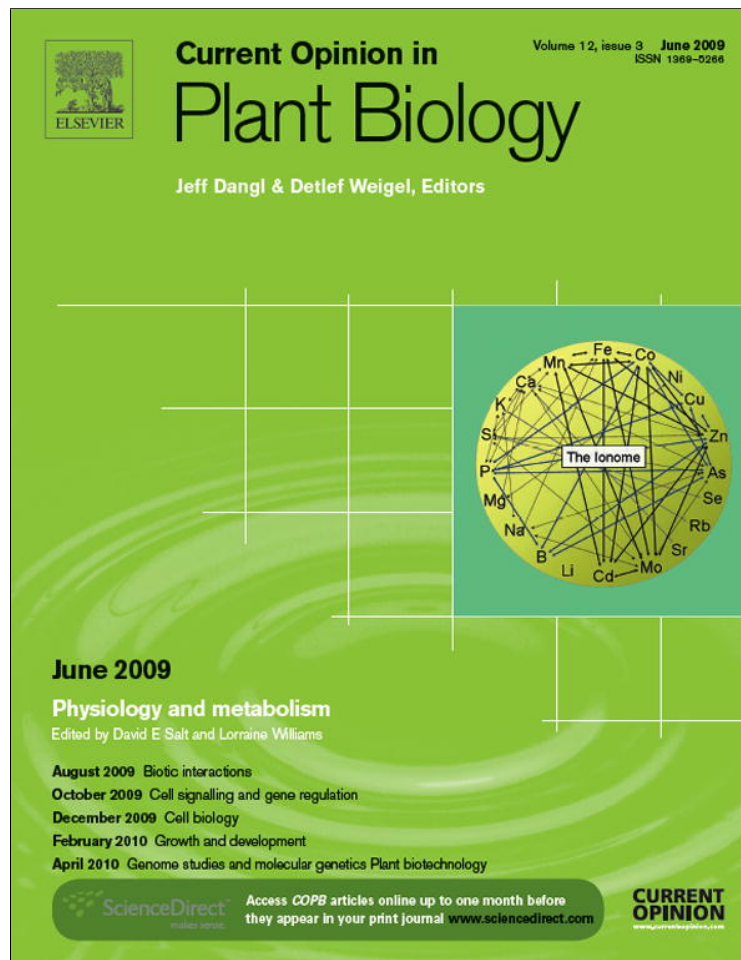


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**Current Opinion in
Plant Biology**

Physiological functions of beneficial elements

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Aluminum (Al), cobalt (Co), sodium (Na), selenium (Se), and silicon (Si) are considered beneficial elements for plants: they are not required by all plants but can promote plant growth and may be essential for particular taxa. These beneficial elements have been reported to enhance resistance to biotic stresses such as pathogens and herbivory, and to abiotic stresses such as drought, salinity, and nutrient toxicity or deficiency. The beneficial effects of low doses of Al, Co, Na and Se have received little attention compared to toxic effects that typically occur at higher concentrations. Better understanding of the effects of beneficial elements is important to improve crop productivity and enhance plant nutritional value for a growing world population.

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Current Opinion in Plant Biology 2009, **12**:267–274

This review comes from a themed issue on
Physiology and metabolism
Edited by David Salt and Lorraine Williams

Available online 26th May 2009

1369-5266/\$ – see front matter
Published by Elsevier Ltd.

DOI [10.1016/j.pbi.2009.04.009](https://doi.org/10.1016/j.pbi.2009.04.009)

Introduction

Essential elements are required to complete an organism's life cycle. Of the 92 known elements on earth, 17 are known to be essential to all plants. They are divided into macronutrients and micronutrients. The macronutrients include C, H, O, Ca, K, Mg, N, S, and P, of which C, H and O make up roughly 95% of plant dry matter and the others are typically present at $>1000 \text{ mg kg}^{-1}$ dry weight. The micronutrients (also called trace elements) include Cl, B, Cu, Fe, Mn, Mo, Ni, and Zn, which are typically present at $<100 \text{ mg kg}^{-1}$ dry weight. Owing to their requirement at very low levels, it is possible that additional micronutrients will be identified in the future.

Elements that promote growth and may be essential to particular taxa but are not required by all plants are called beneficial elements. The five most investigated beneficial

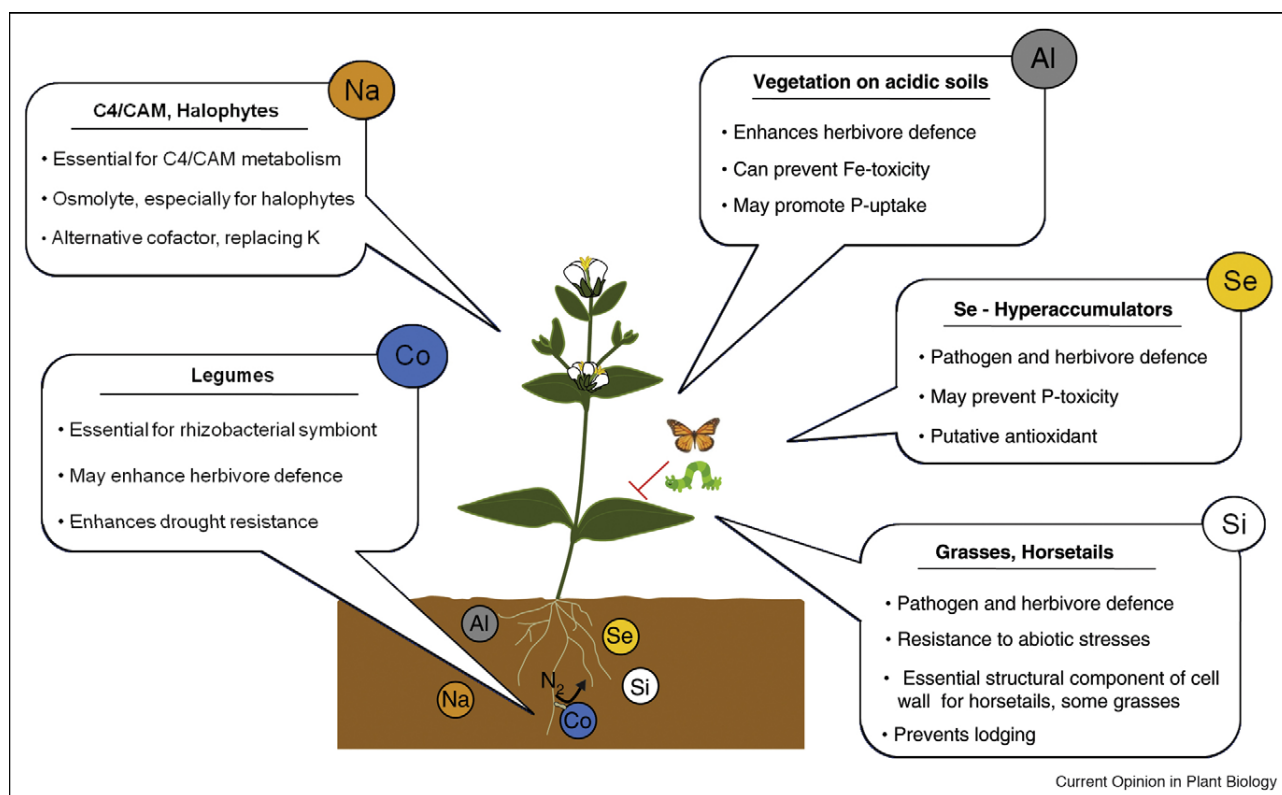
elements are Al, Co, Na, Se, and Si. All of these elements promote growth for various taxa under certain environmental conditions, however, the function and concentration varies for each element and plant species. Clues to the mechanisms that underlie the growth-promoting effects of beneficial elements have been obtained using various approaches. For instance, phenotypic differences were studied between plants growing in the absence or presence of the element, and tissue levels were determined at which the elements have a positive effect. Beneficial effects that require high tissue concentration suggest a structural or osmotic role, while effects at low tissue concentration may indicate a role as cofactor for specific enzymes. Furthermore, the plant taxa for which the elements are beneficial were determined, giving clues to the function of an element in a particular metabolic pathway or a particular microbial symbiont. In addition, determining the growth conditions under which the elements have their beneficial effect, and studying the beneficial effects in the context of plant ecology has been useful, since some beneficial elements affect abiotic stress resistance, or the interactions of plants with herbivores, pathogens or symbionts. Below, and depicted in [Figure 1](#), is a summary of our current knowledge about the beneficial effects of Al, Co, Na, Se, and Si on plants.

Aluminum

Aluminum (Al) is the third most abundant element in the earth's crust. At elevated levels Al is toxic to both plants and animals, and most research on the metabolism of Al in plants has focused on toxicity or tolerance mechanisms. The bioavailability of Al is highest on acidic soils ($\text{pH} < 5.5$), and much research has focused on anthropogenic factors that enhance Al levels in the environment, such as mining and acid precipitation. Soluble Al is released from acidic soils in the form of Al^{3+} , $\text{Al}(\text{OH})^{2+}$ and $\text{Al}(\text{OH})_2^+$ [1]. Aluminum toxicity results in inhibition of root growth, by altering root architecture and disrupting root elongation. Many plants that live on acidic soils have developed Al tolerance via either apoplastic or symplastic detoxification mechanisms. Apoplastic mechanisms include cell wall binding of Al (preventing transfer of Al into the symplasm), root secretions that raise proximal soil pH (making Al less bioavailable), and exudation of organic acids or mucilage that complex Al (reducing Al mobility) [1–5]. Some species tolerate Al in the symplast, often by storing it in less toxic forms, complexed with organic acids [5].

While toxic at high levels, Al has been shown to be beneficial to some plant species when supplied at low

Figure 1



Overview of the mechanisms responsible for the growth promoting effects of the five beneficial elements Al, Co, Na, Se, and Si. The classes of plants for which the growth promoting effect is (particularly) dramatic is shown at the heading of each balloon text, and the roles/effects on plant metabolism or anatomy are listed for each of the five elements in the respective balloons.

concentration. As early as 1937, Al was shown to increase growth in *Miscanthus sinensis* (maiden grass) [6]. Since then, multiple species, especially those native to acidic soils, have shown enhanced growth in the presence of Al, often coinciding with increased leaf phosphorus (P) concentrations [7]. In the presence of Al the tea plant, *Camellia sinensis*, showed increased antioxidant enzyme activity, which may contribute to increased plant growth [8]. *Melastoma malabathricum* uses secreted mucilage to accumulate high levels of Al from soils with low Al availability; the accumulated Al increases root and shoot growth, and prevents iron (Fe) toxicity [9–11]. It has been suggested that Al is essential for the growth of *M. malabathricum* [10]. Other species have also been shown to accumulate Al to substantial levels, typically much higher than the surrounding vegetation. Jansen *et al.* [12] proposed that plants with more than 1000 mg Al per kg dry weight in their leaf tissues be termed hyperaccumulators. Hyperaccumulators may use the Al in their tissues to deter herbivory, similar to other metals that are hyperaccumulated by plants. In support of this hypothesis, Al application prevented herbivory of tall fescue (*Festuca arundinacea*) [13]. Aluminum accumulators often account

for a high percentage of plants growing on acidic soils and it is possible that a plant's ability to accumulate Al is a competitive advantage on soils with high Al availability [14].

Cobalt

Cobalt (Co) is not very abundant: its concentration ranges between 15 and 25 ppm in soils, and is around 0.04 ppm in natural waters. Co concentration in plants is typically in the range of 0.1–10 ppm on a dry weight basis [15]. A recent study on 670 species of terrestrial plants showed that leaf Co concentration was in general less than 0.2 ppm, with the exception of Ericales, Euasterids and Asparagales clades, where 0.3–0.5 ppm of Co was measured [16••]. Also, Baker *et al.* [17] have reported a list of 26 Co hyperaccumulators, containing more than 1000 ppm Co in leaf tissues and for the majority belonging to the families of Lamiaceae, Scrophulariaceae, Asteraceae, and Fabaceae.

In higher plants, Co has been reported to strongly bind to roots, and to be mainly absorbed from the soil solution through passive transport. As Co shares high chemical

similarity with nickel (Ni), it may be envisioned that the two elements enter cells by the same plasma membrane carriers. Indeed, transporters for both Co and Ni were found in prokaryotes and fungi, and recently it has been hypothesized that Co and Ni may be co-regulated in *L. japonicus* [18]. Also, Baxter *et al.* [19] found that in *Arabidopsis* plants grown under reduced Fe concentration in the fertilizer solution the shoot concentration of Co increased. The concurrent increase in expression of the Fe transporter IRT1 lead the authors to conclude that Co may be transported by IRT1.

While it has been known for many years that Co is an essential element for animals and prokaryotes, a physiological function for this element in higher plants has so far not been established. Similar to other heavy metals, Co causes toxicity to plants at high concentration, and most of the recent literature focuses on the mechanisms through which plants can cope with Co stress [20]. At low levels however, Co can have a number of beneficial effects, particularly in leguminous plants. In a recent study by Gad [21] using pea plants (*Pisum sativum* L.), the application of 8 ppm Co to the soil increased growth, nodule number and weight, plant nutrient levels, as well as seedpod yield and seed quality. These effects could most likely be ascribed to the essentiality of Co for symbiotic Rhizobia that live in the nodules of these leguminous plants. Co is a component of cobalamin (vitamin B₁₂), which is required for the activity of several enzymes in nitrogen-fixing microorganisms such as Rhizobium and cyanobacteria [15].

Other beneficial effects reported for Co include retardation of leaf senescence via inhibition of ethylene biosynthesis, and enhancement of drought resistance in seeds. Co also stimulated isoquinoline accumulation (an alkaloid) in medicinal plants, through upregulation of the biosynthesis of aromatic amino acid precursors of alkaloids [15]. This last effect may suggest that Co could indirectly induce biotic stress resistance, but this hypothesis has not been addressed yet. In hyperaccumulators of Co, the high tissue Co levels may also offer direct protection from herbivory or pathogens, as was shown for other hyperaccumulated elements. This potential elemental defence, too, remains to be investigated. Since Co is essential for mammals, fertilization of crops with Co will have the additional beneficial effect of enhancing its nutritional quality.

Sodium

Sodium (Na) has been studied more for its negative effect at excess levels (salt stress) than as a beneficial or essential element. Na⁺ is chemically similar to potassium (K⁺) and likely enters plants mainly via non-selective cation transporters, particularly K⁺ channels [22,23]. However, there are also transporters in plants that are thought to specifically transport Na⁺. These Na⁺ transporters probably

have a main function in salt tolerance, by transporting Na out of the root, into the vacuole, or into the shoot phloem for export to the root.

Sodium has been shown to be an essential element for plants that use C4 or CAM photosynthetic pathways [24]. These C4/CAM plants use phosphoenolpyruvate (PEP) to fix atmospheric carbon for photosynthesis, and Na is needed for the regeneration of PEP from pyruvate. There are also numerous studies that show Na can act as a beneficial element for plant growth in general. Owing to the similarity of Na⁺ to K⁺, Na⁺ can replace K⁺ as a cofactor for certain enzymes, and as osmoregulator for, for example, stomatal movement and cell expansion. This is particularly beneficial when K levels are limiting. There is substantial variation between plant species in the extent to which they can replace K⁺ with Na⁺ (natrophilic vs. natrophobic species), and this ability is correlated with the beneficial effect of Na on growth [25]. Even addition of Na to K-replete plants can have a positive effect on growth, perhaps because Na⁺ affects stomatal movement somewhat differently than K⁺, leading to an overall higher leaf water status, improving water use efficiency.

In certain halophytes (salt-loving plants, e.g. *Atriplex*) Na is accumulated to high levels in the vacuoles, contributing substantially to plant osmotic potential. This allows the plant to take up water from salty or dry soils, which have low water potential. Some aquatic halophytes have also been reported to use Na to facilitate nitrate uptake, via a Na⁺/NO₃⁻ cotransporter [26]. Another group of specialized plants that may have a particular use for Na are certain parasites such as dodder (*Cuscuta attenuata*). Kelly and Horning [27] noted that parasites generally have a higher Na concentration than their host plants, and hypothesized that osmoregulatory dynamics may contribute to the extraction of water and nutrients from hosts.

In summary, Na is an essential trace element for certain plants that use the C4 or CAM pathway. Some halophytic plant species may also require Na to survive in their natural habitat, since they accumulate high levels of Na as a salt resistance mechanism. For the remaining plant species, low levels of Na can have a beneficial effect on growth, particularly in natrophilic species and under K-deficient conditions or moderate drought stress. Thus, depending on the crop species, fertilization with Na may boost crop productivity. Fertilization with Na has an additional beneficial effect on the plant's nutritional value and palatability, since animals require Na as an essential nutrient.

Selenium

Selenium (Se) is not a very abundant element; soil levels are typically below 1 ppm (mg/kg soil), but 4–100 ppm can be found in seleniferous soils. Vegetation on most soils contain less than 1 ppm Se (mg/kg plant dry weight).

On seleniferous soils most plant species contain 1–10 ppm Se, but so-called Se hyperaccumulator plants (e.g. from the genera *Stanleya* and *Astragalus*) can accumulate 1000–15 000 ppm (0.1–1.5% Se), even from low external concentrations. Selenium is chemically similar to sulfur (S) and metabolized via the same mechanisms. While the stoichiometry of Se and S in plants generally reflects that of their environment, hyperaccumulators typically contain elevated Se/S ratios, suggesting they can preferentially take up Se by means of specialized transporters. The main bioavailable form of Se in soils is selenate, which can be taken up by plants via sulfate transporters and assimilated into selenocysteine (SeCys) and selenomethionine (SeMet). While Se is essential for many animals and bacteria as well as the green alga *Chlamydomonas reinhardtii*, it has not been shown to be an essential element for higher plants [28]. The reason for Se's essentiality for some organisms is that it is a structural component of specific selenoproteins and seleno-tRNAs. Selenoproteins contain SeCys in their active site and often have a redox function, such as the scavenging of free radicals that cause oxidative stress and cancer. The SeCys in selenoproteins is encoded by the opal stopcodon when present in the context of a specific secondary mRNA structure (SeCys insertion sequence). In higher plants, SeCys insertion sequences have not yet been found, and plant homologues of selenoproteins (e.g. glutathione peroxidase, GPX) were found to contain Cys instead of SeCys in their active site [29**].

While there is no proof of essentiality for Se in plants, there have been reports of beneficial effects of Se on plant growth. Among higher plants, the largest beneficial effects of Se on growth (up to 2.8-fold higher biomass with Se) have been observed in the Se hyperaccumulator plants, and Se has been suggested to be essential for these species [30]. Since the beneficial effect of Se on hyperaccumulator growth was much less when the plants were grown at lower phosphate levels, it has also been suggested that Se may act as an antagonist against phosphate toxicity in hyperaccumulators [31]. Trace amounts of Se also stimulated growth in a variety of non-hyperaccumulator species including ryegrass, lettuce, potato, and duckweed (for a review see [32]). The Se-supplied plants showed lower levels of lipid peroxidation and higher levels of GPX activity, and were more resistant to ultraviolet radiation. The mechanism of this apparent positive effect of Se on antioxidant capacity may be direct, owing to antioxidant activity of selenocompounds, or indirect, via Se-induced upregulation of general stress resistance mechanisms.

There is mounting evidence that Se can also protect plants from biotic stresses. Supply of Se to hyperaccumulator and non-hyperaccumulator species protected the plants from a wide variety of herbivores, as well as from fungal infections [33*]. The protective action of Se

against biotic stresses may again be a combination of direct and indirect effects. Volatile Se (dimethylselenide) emitted by plants deters herbivores, and plant-accumulated Se is toxic to herbivores and pathogens. Se treatment has also been shown to upregulate plant JA and ethylene production and the production of defence-related proteins and upregulation of sulfate/selenate assimilation [34]. Thus, fertilization with low doses of Se may promote plant growth and increase resistance to pests and other stresses.

While Se is generally metabolized by sulfur pathways, there is some evidence that plants have evolved Se-specific enzymes that facilitate Se accumulation, perhaps to serve an ecological or physiological function. Hyperaccumulators such as two-grooved milkvetch (*Astragalus bisulcatus*), but also broccoli (*Brassica oleracea*) have a Se-specific selenocysteine methyltransferase, leading to accumulation of Se as relatively non-toxic methyl-selenocysteine [35,36]. There is also a report of an *Arabidopsis thaliana* Se-binding protein that conferred Se tolerance when overexpressed [37].

Since Se is essential at low levels for humans and other mammals, fertilization of crops with Se may not only benefit plant productivity but may have the additional benefit of enhancing its nutritional value [38]. The window between deficiency and toxicity is relatively narrow for Se, so in case of biofortification with Se it is important to carefully monitor the Se levels in the final food products, to avoid toxicity.

Silicon

Silicon (Si) is one of the earth's most prevalent elements, comprising more than 25% of the earth's crust [39]. Si is mainly available to plants as monosilicic acid, $\text{Si}(\text{OH})_4$, at a typical concentration of 0.1–0.6 mM in soil water [40]. Once absorbed, Si is deposited as amorphous silica ($\text{SiO}_2 \cdot n\text{H}_2\text{O}$) throughout the plant, mainly in the cell walls, where it interacts with pectins and polyphenols, and enhances cell wall rigidity and strength [41]. Si concentration in the plant ranges from 0.1 to 15% of dry weight, depending on the species [42]. In general, monocots show higher levels of Si accumulation (10–15%) compared to dicots (0.5% or less), particularly members of the comelinids clade orders Arecales and Poales [42]. Differences in Si accumulation among species have been ascribed to differences in the root density of Si transporters, as well as to distinct mechanisms of Si loading into the xylem (for a review see [43*]).

Although silicon is a major constituent of plants, to date its essentiality has been proven only in members of the Equisetaceae (e.g. horsetail, *Equisetum arvense*) and in wetland Poaceae (e.g. paddy rice, *Oryza sativa*) [44,45]. However, on the basis of the definition of essentiality given by Epstein and Bloom [40], Si may be considered a

'quasi essential' element for plants because its deficiency can cause various abnormalities with respect to plant growth, development and reproduction. Supplementation with Si exerts a number of beneficial effects on growth and yield of several plant species, which include improvement of leaf exposure to light, resistance to lodging, decreased susceptibility to pathogens and root parasites, and amelioration of abiotic stresses [25,46,47]. Si depositions in the epidermal layer of the leaves are thought to be responsible for the reduction of mutual leaf shading by keeping leaves more erect, while in the roots they can increase cell wall elasticity during root cell elongation [25].

The most extensively studied beneficial effect of Si on plant health is its role in reducing plant susceptibility to fungal diseases [47,48]. Two possible mechanisms of Si-enhanced plant resistance to pathogens have been proposed. One is that polymerized Si can reinforce the cell walls by physically inhibiting fungal germ tube penetration of the epidermis, thereby impeding infections [49]. The other is that Si may act locally as a signal in triggering natural defence responses in both dicots and monocots, by stimulating the activity of such enzymes as chitinases, peroxidases, polyphenol oxidases, and/or by increasing the production of phenolic compounds, phytoalexins, antimicrobial compounds and systemic stress signals (salicylic acid, jasmonic acid and ethylene) [49,50,51]. Silicon

bioactivity has been compared to that of the known activator/secondary messengers of systemic acquired resistance (SAR), which can be considered the plant's equivalent of an immune system. Si has a similar saturable effect and can significantly modulate the activity of post-elicitation intracellular signaling systems, including the mitogen activated protein (MAP) kinases [52]. However, different from SAR activators, the effect of Si on plant-induced resistance to pathogens vanishes when Si supply to plants is stopped, even though Si had irreversibly accumulated [52]. This is because only the soluble form of Si within plants can induce defence responses, while the polymerized fraction is almost inert.

Silicon can also prevent abiotic stress in plants. For instance, Si can alleviate heavy metal toxicity symptoms [46]. Several mechanisms have been proposed for this phenomenon, which include reduction of metal availability to plants in the growth medium, regulation of metal uptake and root-to-shoot transport, modulation of the cation binding capacity of the cell wall, stimulation of antioxidants, both enzymatic (e.g. superoxide dismutase, ascorbate peroxidase, dehydroascorbate reductase and glutathione reductase) and non-enzymatic (e.g. ascorbate and glutathione), and complexation or co-precipitation of toxic metal ions with Si in the cytoplasm (e.g. Zn, Cd and Al silicates), followed by sequestration of the metals in the vacuoles [41,46,53]. Other abiotic stresses that may be

Table 1

Overview of mechanisms proposed to be responsible for the beneficial effects of the elements Al, Co, Na, Se, and Si.

| Element | Plant concentration | Beneficial functions | Mechanisms hypothesized |
|---------|--|--|---|
| Al | <0.1% non-accumulators ≥0.1% Al accumulators | Increases plant growth Resistance to herbivory | Increases antioxidant activity Increases P availability Decreases Fe toxicity |
| Co | 10 ⁻⁶ -0.001% non-accumulators >0.1% Co accumulators | Increases growth in legumes Retardation of leaf senescence Seed drought resistance Resistance to herbivory | Essential co-factor for bacterial nitrogenase Inhibition of ethylene biosynthesis |
| Na | <0.05% non-halophytes >0.25% in halophytes | Increases plant growth Essential for C4 in CAM plants Can replace K as osmoregulator Can facilitate nitrate uptake | Regeneration of PEP |
| Se | ≤0.01% non-Se accumulators 0.01% - 0.1% Se accumulators ≥0.1% Se hyperaccumulators | Increases plant growth Resistance to pathogen and herbivore attack | Increases antioxidant activity Prevents P toxicity Volatile Se deters herbivores, accumulated Se is toxic |
| Si | <0.5% most species 10-15% horsetails, commelinid monocots | Increases plant growth Resistance to pathogen and herbivore attack Resistance to abiotic stress (heavy metals, salinity, drought, UV radiation, extreme temperature) | Strengthens cell walls Activation or synthesis of stress-related molecules SAR-like bioactivity Regulation of metal transport Increases antioxidant activity Sodium exclusion from roots |

alleviated by silicon include salt, nutrient imbalance, drought, high and low temperature, and UV radiation. In particular, Si was recently proven to mitigate salinity stress by enhancing sodium exclusion and decreasing lipid membrane peroxidation through stimulation of enzymatic and non-enzymatic antioxidant molecules [54*].

In summary, Si has several well-established beneficial effects on plants, and is even considered to be quasi-essential for certain taxa, particularly grasses, sedges, and horsetails. Si is accumulated to high levels, particularly in cell walls, and promotes plant sturdiness and resistance to a variety of biotic and abiotic stresses. While not essential, Si is also considered a beneficial nutrient for animals, and thus Si fertilization of crops may enhance their nutritional value.

Conclusions and future prospects

Al, Co, Na, Se, and Si all have documented positive effects on plant growth and stress resistance, and in some cases the underlying mechanisms are known, as summarized in Table 1. While none of these elements is essential for all plants, Na and Si are essential for certain plant taxa, and Al and Se have been suggested to be essential for certain hyperaccumulator species. Co is essential for the microbial partners of some plants, rather than for the plants themselves. Even in taxa for which they are not essential, these five elements can have a significant beneficial effect on plant growth, and thus may be applied as fertilizer.

The mechanisms behind the beneficial effects to the plant are relatively underinvestigated, compared to the toxic effects that many beneficial elements have at high levels. The effects of beneficial elements at low levels deserves more attention, not only because this will shed more light on basic processes of plant nutrition but also because fertilizing with beneficial nutrients may boost crop production and affect plant nutritional value as feed or food. Lack of nutritional value is one of the top ten problems identified by the World Health Organization, particularly in developing countries (the 'hidden hunger'). Dietary supplementation of Se, for instance, significantly reduces the occurrence of cancer and male infertility, as well as the susceptibility to viruses including the AIDS-causing virus, HIV.

The roles of beneficial elements in plant ecological processes may be another interesting area of continued study. The effects of beneficial elements have so far often been investigated in a laboratory setting using isolated plants, which overlooks any beneficial effects on positive or negative interactions of the plant with other species. Another potential area of further study is the identification and functional characterization of additional beneficial elements. There are reports that other

elements than the ones discussed above may have beneficial effects on plants, but more evidence is needed to confirm these results [55]. These other potentially beneficial elements include silver (Ag), cerium (Ce), chromium (Cr), fluor (F), iodine (I), lanthanum (La), rubidium (Rb), tin (Sn), strontium (Sr), titanium (Ti), vanadium (V), and tungsten (W). It is interesting to note in this context that leaf elemental composition was surveyed in over 670 species of terrestrial plants, and over 25% of the total variation could be assigned to the family level and above for 21 of the 42 elements [16**]. Thus, certain plant families preferentially take up particular elements. If any of these elements are indeed confirmed to be beneficial to plants, the cellular basis for the positive effects of these elements will be an interesting area of future study.

Acknowledgement

The writing of this manuscript was supported by National Science Foundation grants # IOB-0444471 and IOS-0817748 to EAHP.

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