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Essential and Beneficial Trace Elements in Plants, and Their Transport in Roots: a Review

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Abstract The essentiality of 14 mineral elements so far have been reported in plant nutrition. Eight of these elements were known as micronutrients due to their lower concentrations in plants (usually ≤100 mg/kg/dw). However, it is still challenging to mention an exact number of plant micronutrients since some elements have not been strictly proposed yet either as essential or beneficial. Micronutrients participate in very diverse metabolic processes, including from the primary and secondary metabolism to the cell defense, and from the signal transduction to the gene regulation, energy metabolism, and hormone perception. Thus, the attempt to understand the molecular mechanism(s) behind their transport has great importance in terms of basic and applied plant sciences. Moreover, their deficiency or toxicity also caused serious disease symptoms in plants, even plant destruction if not treated, and many people around the world suffer from the plant-based dietary deficiencies or metal toxicities. In this sense, shedding some light on this issue, the 13 mineral elements (Fe, B, Cu, Mn, Mo, Si, Zn, Ni, Cl, Se, Na, Al, and Co), required by plants at trace amounts, has been reviewed with the primary focus on the transport proteins (transporters/channels) in plant roots. So, providing the compiled but extensive information about the structural and functional roles of micronutrient transport genes/proteins in plant roots.

Keywords Toxicity · Deficiency · Micronutrient · Beneficial element · Broad range affinity

Introduction

Plants are usually reported to need about 14 essential mineral elements for healthy growth and development [1]. From these elements, eight such as boron (B), chlorine (Cl), copper (Cu),

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iron (Fe), manganese (Mn), molybdenum (Mo), nickel (Ni), and zinc (Zn) are known as micronutrients since they are found in plants at lower concentrations (usually ≤100 mg/kg/dry weight (dw)) [1]. However, it is still challenging to mention an exact number of the micronutrients since some elements have not been strictly proposed yet either as essential or beneficial. For example, some authors report silicon (Si) in the micronutrient list while others mention it as a beneficial element [1–3]. Further molecular and physiological studies are thus required whether to include or exclude these controversial elements in the micronutrient list. Micronutrients participate in a number of metabolic processes, including primary and secondary metabolism, cell defense, signal transduction, energy metabolism, hormone perception, and gene regulation [1–4]. Taking into account that the very diverse group of physiological events in plant metabolism are directly or somewhat associated with the mineral elements, elucidating the molecular mechanism behind the element uptake and transport appears to have great significance in terms of basic and applied plant sciences [4, 5]. In addition, the element deficiencies or toxicities seriously affect the plant life cycle by causing the various symptoms, even plant death if not treated, and millions of people around the world also suffer from the plant-based element deficiencies or toxicities [6–8]. Regarding the essentiality and/or beneficial effects of the micronutrients in plants, this study has attempted to review 13 mineral elements such as iron (Fe), boron (B), copper (Cu), manganese (Mn), molybdenum (Mo), silicon (Si), zinc (Zn), nickel (Ni), chlorine (Cl), selenium (Se), sodium (Na), aluminum (Al), and cobalt (Co) with an emphasis on the micronutrient transporters or channels in plant roots. In this context, the very diverse group of root uptake micronutrient transporters or channels from various protein families was compiled and provided an easy-access information about their structural and functional roles in plants.

Iron (Fe)

Fe is one of the important essential micronutrients in plants and also crucial for the plant growth and development [9, 10]. It participates in a number of biological processes, including respiration, photosynthesis, hormone production, nitrogen fixation, and chlorophyll and DNA syntheses. In addition, it functions as structural element in iron-sulfur clusters, heme cofactor, and other iron-binding sites [11–13]. Plants require about 10^{-9}–10^{-4} M of Fe concentration to maintain the normal growth and development. Its deficiency causes the interveinal chlorosis in plant leaves and reduces the crop productivity; if not treated, even it could lead to plant death [14]. The Fe^{3+} form is abundant in nature but it is not directly available by plants at normal physiological conditions due to its less solubility [15]. Thus, iron transport necessitates either its reduction to Fe^{2+} or its chelation at root rhizosphere [16]. Moreover, Fe is a suitable element for redox reactions due to its chemical properties. However, its large quantities in free-state could also lead the generation of reactive oxygen species (ROS) [5]. So, its uptake, mobilization, utilization, and partitioning in plants require a tight regulation at cellular and molecular levels [11, 12, 17]. Regarding Fe uptake, two different strategies have been proposed for graminaceous and non-graminaceous plants [18]. In graminaceous plants, its uptake depends on the secretion of phytosiderophores (MAs) which are synthesized by S-adenosyl-L-methionine (SAM) pathway with three consecutive enzymatic reactions such as nicotianamine synthase (NAS), nicotianamine aminotransferase (NAAT), and deoxymugineic acid synthase (DMAS) [19–21]. The secreted MAs in rhizosphere solubilized the Fe^{3+} and formed an Fe^{3+}-MA complex followed by its uptake into the root cells by Yellow Stripe 1-like (YSL) and Yellow Stripe 1 (YS1) transporters [22–24]. In non-graminaceous plants, Fe chelates are

reduced at the root surface and the resulting ferrous ions (Fe^{2+}) are taken into the cells through the plasma membrane. The phenolic compounds and protons, secreted into rhizosphere, also accompany this process to increase the ferric ions (Fe^{3+}) solubility [12, 25]. Besides, some plants like rice demonstrate both types of mechanisms such as Fe^{3+}-DMA uptake by OsYSL15 transporter as graminaceous plants and uptake by ferrous transporter OsIRT1 as non-graminaceous plants [22, 23]. For cytosolic Fe transport, several transporter families such as iron-regulated transporter (IRT)-like protein (ZIP), zinc-regulated transporter (ZRT), natural resistance-associated macrophage protein (NRAMP), and oligo peptide transporters (OPTs) have been reported so far [26]. ZIP family is a type of broad range metal transporters carrying the Fe^{2+}, Zn^{2+}, Mn^{2+}, and Cd^{2+} [26, 27]. This family proteins are 309–476 residues long with eight putative TMDs and extracellular N- and C-terminals [27]. They contain a variable cytosolic region between TMD3 and 4 with a putative His-rich metal-binding domain [27]. TMD4 also harbors the most conserved part of the ZIP proteins with an amphipathic helix including a full conserved His residue. It has been also reported that this His amino acid and a semi polar adjacent residue could form an intramembranous metal-binding site [28]. As for the NRAMP family, they also contain metal transporters with broad subtract range such as Fe^{2+}, Mn^{2+}, Cu^{2+}, Zn^{2+}, Cd^{2+}, Ni^{2+}, Al^{3+}, and Co^{2+} [29–31]. These family members have 10–12 putative TMDs with a consensus transport residue between TMD8 and 9 [32]. Members of the OPT family transport the metal ions such as Fe, Zn, Mn, Ni, Cd, and Cu, and amino acid-containing compounds and their derivatives [33, 34]. Thinking that most iron transporters have broad subtract range for different metals, therefore, plants could have developed a sophisticated iron homoeostasis maintaining the physiological iron limits.

Zinc (Zn)

Like Fe, Zn is also a crucial micronutrient in the plant life cycle due to its essentiality [35]. As a catalytic element, it functions in more than 300 enzymes, including alkaline phosphatase, alcohol dehydrogenase, carbonic anhydrase, and Cu-Zn superoxide dismutase. It also plays a structural role in stabilization of many proteins such as Zn cluster, Zn finger, and RING finger domains/motifs [36]. Its plant deficiency could cause the chlorosis, the formation of necrotic spots, and could reduce the plant growth [37]. From soil, it is taken as divalent cations (Zn^{2+}) which also determine its physiological role since it is neither further reduced nor oxidized intracellularly [5, 36]. Zn homeostasis in plants is mainly maintained by the coordinated regulation of ZIP family uptake transporters [27, 38; refer to Fe (iron)]. In model organism *Arabidopsis thaliana*, seven ZIP family genes *ZIP1–4* and *IRT1–3* were characterized as functional Zn transporters with different affinities [6, 38–40]. *ZIP1–3* genes were able to complement the Zn uptake in yeast and they were also overexpressed in Zn-deficient roots, while *ZIP4* was expressed in roots and shoots of the Zn-deficient plants and also referred a role in intracellular Zn transport [6]. Although IRT1 is a high affinity iron transporter in roots, its overexpression was also able to accumulate the high levels of Zn and Cd in Fe-deficient *Arabidopsis* plants [41, 42]. *IRT2* was reported to be expressed under Fe deficiency in *Arabidopsis* as well as could transport the Zn and Fe in yeast [42]. *A. thaliana* and *Arabidopsis halleri IRT3* gene functionally complemented the Zn and Fe uptake in yeast, suggesting a Zn/Fe transport activity [39]. Moreover, Zn transporter homologs have been also reported in many plant species [43–47] but most are still waiting for their experimental characterization. Furthermore, taking into the account that reported Zn transporters have broad range affinity as well as have cross-talks with other metals, therefore it seems more challenging to propose a single specialized Zn transporter.

Boron (B)

Another important essential element involving in the healthy plant growth and development is boron [48]. It involves in many physiological processes, including the ammonium and nitrogen assimilation [49, 50], cytoskeleton polymerization [51], cellular signaling [52], regulation of the membrane potential and permeability [53, 54], control of the cell wall porosity and tensile strength [55, 56], and changes of the phenolic compounds [57]. B-deficiency forms one of the most widespread micronutrient deficiencies in the world and causes the significant losses in crop yield and quality [48]. It affects the vegetative and reproductive growth in plants; inhibits the cell expansion, reduces the plant fertility, and causes the meristem death [5]. In soil solution, B is present as boric acid ($B(OH)_3$) or borate but boric acid is the most accepted form by plants since it is abundant in soil at optimum pH (5.5–7.5). Based on the B availability, three different mechanisms have been proposed for boric acid uptake; (i) passive diffusion by plasma membrane, (ii) facilitated transport by MIP proteins, and (iii) active transport by BOR transporters [58]. In case of B availability, boric acid is taken up via passive diffusion and facilitated transport, and under B deficiency, BOR transporters mainly involve in the boron uptake [59]. In model organism *A. thaliana*, B uptake was achieved by two transport molecules NIP5;1 and BOR1 [60, 61]. NIP5;1 is a boric acid channel protein from major intrinsic protein (MIP) family. It is localized to epidermal cell and root cap plasma membranes with a soil-facing polarity and significantly upregulated under B-deficient conditions [60, 61]. This family (MIP/aquaporin) members are characterized with six putative TMDs and an NPA (Asn-Pro-Ala/Ser/Val) motif [62]. BOR1 transporter was first characterized in B-deficient *Arabidopsis* roots [60]. *Arabidopsis BOR1* gene encoded a protein of 704 amino acid residues including 10 putative TMDs. Besides, *Arabidopsis* AtBOR2–7 sequences also demonstrated the similarity to AtBOR1 [60]. Additionally, under B-deficient conditions, rice NIP3;1 channels and BOR1 transporters participated in B uptake [63, 64]. They also showed high homology to *Arabidopsis* NIP5;1 boric acid channels and BOR1 transporters, respectively [65]. Grapevine *VvBOR1* gene, which is an *AtBOR1* ortholog, encoded a polypeptide of 720 amino acid residues in *Arabidopsis* root pericycle cells [66]. In addition, functional BOR1 transporter homologs were also reported in some other species, including baker's yeast [60], *Brassica napus* [67], and *Eucalyptus* [68]. Moreover, maize mutants *tls1* and *rte* encoded the NIP3;1 and boron transporter proteins, homologous to AtNIP5;1 and AtBOR1, respectively, with some vegetative and reproductive defects like B deficiency [69–71]. Furthermore, boron transporter genes were reported to have great importance from agricultural perspectives to alleviate the B-deficiency symptoms and enhance the B tolerance.

Copper (Cu)

Cu stands another crucial element in plant micronutrient list [72]. It participates in a number of metabolic processes such as mitochondrial respiration, hormone signaling, photosynthetic electron transport, cell wall metabolism, and superoxide scavenging. It also functions as structural component in variety of enzymes, including cytochrome c oxidase, laccase, amino oxidase, plastocyanin and polyphenol oxidases, and Cu/Zn superoxide dismutase [5, 73]. Cu deficiency mainly affects the reproductive organs and younger leaves while its toxicity causes the necrosis, chlorosis, leaf discoloration and stunting, inhibits the root growth, and incites the ROS generation [5, 72]. Thus, plants could have acquired a sophisticated Cu network to

maintain its uptake, mobilization, utilization, and storage [74]. In model species *A. thaliana*, Cu is transported into the cytosol by six high affinity transporters COPT1–6 while it is effluxed by P-type ATPases such as HMA1, HMA5, PAA1, PAA2, and RAN1. In addition, its intracellular distribution occurs with the help of metallochaperones such as CCS1, ATX1, and CCH [75–78]. COPT transporters are the members of CTR protein family with three putative TMDs and they include an extracellular N-terminal and a cytosolic C-terminal region [79–81]. With the exception of AtCOPT4, all *Arabidopsis* COPT proteins contain the His-rich residues and variable number of Met-rich motifs in their N-terminal regions. Yeast studies have demonstrated that Met-rich motifs in CTR family involve in Cu translocation into the cytosol by selectively sequestering copper ions from environment and stabilizing them with thioester groups in Met residues [80, 82, 83]. Green algae CTR1 and 2 transporters contained the six Met- and Cys-rich copper binding motifs [84]. In *Arabidopsis*, a Met residue before TMD1 (around 20 amino acids) and an Mx_3M motif in TMD2 were essential in copper transport [85]. In yeast *ctr1* mutants, a conserved Gx_3G motif in TMD3 functioned as glycine zipper in helix packing and trimer assembly, and involved in delivery of transporters to their targets [86]. $Mx_3Mx_{12}Gx_3G$ motif was also highly conserved in CTR proteins [85]. In addition, many CTR sequences contained the Cys-rich (CxC) motif in their C-terminal regions. Yeast CTR1 studies demonstrated that this motifs (CxC) could involve in regulation of intracellular copper concentrations as well as could function in copper delivery to cytosolic metallochaperones [87]. Moreover, transcriptional activation of copper deficiency responsive genes, including COPT1 and 2 in *Arabidopsis*, is regulated by SPL7 transcription factor. This transcription factor also modulates a group of Cu-microRNAs such as miR397, 398, 408, and 857, causing the degradation of messenger RNAs (mRNAs) encoding the non-essential cuproproteins [88, 89]. All these mechanisms suggest the dynamic regulation of intracellular copper concentrations in response to plant physiological demand.

Molybdenum (Mo)

In essential plant micronutrient list, Mo is another important element with crucial metabolic functions [1]. It is used in synthesis of molybdenum cofactor (Moco), which forms the active sites of molybdoenzymes such as sulfite oxidase (SOX), aldehyde oxidase (AO), xanthine dehydrogenase (XDH), and nitrate reductase (NR) [90]. These enzymes participate in many substantial metabolic processes, including the phytohormone biosynthesis, purine metabolism, sulfite detoxification, and nitrate assimilation [91]. Thus, its deficiency or toxicity hinders the plant growth and development, and decreases the agricultural productivity [92]. Mo is present in soil at various forms but only molybdate (MoO_4^{2-}), a dissolved form of the molybdenum, is taken up by the plants [93]. In model plant *A. thaliana*, MOT1 (previously SULTR5;2) is a high-affinity molybdate transporter in plasma membrane or endomembranes [94, 95]. Another *Arabidopsis* protein reported was the MOT2 in vacuoles; its accumulation in leaves and decrease in seed as well as the increased *MOT2* activity in senescing leaves in *mot2*-deficient plants suggested that MOT2 may export the molybdate from vacuole into the cytosol [96]. In addition, MOT1 and 2 homologs have been also identified as in silico in a number of plant species [97]. Previously, MOT1 and 2 proteins were included into the sulfate transporters under SLC26A/SulP transporter family but they were separated from them with the absence of a C-terminal STAS (sulfate transporter and anti-sigma factor antagonist) domain [98]. SLC26A/SulP family members were reported to have 10–12 putative TMDs with STAS domain [99]. However, recently, Mo transporters were included into the molybdate transporter

family (Pfam: PF16983) [100]. Molybdate (MoO_4^{2-}) and sulfate (SO_4^{2-}) show high-degree similarity due to their double negative charges and tetrahedral structures. Thus, sulfate transporters are reported to facilitate the molybdate uptake and distribution [96]. Green algae CrMOT1 included nine putative TMDs, and residues PXPVQPMKX(I/L)(A/G)AXA between TMD1 and 2, and residues FGXMPXCHG(S/A)GGLAXQ(Y/H)XFG(A/G)RXG between TMD6 and 7 showed the significant conservation in plants, algae, fungi, and bacteria [101]. Overall, further molecular and physiological studies are required to more elaborately elucidate the molybdenum transporters from the sulfate transporters.

Silicon (Si)

Among the plant micronutrients, Si is usually regarded as beneficial element [102]. It improves the canopy photosynthesis, reduces the transpiration loss, and increases the plant resistance against various biotic/abiotic stresses such as cold, drought, salinity, temperature, and various bacterial and fungal diseases [102–105]. However, beneficial effects of the silicon are related with the accumulation capacity of the plants; effects are clearer in high Si accumulators while less in low accumulating plants [106]. Silicon is taken up and transported to the shoots as silicic acid ($Si(OH)_4$) and there it is converted to hydrated amorphous silica and stored on cell the walls, which forms the silica cuticle and silica cellulose double layers on stem, leaf and hull surfaces [104, 107]. Si transporter Lsi1 (NIP2;1) was first characterized in the root plasma membrane of the rice [108]. This transporter is a member of nodulin 26-like intrinsic proteins (NIPs) from plant aquaporins, which carry the water and small uncharged solutes such as silicic and boric acids, glycerol, and ammonia [109]. Substrate preference in NIP members were associated with two pore forming sites; (i) two conserved NPA (Asn-Pro-Ala) motifs and (ii) an aromatic/arginine (ar/R) region [110]. Adjacent Asn residues in two NPA motifs constitute the conserved NPA site. Besides, these residues are reported to make H bond with the molecules to be transported and function as proton exclusion [111, 112]. ar/R region is composed of four residues from helix 2, helix 5, loops E1 and E2, and forms a selectivity filter for substrate molecules [113, 114]. It plays a barrier role, regulates the transport rate, and makes van der Waals and H bonds [115, 116]. In Si transport, only Gly-Ser-Gly-Arg (GSGR) residues are reported to form the correct specificity filter with high conservancy in all known silicon transporters [114]. Two silicon transporters, Lsi1 and Lsi2 were reported to involve in efficient silicon uptake in rice; knockout of either transporter resulted in the decreased silicon uptake [108, 117, 118]. Besides, these transporter (Lsi1 and 2) homologs were also identified in some silicon accumulators including maize, barley, and pumpkin [119–122]. Moreover, plants absent with Lsi1 or Lsi2 homologs were either low accumulators or inefficiently accumulated the silicon [108, 117]. Although many studies so far have reported the beneficial effects of silicon in plant stress tolerance; however, its accumulation by different plants still waits to be elucidated. Besides, up to date, silicon transporters were mainly characterized in monocots therefore we have limited knowledge about many dicot species.

Manganese (Mn)

Mn is considered as an essential element in the list of major plant micronutrients [8, 123]. It functions in biosynthesis of the lipids, lignins, and carbohydrates, and involves in photosystem II (PSII) as well as it plays a structural role as cofactor in many enzymes. Its deficiency or toxicity hinders the plant growth, reduce the biomass, and causes the tissue necrosis, and

interveinal chlorosis [8, 124–126]. Several transporter families, with broad range substrate affinities have been reported in influx and efflux of Mn. The NRAMP, ZIP, and YSL families were in Mn influx, and cation exchanger (CAX), cation calcium exchanger (CCX), P-type ATPases, and vacuolar iron transporter (VIT), and cation diffusion facilitator/metal tolerance protein (CDF/MTP) families were in Mn efflux [126]. Many studies have also reported the crucial roles of NRAMP, ZIP, and YSL families in Mn uptake. In NRAMP family, *NRAMP1* is a high-affinity Mn transporter in *Arabidopsis* root plasma membrane [127, 128]. *Arabidopsis NRAMP3* and *4* are reported to complement the Mn/Fe deficiency in yeast [129, 130]. NRAMP3 and 4 proteins are shown to involve in the Mn/Fe remobilization from vacuole [129]. Rice NRAMP3 differentially transports the Mn depending on the environmental conditions [131] while rice NRAMP5 is an essential Mn root uptake transporter from the soil [132]. In the ZIP family, *Arabidopsis* high-affinity iron transporter IRT1 was also to have low affinity for Mn [133]. Besides, *Arabidopsis* ZIP1, 2, 5–7, and 9 were reported to restore the Mn uptake in yeast mutants [134]. In YSL family, rice *YSL2* and *6*, and *Arabidopsis YSL4* and *6* were implicated in Mn homeostasis [135–137]. Moreover, Ca^{2+}-permeable channels were also reported to involve in the Mn transport in *Arabidopsis* and maize roots [138, 139]. *NRAMP* genes encode the highly hydrophobic membrane proteins with 10–12 putative TMDs possessing a consensus transport residue between TMD8 and 9 [29, 32]. *Arabidopsis* NRMAP1 and 2 transporters, respectively, are 532 and 530 residue proteins with 12 putative TMDs and a consensus transport residue between TMD8 and 9 [140]. Despite the reports of several transporter families in Mn uptake in some plants, we still have limited knowledge in many other plant species.

Nickel (Ni)

Ni has been proposed as essential plant micronutrient. It involves in the structure of many enzymes, including glyoxalases (family I), ureases, methyl-CoM reductase, superoxide dismutases, peptide deformylases, and some hydrogenases [141–143]. It plays crucial roles in ureolysis, methane biogenesis, acitogenesis, and hydrogen metabolism as well as in maintaining the cellular redox state, stress tolerance/defense, and optimum nitrogen use efficiency (NUE) [143–148]. Its deficiency was reported to cause the accumulation of urea and necrotic lesions in plant leaves [143], while toxicity reduced the plant growth and photosynthesis, induced the oxidative stress, inhibited the nitrogen metabolism, and enzymatic and mitotic activities, and interfered with other metals uptake [149–152]. Thus, nickel seems to play substantial role/s in plant growth and development. Nickel uptake could be achieved by active transport or passive diffusion depending on the plant species, soil pH, nickel form and concentration, and availability of other metals [153–155]. Solubilized nickel compounds could be transported by various cation transport systems such as Fe^{2+}, Mg^{2+}, Cu^{2+}, and Zn^{2+}, by chelators such as citric acid, histidine (His), and nicotianamine (NA) as well as with various other proteins such as permeases, metallothionein (MT), YS1-like (YSLs) and metallochaperones [151–156].

Chlorine (Cl^-)

Cl, as being an essential micronutrient, involves in regulation of the pH and turgor pressure, and cytoplasmic enzyme activities, helps to stabilize the membrane potential, and plays a cofactor role in photosynthesis [5, 157–160]. Its deficiency causes the reduced leaf growth and

wilting resulted with chlorosis and necrosis, and causes the stunted roots and reduced fruit size. However, its deficiency rarely occurs in normal conditions because the chlorine concentrations in soil are usually high and plants only require the trace amounts [160]. Besides, higher concentrations are reported to be toxic to plants, particularly many economically valuable cereals, vegetables, and fruit crops are susceptible to chlorine toxicity (4–7 mg/g/dw for sensitive species and 15–50 mg/g/dw for tolerant plants) [159]. In plants, several transporter families have been reported to participate in anion transport thereby in chlorine transport. These anion transporters include the slow anion channel associated protein (SLAC1), aluminum activated malate channels (ALMT), anion/H+ antiporters, ATP-binding cassette (ABC) transporter family, CLC anion channels, cation-coupled Cl^- (CCC), voltage-dependent anion channels (VDAC), NRT (NOD)s nitrate and peptide transporter family, and MscS-like mechanosensitive channels [161]. Moreover, some other channels such as stretch-activated anion channels, slowly activated anion channels (S-type) and rapidly activated anion channels (R-type) were also shown to involve in chlorine ion efflux in plasma membranes of guard cells [160]. Furthermore, chlorine homeostasis in plants was also reported to be closely related with the salt tolerance [162–166].

Selenium (Se)

Se is regarded as a beneficial element for plants but non-essential. It involves in antioxidant and ROS regulation, heavy metal uptake and transport inhibition, photosynthetic system improvement, and construction of chloroplast components and cell membrane [167]. Besides, it also helps plants to alleviate the abiotic stress factors such as cold [168], drought [169], temperature [170], desiccation [171], salinity [169], heavy metals [172], water [173], senescence [174], and UV [175]. Its low concentrations improve the plant growth and development, and alleviate the stress factors, while higher concentrations could be toxic to plants [167]. For example, 1 mg/kg H_2SeO_4 addition to soil showed the toxic effect in ryegrass [174]. However, application of 1 mg/L Se with foliar or fruit spray was reported to improve the fruit quality in pears and peaches [176]. Besides, Se levels (up to 5 mg/L) were beneficial for some Se accumulators such as *Spirulina platensis*, red seaweed, and *Pteris vittata* [172, 177, 178]. Thus, plants demonstrate the variations for its accumulation and effects. Its concentration was reported to usually vary of 0.01–2.0 mg/kg in most soils [179]. Se is mainly present as selenate in alkaline and well-oxidized soils, as selenite in well-drained mineral soils, and as selenide in strongly reduced soils [180]. Plants could transport the selenate by sulfate transporters since both (sulfate and selenate) demonstrate the chemical similarity [181]. Sulfate selectivity over selenate is low under high sulfate availability. In addition, inducible sulfate transporters have higher selectivity than constitutive sulfate transporters for sulfate over selenate [182]. So, it is of great importance to characterize the sulfate transporter homologs particularly in Se hyperaccumulators [183]. Besides, plant selenite uptake is less known. Some studies suggested that its uptake is not metabolically associated [184]. Additionally, phosphate and carbonyl cyanide m-chlorophenyl hydrazone (CCCP) are reported to hinder the selenite uptake in wheat while P-deficiency improves it [185].

Sodium (Na)

Na significance is usually associated with the soil salinity (mainly with NaCl) because excessive Na^+ concentrations are toxic to plants [186]. In woody plants citrus and grapevine, Na^+ accumulated in roots and stems, and Cl^- in shoots are harmful to plants [187]. In many

higher plants, Na^+ was also reported to cause an ion-specific damage [188]. However, some C4 plants and dicotyledonous halophytes were also reported to show considerable growth in response to high Na^+ treatments [189]. Some specific/non-specific channels and transporters such as voltage-independent channels (VICs), nonselective cation channels (NSCCs), low-affinity cation transporter 1 (LCT1), KUP/HAK/KT, HKT1, HKT2, AKT1, and CCCs were suggested to involve in Na^+ uptake in plants [186, 190]. Electrophysiological studies demonstrated that Na^+ flows through NSCC/VIC channels in the root cortical cell plasma membranes [191–193]. It was therefore suggested that salt stress in plants can be alleviated by manipulation of NSCCs channels [193]. Despite the implication of LCT1 in Na^+ influx, it was mainly reported to involve in Ca^+ acquisition and Cd^{2+} toxicity recovery [194]. HKT1 via K^+-independent way and HKT2 via K^+-dependent way were involved in Na^+ transport [195]. KUP/HAK/KT and AKT1 transporters involved in low and high affinity K^+ uptake, and were relatedly sensitive to Na^+ [191, 196, 197]. Cation-Cl–cotransporters (CCCs) participated in Na^+, K^+, and Cl^- ions uptake in plants [198]. In light of these studies, a number of specific/non-specific transporters and channels appeared to involve in Na^+ uptake in plants.

Aluminum (Al)

No experimental studies have been available so far showing the essentiality of Al in plants [199]. But its toxicity was demonstrated to be a major problem for many crops, particularly those growing in the acidic soils [200–202]. However, Al also stimulated the plant growth in Al accumulators [203, 204]. For example, tea plants responded by growth stimulation to the Al accumulation in shoots [205, 206]. Several reports have been proposed about the Al-induced growth mechanisms in plants. For example, Al-associated growth stimulation in tea plants could have derived from the improvement of latent iron toxicity [207]. In a different study, amelioration of proton toxicity was regarded as reason of Al-induced root elongation in proton-sensitive plants [208, 209]. In some other studies, improved antioxidant defense system was attributed as the reason of Al-related growth simulation in plants [199, 204, 210]. Thus, further molecular and physiological studies are required with more Al accumulator plants to demonstrate whether Al has any beneficial effects in plants.

Cobalt (Co)

Co is not regarded as essential element but reported as beneficial for plants. Its plant concentrations have importance because of its essentiality in animal nutrition; it is a vitamin B_{12} component required by all animals [211]. Normal Co concentrations in plants were as low as 0.1–10 μg/g/dw [212]. Thus, its higher concentrations were toxic to plants, severely interfering with the metabolic functions [213–215]. It hinders the plant growth, photosynthesis, and seed germination [216] as well as could cause the neurotoxicity in animals and memory deficit in humans [217]. Co transport in plants is physiologically regulated at a species-specific way. Co as divalent cation (Co^{2+}) could be transported into the cells by various broad range transporters thereby its homeostasis in plants are regulated by different metabolic pathways [211]. Besides, it is reported to be distributed in plant body via organic complexes due to its low mobility [212, 218, 219]. However, its precise transport mechanism from soil to root and to plant organs still awaits for further elucidation. In addition, soil properties significantly affect the Co bioavailability by plants [220, 221] therefore eliminating soil properties in Co studies could lead to the incorrect reports of toxicity thresholds [222]. So, cobalt being a heavy metal as well as a micronutrient, its elaborative control is required by plants for normal plant cycle.

Conclusion

Present study has extensively reviewed the 13 mineral elements (Fe, B, Cu, Mn, Mo, Si, Zn, Ni, Cl, Se, Na, Al, and Co) that are required by plants at trace amounts, with an emphasis on their transport proteins (transporters/channels) in plant roots. Although the essentiality of some micronutrients have been well established by many studies while some others have not been strictly proposed yet. Thus, it is still challenging to mention an exact number of the micronutrients in plants. Further molecular and physiological studies are needed to elucidate the roles of some elements in plant nutrition whether as essential or beneficial. In addition, transporter or channel proteins involved in the micronutrient transport usually demonstrate the broad range affinity for various other metals. Therefore, the cellular element uptake and its metabolism in plants are physiologically regulated depending on the plants demand, availability of other elements, physiological state of the plants, and other environmental conditions.

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