DGT) with membrane analysis techniques (such as glue-cutting analysis, computer/colorimetric imaging densitometry, and LA-ICP-MS) can be used to monitor changes in soil properties and element spatial distributions caused by plants and microorganisms (Guan *et al.* 2022). There is also an emerging microfluidic technology that grows roots in the root chambers of microfluidics devices (Massalha *et al.* 2017). Subsequently, researchers can introduce microorganisms into the root chamber and use various techniques for imaging, such as dark-field and confocal microscopy. This technology not only enables high-resolution cell imaging, but also dynamically depicts the spatial and temporal interactions of elements, microorganisms, and roots (Dai *et al.* 2024).

Technological progress in materials science has also stimulated the development of beneficial element products with new functionalities. Due to the spontaneous fluorescence properties of some REE such as europium (Eu), doping Eu into microplastics can allow the quantitative tracing of microplastic uptake and transport in plants (Luo *et al.* 2022). In addition, many newly developed nanofertilizers which contain beneficial elements exhibit characteristics that are different from conventional fertilizers in terms of promoting plant growth and stress resistance. For example, mesoporous Si nanoparticles can be used as a green and efficient fungicide to control potato late blight by inducing intracellular peroxidation damage (Fig. 4-G) (Chen *et al.* 2023). Identifying the absorption, effects, and mechanisms of beneficial elements at the nanoscale is one of the hotspots for future research (Mukarram *et al.* 2022).

5.2. Expanding the application scope and element types

Excluding certain elements from nutrient solutions during cultivation helps to distinguish between essential and nonessential elements (Kirkby 2023). However, several factors may affect such assessments. For example, limitations in filtering technology make it difficult to completely remove certain elements from the environment; and similarly, due to the limitations in detection technologies, elements that do not exceed the detection threshold cannot be detected (Welch and Shuman 1995; Kirkby 2023). In addition, the narrow definition of essential elements in the past has prevented many beneficial elements from being legally referred to, marketed, or sold as plant nutrients. Brown *et al.* (2022) proposed an expanded definition of plant nutrients,

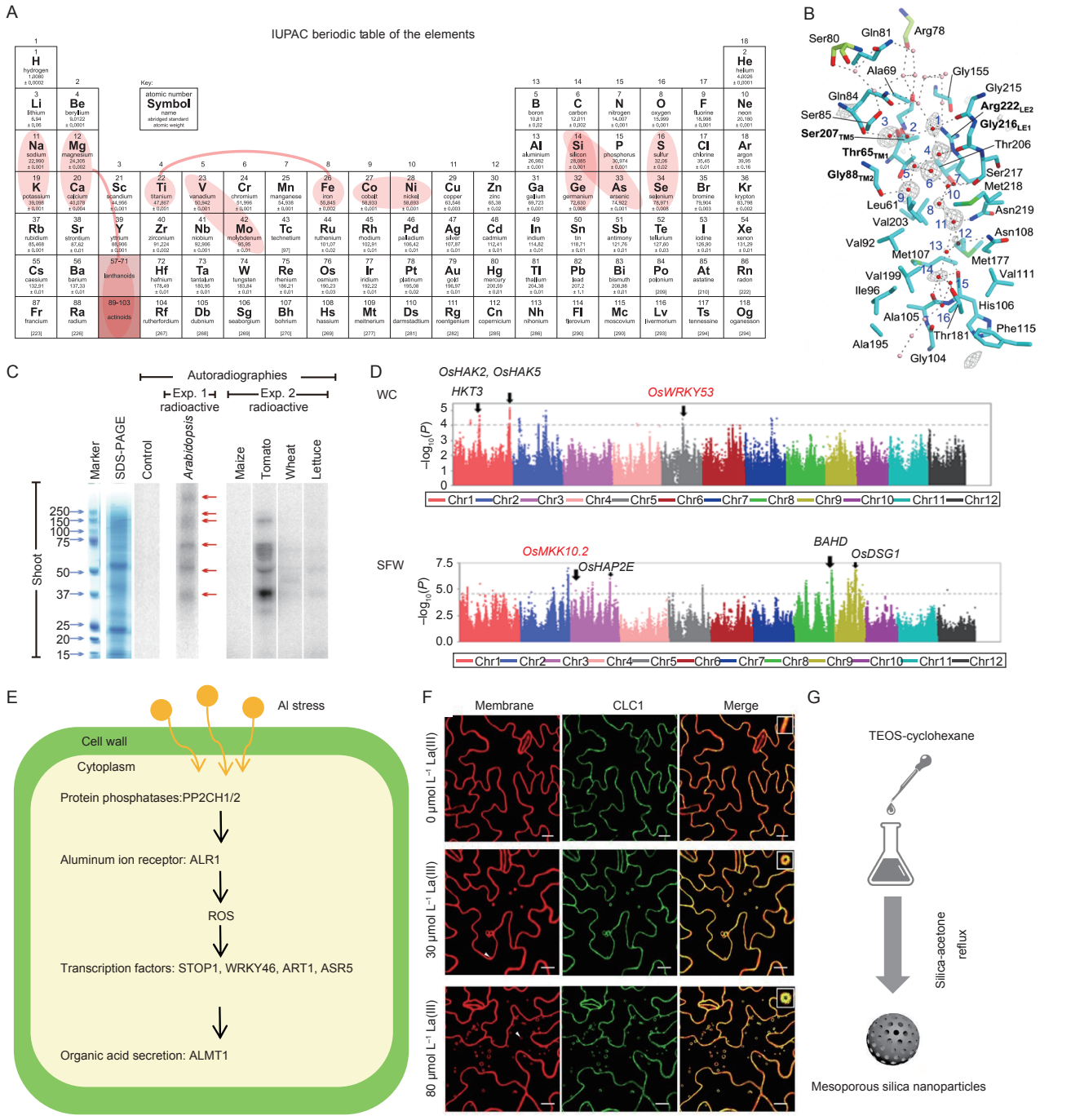


Fig. 4 Techniques for studying beneficial elements in the molecular dimension. A, using similarities in the properties of different elements to study the element absorption pathways and mechanisms of action (Lyu *et al.* 2017), for example, silicon (Si) and arsenic (As), Si and germanium (Ge), titanium (Ti) and iron (Fe), sodium (Na) and potassium (K), selenium (Se) and sulfur (S), and cobalt (Co) and nickel (Ni). B, using synchrotron radiation to analyze the structure of the Si transporter Lsi1 (Saitoh *et al.* 2021). C, presence of iodinated proteins in plants demonstrated using radiolabeled ^{125}Iodine (Kiferle *et al.* 2021). D, candidate genes related to salt tolerance traits identified through a genome-wide association study (Yu *et al.* 2023). E, model illustrating putative aluminum (Al)-mediated signaling pathways involved in the perception and triggering of Al stress and resistance responses in roots (Kochian *et al.* 2015; Xu *et al.* 2025). F, observing the endocytosis of lanthanum (La) in cells using fluorescence labeling and confocal laser scanning microscopy (Wang *et al.* 2019). G, using material science methods to create new mesoporous silica nanoparticles that can induce intracellular peroxidation damage in *Phytophthora infestans* (Chen *et al.* 2023).

stating that “elements that are essential or beneficial for plant growth and development, or for the quality attributes of the plant or harvested product of a given plant species grown in its natural or managed environment, can be considered plant mineral nutrients”. In the future, with the upgrading of filtering and detection technologies, we can use this concept to evaluate the existing beneficial elements, undefined elements, and harmful elements.

Many beneficial elements affect only a few specific plants or accumulate in only a few plant species. If technological

means can be used to facilitate the accumulation of beneficial elements in more plants, it will greatly expand the application range of beneficial elements and contribute to human nutritional intake. For example, methods have been developed that allow low-Si plants to quickly establish Si-based defensive barriers in the roots, allowing these plants to use Si to resist stress like high-Si plants (Pang *et al.* 2024c). In addition, considering the important roles of Se and I in human health, many breakthroughs have been made in increasing their accumulation in the edible parts of plants (White 2016; Zhang *et al.* 2023).

With industrialization in the Anthropocene, crops now encounter certain elements that were previously absent or present only at low levels in field soils (Anjum *et al.* 2015). There is still a lack of research on the effects of many of these elements on plants (referred to as undefined elements) which complicates the assessment and timely management of their effects and potential hazards. For example, germanium (Ge) has not been characterized as an essential element for any organism or as a highly-toxic element in the environment; thus, considerably less attention has been paid to this element (Wiche *et al.* 2018). Studies have reported its positive effects on growth, the regulation of antioxidant enzyme activities, and resistance to strong light and salt stress (Wang *et al.* 2018). However, Ge can also cause toxic symptoms (such as characteristic brown spots on leaves) in Si accumulating species such as rice. Using this characteristic and the similarity between Ge and Si, researchers successfully identified rice mutants with defects in Si transporters (Ma *et al.* 2002). Due to the promising effects of Ge in anticancer treatments and free radical scavenging, we anticipate that Ge can accumulate in plants and be transferred to humans through the food chain (Menchikov and Popov 2023). In addition, chromium (Cr) is a toxic metal with various valence states. Hexavalent Cr is toxic to both plants and humans, but trivalent Cr has beneficial effects on human health, including promoting insulin synthesis and maintaining blood sugar levels (Ao *et al.* 2022). Another example is silver (Ag). Although Ag nanoparticles have attracted attention as a novel nutrient and growth promoter, controversy over whether they are beneficial or harmful remains (Siddiqi and Husen 2022). Therefore, elucidating the processes of uptake, transport, and morphological transformation of undefined elements such as Ge, Cr, and Ag in plants, identifying the appropriate concentrations for their beneficial effects, improving plant tolerance, and regulating plant accumulation ability are crucial for better utilizing and managing these elements.

Many elements that were previously considered toxic should be reassessed, as they may have beneficial effects in specific scenarios. For example, cadmium (Cd) and arsenic (As) are considered harmful in most plants. However, researchers have also reported beneficial effects of Cd on resistance to aphids, powdery mildew, and high-temperature stress in *Sedum alfredii* (Xu *et al.* 2023), and As on promoting the enrichment of key diazotrophs in the rhizosphere, and growth and resistance to natural enemies in *Pteris vittata* (Zhao *et al.* 2023; Lin *et al.* 2024). Studying the mechanisms of action of these elements in specific plant species has important practical application value for metal mining and soil remediation (Rylott and Bruce 2022; Pang *et al.* 2025c).

5.3. Expanding the spatial and temporal scales of research

Most studies on beneficial elements are performed in the laboratory or in the field, but there is a lack of research on beneficial elements on large spatial and temporal scales (Liang *et al.* 2015). Researchers need to explore the geographical distributions and evolutionary histories of plants with different potentials for utilizing beneficial elements to uncover the correlations between environmental factors (such as soil and climate) and the utilization of beneficial elements by plants. For example, in the field of microbiology, researchers have identified the relationship between the molecular mechanism of As tolerance in microorganisms and the Earth's great oxygenation event by tracing its evolutionary history (Chen *et al.* 2020). In the field of botany, phylogenomic and paleontological evidence suggest that the evolution of plant traits such as stomata, plant height, seed size, seed number, and N and P concentrations is closely associated with historical climate change events (Clark *et al.* 2022; Joswig *et al.* 2022). The field of beneficial elements has also made some progress. For example, using field sampling and controlled experiments, researchers found a positive correlation between leaf Si concentration and temperature (Brightly *et al.* 2020; Pang *et al.* 2025b). Given that Si deposition in cell walls can enhance plant resistance to high temperatures by blocking thermal radiation (Wang *et al.* 2005; Wang *et al.* 2010), a connection between the Earth's historical temperatures and plant silicification is plausible (Pang *et al.* 2025b). Based on various lines of evidence, we propose a putative model for the interaction between plant silicification, carbon cycling, and the Earth's temperature on extensive spatial and temporal scales (Fig. 5). Specifically, the increase in atmospheric CO_2 leads to global warming. Global warming may promote the emergence and expansion of high-Si plants. High-Si plants can promote the weathering of silicates by absorbing H_4SiO_4 from the soil. The cations released by silicate weathering fix CO_2 in the form of carbonates and promote a reduction in temperature. Although some connections in this model require further evidence, it serves as a valuable framework for advancing research on beneficial elements.

5.4. Incorporating beneficial elements into the soil health evaluation system

The evaluation of soil health, which refers to the soil's ability to support the growth of plants, animals, and humans and continuously perform ecosystem functions, is currently receiving widespread attention from the government, scientific community, and public (Guan *et al.* 2023). Most beneficial elements exhibit closed biogeochemical cycles and do not return to the soil unless applied as amendments or fertilizers. Continuous farming and harvesting over many years may deplete the plant-available beneficial elements in the soil (Sharma *et al.* 2023). Therefore, incorporating beneficial elements into the soil health evaluation system is crucial for encouraging farmers and governments to

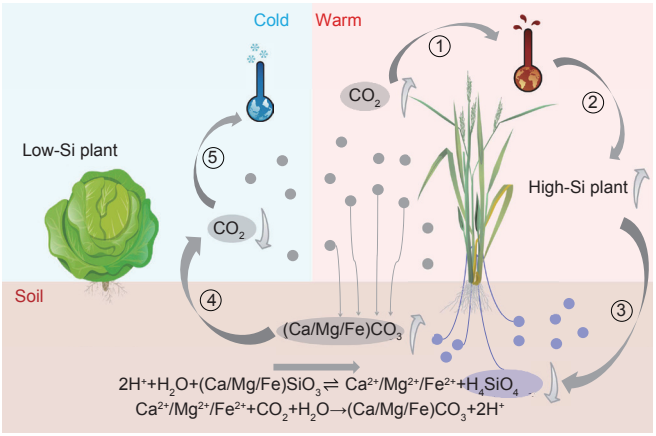


Fig. 5 Putative model describing the coupling of plant silicification and the Earth's carbon cycles. The reaction equations at the bottom of the figure represent the process for CO_2 reacting with silicates (Batool *et al.* 2024). ① The increase in the atmospheric CO_2 concentration leads to global warming. ② The increase in temperature promotes the emergence and expansion of high-Si plants. ③ High-Si plants absorb more H_4SiO_4 from the soil than low-Si plants, promoting the weathering of silicates. ④ The cations released by silicate weathering fix CO_2 in the form of carbonates. ⑤ The decrease in the atmospheric CO_2 concentration reduces global temperatures.

accept beneficial element fertilizers and guiding timely and rational fertilization. Although current soil health assessment methods, such as soil health cards (Purakayastha *et al.* 2019), Solvita soil health tests (Chahal *et al.* 2021), Haney soil health tests (Haney *et al.* 2008), and comprehensive assessments of soil health (Fine *et al.* 2017), consistently prioritize soil nutrients as the most crucial indicator, they often overlook the beneficial elements (Guo 2021). This exclusion arises not only from an underestimation of their significance but also from the challenges in determining their optimal concentrations.

Healthy soils should contain the appropriate crop-specific effective concentrations of beneficial elements which are defined as *c*. The actual concentrations of beneficial elements in the soil can be denoted as *ρ*. The difference between *c* and *ρ* can be used to determine the health status of the beneficial elements in the soil. Fig. 6 shows a potential method for incorporating beneficial elements in the soil health evaluation system, and the higher the final score, the healthier the soil. Therefore, the key task for the future is to establish the *c* of various beneficial elements in different soil types. This can be achieved through methods such as chemical extraction (e.g., 0.001–0.01 mol L^{-1} $CaCl_2$ and 0.05 mol L^{-1} EDTA), *in situ* measurements (e.g., the diffusion gradient in thin films technique and the Donnan membrane technique), model simulations (e.g., Visual MINTEQ), and plant experiments (Kim *et al.* 2015). In addition, the Beneficial Element Health Value (BEHV) needs to be graded. Specifically, if the value is above a certain level, the soil can be considered healthy; if the value is below that level, the soil is considered to require additional attention.

5.5. Shifting from single to combined applications of beneficial elements

In agriculture, 75% of all fertilizers used are complexes of compounds or blends of compounds containing multiple elements (Finch *et al.* 2014). However, current research on the effects and mechanisms of beneficial element interactions remains inadequate. Some combinations of beneficial elements may be more effective than the individual elements in promoting plant growth and enhancing stress resistance. For instance, the synergy between Si and Se enhances rice yield and affects dry weight accumulation, antioxidant properties, and quality characteristics, whereas Si facilitates Se uptake and mitigates Se-induced lodging (Liu *et al.* 2020). In addition, the combination of Si and Se has a highly synergistic effect in helping plants resist salt and toxic metal stress (Huang *et al.* 2021; Xu *et al.* 2021). Similarly, the combined application of Se and I inhibits nitrate accumulation in mustard, activates flavonoid synthesis, and reduces strontium (Sr) and Cd accumulation (Golubkina *et al.* 2018). Future studies should identify the optimal combinations of beneficial elements to highlight their synergistic effects, reduce fertilizer dosages, and prevent them from interfering with each other in a way that weakens their individual effects. In addition, the mechanisms of element interactions within plants should also be explored.

6. Conclusion

The accumulated evidence from agricultural production and scientific research indicates that beneficial elements have significant implications for plant growth and stress resistance. We suggest that future research on beneficial elements should closely follow the "mechanism+application" framework. On the one hand, we need to identify more beneficial elements and reveal their mechanisms of action by adopting multidisciplinary approaches and expanding research in terms of temporal and spatial scales. On the other hand, it is necessary to accelerate the inclusion of beneficial elements in the evaluation system of soil health, design more combination strategies, and develop environmentally friendly, multifunctional, and cost-effective products to encourage farmers and governments to accept and use beneficial elements.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

Declaration of generative AI and AI-assisted technologies in the writing process

The authors declare that they did not use AI in the preparation and writing of this manuscript.

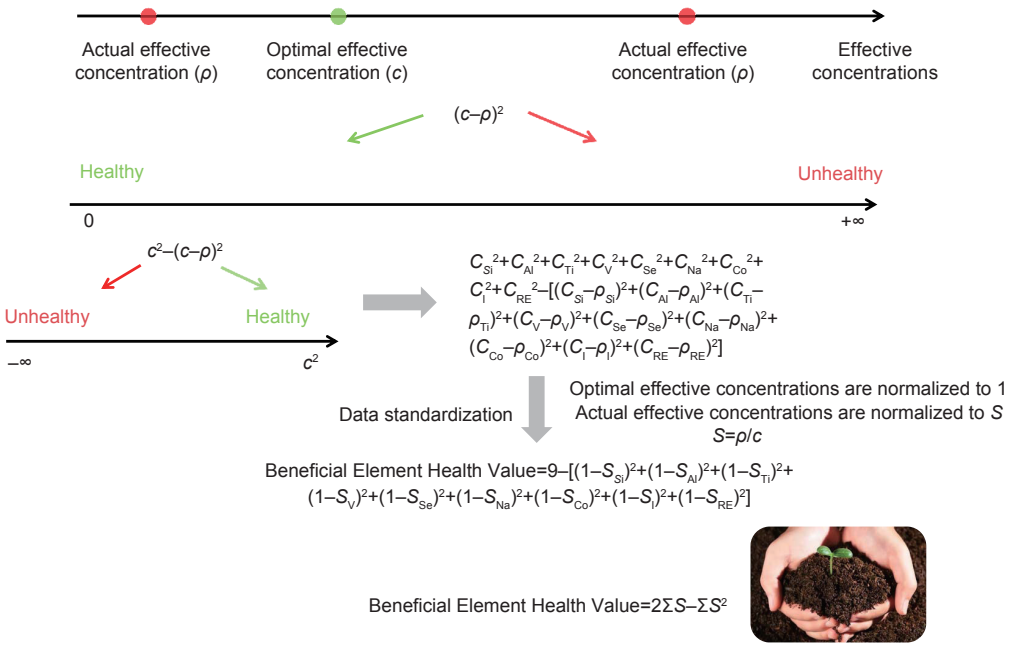


Fig. 6 Incorporating beneficial elements into the soil health evaluation system. Basically, the greater the difference between the actual effective concentration (ρ) and the optimal effective concentration (c) in the soil, the less healthy the soil. Therefore, the larger the value of $c^2-(c-\rho)^2$, the healthier the soil. After normalizing the optimal concentrations and the actual concentrations to 1 and S, a composite index of soil health based on beneficial elements is obtained. Larger values represent superior soil health. In addition, there are currently no reports of the harmful effects of silicon (Si) at high concentrations. Therefore, when ρ_{Si} is greater than c_{Si}, $(c_{Si}-\rho_{Si})$ can be considered 0.

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