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OVERVIEW: PART OF A SPECIAL ISSUE ON PLANT NUTRITION

# Plant nutrition for sustainable development and global health

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• *Background* Plants require at least 14 mineral elements for their nutrition. These include the macronutrients nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg) and sulphur (S) and the micronutrients chlorine (Cl), boron (B), iron (Fe), manganese (Mn), copper (Cu), zinc (Zn), nickel (Ni) and molybdenum (Mo). These are generally obtained from the soil. Crop production is often limited by low phytoavailability of essential mineral elements and/or the presence of excessive concentrations of potentially toxic mineral elements, such as sodium (Na), Cl, B, Fe, Mn and aluminium (Al), in the soil solution.
• *Scope* This article provides the context for a Special Issue of the *Annals of Botany* on 'Plant Nutrition for Sustainable Development and Global Health'. It provides an introduction to plant mineral nutrition and explains how mineral elements are taken up by roots and distributed within plants. It introduces the concept of the ionome (the elemental composition of a subcellular structure, cell, tissue or organism), and observes that the activities of key transport proteins determine species-specific, tissue and cellular ionomes. It then describes how current research is addressing the problems of mineral toxicities in agricultural soils to provide food security and the optimization of fertilizer applications for economic and environmental sustainability. It concludes with a perspective on how agriculture can produce edible crops that contribute sufficient mineral elements for adequate animal and human nutrition.

**Key words:** Biofortification, fertilizer use efficiency, mineral nutrition, pollution, toxicity, transport protein.

## INTRODUCTION

In addition to oxygen, carbon dioxide and water, plants require at least 14 mineral elements for adequate nutrition (Marschner, 1995; Mengel *et al.*, 2001). Deficiency in any one of these mineral elements reduces plant growth and crop yields. Plants generally acquire their mineral elements from the soil solution. Six mineral elements, nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg) and sulphur (S), are required in large amounts, whilst chlorine (Cl), boron (B), iron (Fe), manganese (Mn), copper (Cu), zinc (Zn), nickel (Ni) and molybdenum (Mo) are required in smaller amounts (Table 1). In geographical areas of low phytoavailability, essential mineral elements are supplied to crops as fertilizers to achieve greater yields. In addition, fertilizers containing essential mineral elements for human nutrition are occasionally supplied to crops to increase their concentrations in edible portions for the benefit of human health (see 'Plant nutrition for human health').

Inorganic N-fertilizers are generally produced from gaseous nitrogen by the energy-intensive Haber–Bosch process, most inorganic P-fertilizer is produced from rock phosphates using sulphuric acid, and K is mined from ores of largely marine origin (Lægreid *et al.*, 1999). It has been suggested that commercially viable reserves of sulphate and phosphate rocks are being used so rapidly that these will be exhausted within the next 25–100 years (Kesler, 2007). Fluctuating costs of energy and raw materials cause dramatic increases and uncertainty in the costs of agricultural fertilizers, with negative impacts on agricultural sustainability. The use of fertilizers in agriculture can also contribute to environmental pollution. The synthesis of N-fertilizers contributes significantly to the production of greenhouse gasses (GHG) and nitrogenous fertilizers are the largest single source of GHG emissions from arable agriculture (Galloway *et al.*, 2008; Smith *et al.*, 2008). The use of N- and P-fertilizers in agriculture is a major contributor to eutrophication processes in waters of both developed and developing nations (Conley *et al.*, 2009; White and Hammond, 2009). For both commercial and environmental reasons, it is clear that fertilizers should be used with caution, and that crop production for future food security will require sustainable fertilizer management, which might include more sophisticated decision support tools, improved agronomic practices and crops or cropping systems that require less fertilizer input (see 'Fertilizer management for optimal productivity and sustainability').

High concentrations of mineral elements in the soil solution can inhibit plant growth and reduce crop yields (Table 1; MacNicol and Beckett, 1985; Marschner, 1995; Mengel *et al.*, 2001). In particular, toxic concentrations of Mn, aluminium (Al), B, sodium (Na), Cl and Fe occur frequently on agricultural soils. Toxicities of Mn and Al occur on acid mineral soils, toxicities of B and Na occur on sodic (Na-rich) soils, and toxicities of Na and Cl occur on saline soils, throughout the world. Na, B and Cl toxicities and imbalances of Ca, Mg and K also occur in irrigated agriculture. In addition, Mn and Fe toxicities can occur on waterlogged or flooded soils and specific geological formations can result in

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TABLE 1. *Critical leaf concentrations for sufficiency and toxicity of mineral elements in non-tolerant crop plants*

| Element | Essentiality | | Critical leaf concentrations (mg $g^{-1}$ DM) | |
|---|---|---|---|---|
| | Plant | Animal | Sufficiency | Toxicity |
| Nitrogen (N) | yes | yes | 15 − 40 | |
| Potassium (K) | yes | yes | 5 − 40 | >50 |
| Phosphorus (P) | yes | yes | 2 − 5 | >10 |
| Calcium (Ca) | yes | yes | 0·5 − 10 | >100 |
| Magnesium (Mg) | yes | yes | 1·5 − 3·5 | >15 |
| Sulphur (S) | yes | yes | 1·0 − 5·0 | |
| Chlorine (Cl) | yes | yes | 0·1 − 6·0 | 4·0 − 7·0 |
| Boron (B) | yes | suggested | $5 - 100 \times 10^{-3}$ | 0·1 − 1·0 |
| Iron (Fe) | yes | yes | $50 - 150 \times 10^{-3}$ | >0·5 |
| Manganese (Mn) | yes | yes | $10 - 20 \times 10^{-3}$ | 0·2 − 5·3 |
| Copper (Cu) | yes | yes | $1 - 5 \times 10^{-3}$ | $15 - 30 \times 10^{-3}$ |
| Zinc (Zn) | yes | yes | $15 - 30 \times 10^{-3}$ | $100 - 300 \times 10^{-3}$ |
| Nickel (Ni) | yes | suggested | $0{\cdot}1 \times 10^{-3}$ | $20 - 30 \times 10^{-3}$ |
| Molybdenum (Mo) | yes | yes | $0{\cdot}1 - 1{\cdot}0 \times 10^{-3}$ | 1 |
| Sodium (Na) | beneficial | yes | – | 2 − 5 |
| Selenium (Se) | beneficial | yes | – | $10 - 100 \times 10^{-3}$ |
| Cobalt (Co) | beneficial | yes | – | $10 - 20 \times 10^{-3}$ |
| Iodine (I) | – | yes | – | $1 - 20 \times 10^{-3}$ |
| Fluorine (F) | – | suggested | – | 0·1 |
| Lithium (Li) | – | suggested | | $10 - 200 \times 10^{-3}$ |
| Lead (Pb) | – | suggested | – | $10 - 20 \times 10^{-3}$ |
| Arsenic (As) | – | suggested | – | $1 - 20 \times 10^{-3}$ |
| Vanadium (V) | – | suggested | – | $1 - 10 \times 10^{-3}$ |
| Chromium (Cr) | – | suggested | – | $1 - 2 \times 10^{-3}$ |
| Silicon (Si) | beneficial | suggested | – | nd |
| Aluminium (Al) | beneficial | – | – | $40 - 200 \times 10^{-3}$ |
| Cadmium (Cd) | – | – | – | $5 - 10 \times 10^{-3}$ |
| Mercury (Hg) | – | – | – | $2 - 5 \times 10^{-3}$ |

Essential elements for plants and animals are indicated. Mineral elements considered beneficial to plants, which improve the growth of various taxa under certain environmental conditions, are also indicated. The critical concentration for sufficiency is defined as the concentration in a diagnostic tissue that allows a crop to achieve 90 % of its maximum yield. The critical concentration for toxicity is defined as the concentration in a diagnostic tissue above which yield is decreased by more than 10 %. Data are taken from MacNicol and Beckett (1985), Brown *et al.* (1987), Marschner (1995), Mengel *et al.* (2001), White *et al.* (2004) and Pilon-Smits *et al.* (2009). It should be recognized that critical tissue concentrations depend upon the exact solute composition of the soil solution and can differ greatly both between and within plant species. The latter differences reflect both ancestral habitats and ecological strategies.

toxicities of particular mineral elements, such as Ni, cobalt (Co) and chromium (Cr) toxicities on certain serpentine soils and selenium (Se) toxicity on seleniferous soils. Unfortunately, anthropogenic activities have led to toxic concentrations of Zn, Cu, cadmium (Cd), mercury (Hg) and lead (Pb) in particular environments. Often, traditional agronomic countermeasures allowing crop production on such soils are expensive and only partially or temporarily successful. Plant breeders are therefore developing crop genotypes that tolerate these soils (see 'Addressing mineral toxicities in agricultural soils'). As is the case with wild plants, physiological mechanisms that allow crop plants to grow on soils containing high concentrations of mineral elements are based on their exclusion from the plant and/or tolerance of these elements through their sequestration as non-toxic compounds and/or in non-vital cellular compartments (Marschner, 1995).

This Special Issue of the *Annals of Botany* highlights topics of current interest in plant mineral nutrition. It begins with articles describing research to identify the molecular mechanisms and genetic factors influencing the uptake and distribution of mineral elements in plants and the practical uses of this knowledge for sustainable crop production and global health. Several articles then propose strategies to identify crops that tolerate high concentrations of mineral elements in the environment, that are suitable for soils lacking sufficient phytoavailable essential mineral elements and/or that yield well with reduced fertilizer inputs. Finally, there are articles describing genetic strategies for the biofortification of food and feed with mineral elements required for animal nutrition.

## UPTAKE AND DISTRIBUTION OF MINERAL ELEMENTS

The uptake of mineral elements by plant roots and their subsequent distribution within the plant have been the subject of studies for many decades (see Marschner, 1995; Mengel *et al.*, 2001; Karley and White, 2009; Miller *et al.*, 2009; Miwa *et al.*, 2009; Puig and Peñarrubia, 2009; White and Broadley, 2009). Mineral elements are acquired from the soil solution by plant roots. They traverse the root via apoplastic (extracellular) and/or symplastic (intracellular) pathways to the stele, where they are loaded into the xylem for transport to the shoot. All cytotoxic cations must be transported either through the apoplast or through the symplast in a chelated form. Several mineral elements are retained in the roots of some plant species. Examples are Ca, Mo, Na, Cd and Al

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(Marschner, 1995). The xylem delivers mineral elements to transpiring leaf tissues, where these are taken up from the apoplast by specific cell types. Recirculation of mineral elements within the plant, and the delivery of mineral elements to non-transpiring or xylem-deficient tissues, occurs via the phloem. K, Na, Mg, Cd, N, P, S, Se and Cl are transported readily, but Fe, Zn, Cu, Mo and iodine (I) are less mobile, and Mn and Ca are essentially immobile in the phloem of most plant species (Marschner, 1995). The phloem mobility of B varies between species (Brown *et al.*, 2002). Mineral elements that have low phloem mobilities accumulate in tissues with high transpiration rates and are present at low concentrations in fruits, seeds and tubers (Karley and White, 2009; White and Broadley, 2009; White *et al.*, 2009).

The ionome is defined as per Salt *et al.* (2008). It includes all mineral elements, whether essential or non-essential for life, in whatever chemical form these occur. Current interest is primarily focused on quantifying the ionome of different plant species, ecotypes and induced mutants, and on explaining differences in the ionome between and within plant species at the genetic level, although the ionome is also influenced profoundly by developmental and environmental factors (Watanabe *et al.*, 2007; Baxter, 2009; Chen *et al.*, 2009; White and Broadley, 2009; Broadley *et al.*, 2010). It is self-evident that the uptake of mineral elements and their distribution within the plant determine the ionome of both the plant and its tissues. These processes are therefore fundamental not only to the mineral nutrition of the plant, but also for increasing the concentrations of mineral elements in edible tissues for human consumption.

Plants appear to be composed of relatively few different cell types (Martin *et al.*, 2001). Each of these cell types is thought to perform a distinct physiological function and, consequently, to have a unique ionome (Punshon *et al.*, 2009; Karley and White, 2009). In this Special Issue, Conn and Gilliham (2010) review the phenomenon of cell-specific accumulation of mineral elements in plants. They describe the techniques used to determine both the tissue and subcellular distributions of mineral elements and present the tissue distributions of diverse elements including K, P, Ca, Na and Cd. They speculate on the physiological reasons for these distributions and the transport processes that are likely to generate them. They observe that the accumulation and tissue distributions of Ca, Na and Cd can be defined by the expression of key transport proteins and suggest how this phenomenon might be utilized to prevent the accumulation of toxic elements by plants. Similar observations are made by Miwa and Fujiwara (2010), who report that the misexpression of genes encoding B transporters alter the uptake and distribution of B in plants, and by Kobayashi *et al.* (2010), who report that misexpression of the iron deficiency-responsive *cis*-acting element binding factors 1 and 2 (IDEF1 and IDEF2) alters the expression of various genes encoding transport proteins that impact the uptake and distribution of Fe in plants. Indeed, the role of transport proteins in the uptake and distribution of mineral elements is highlighted by many articles in this Special Issue. These articles reveal that the expression of genes affecting transport processes influence plant adaptation to soils with extreme phytoavailabilities of mineral elements (Eticha *et al.*, 2010; Führs *et al.*, 2010; Kobayashi *et al.*, 2010; Miwa and Fujiwara, 2010), fertilizer use efficiencies in crops (Masclaux-Daubresse *et al.*, 2010; White *et al.*, 2010) and the biofortification of edible portions with essential mineral elements (Ding *et al.*, 2010).

## ADDRESSING MINERAL TOXICITIES IN AGRICULTURAL SOILS

Agriculture in many parts of the world is restricted by excessive concentrations of mineral elements in the soil solution. It is estimated that about 5 % of agricultural land is saline or sodic and contains toxic concentrations of Na, Cl or B (Marschner, 1995; Munns and Tester, 2008), that over 40 % of the world's arable land suffers from soil acidity and, therefore, Al and Mn toxicities (Von Uexküll and Mutert, 1995), and that Mn and Fe toxicities affect crop production in many waterlogged or flooded soils worldwide (Marschner, 1995). Traditional agronomic countermeasures can be employed to address these problems and plant breeders are developing crop genotypes that tolerate these adverse abiotic environments better, through either conventional breeding or transgenic strategies.

Crop production on acid soils is primarily limited by Al toxicity (Marschner, 1995; Mengel *et al.*, 2001). The presence of excessive Al in the rhizosphere inhibits root elongation (Marschner, 1995; Mengel *et al.*, 2001). Resistance is generally conferred by the release of organic acids, such as malate, citrate and oxalate, at the root apex that form Al-complexes and reduce the phytoavailability of toxic Al species in the root elongation zone (Ma *et al.*, 2001). In some plant species, such as wheat and maize, the release of organic acids is constitutive, whereas in other plant species, such as soybean, sorghum and rye, it is induced by exposure to Al (Ma *et al.*, 2001). In general, proteins that release malate from root cells into the rhizosphere belong to the Al-activated Malate Transporter (ALMT) family, whereas those that release citrate into the rhizosphere belong to the Multidrug and Toxin Extrusion (MATE) family (Delhaize *et al.*, 2007). In common bean (*Phaseolus vulgaris*), Al-resistance is effected by the Al-inducible release of citrate into the rhizosphere (Rangel *et al.*, 2010). In this Special Issue, Eticha *et al.* (2010) confirm that, following exposure to Al, restoration of root growth in the common bean is correlated with the release of citrate into the rhizosphere. They then reveal that, although the initial restoration of root growth is dependent upon Al-induced expression of genes encoding citrate transporters of the MATE family, in the longer term, Al-tolerance is achieved by the maintenance of citrate synthesis in the roots of resistant genotypes through post-translational regulation. The implication is that continued synthesis and release of organic acids must be achieved to confer Al resistance and the potential for crop production on acid soils.

Mn toxicity also limits crop production on acid soils. Mn is required by plants for the manganese-protein in photosystem II and the manganese-containing superoxide dismutase and also acts as a cofactor for a number of enzymes that catalyse redox, decarboxylation and hydrolytic reactions (Marschner, 1995). Excessive $Mn^{2+}$ is toxic because it can displace $Ca^{2+}$, $Mg^{2+}$, $Fe^{2+}$ and $Zn^{2+}$ in their essential cellular

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functions. Consequently, Mn-induced Ca, Mg and Fe deficiencies are common symptoms of Mn toxicity. Other symptoms of Mn toxicity are caused by the generation of reactive oxygen species in the cell wall. Low $Mn^{2+}$ concentrations must be maintained in metabolic compartments, which can be achieved through its sequestration in the vacuole and/or the cell wall (Marschner, 1995; Pittman, 2005; Puig and Peñarrubia, 2009). Large differences in Mn tolerance exist both between and within plant species (Marschner, 1995). In this Special Issue, Führs *et al.* (2010) observe greater activity of leaf apoplastic peroxidases in barley, a Mn-sensitive species, than in rice, a Mn-tolerant species, and demonstrate that, in rice, the greater Mn tolerance of old leaves than young leaves is related to a greater capacity for binding Mn in the cell wall. They also conducted a proteomic study to identify proteins whose abundance was altered in response to high Mn availability in rice leaves, observing an increased abundance of proteins related to stress responses and changes in the profile of proteins related to photosynthesis.

B is essential for cross-linking the pectic polysaccharide rhamnogalacturonan-II in primary cell walls, but high tissue B concentrations are toxic to plants (Brown *et al.*, 2002). Miwa and Fujiwara (2010) propose that plants maintain their tissue B concentrations within an optimum range by regulating B transport processes and review the properties of B transporters responsible for the uptake and distribution of B in plants. They describe evidence for two types of B transporters: Nodulin-26-like Intrinsic Proteins (NIPs) and Plasma-membrane Intrinsic Proteins (PIPs), several of which behave as boric acid channels, and B exporters (BORs), which remove B from plant cells. They observe that the activity of these transport proteins is finely regulated in response to B phytoavailability, and that the combined over-expresssion of *AtNIP5;1* and *AtBOR1* allows transgenic *Arabidopsis thaliana* to grow better than the wild-type in environments with low B phytoavailability, whereas the over-expression of *AtBOR4* confers increased tolerance of high B concentrations in the environment. Similarly, greater expression of *BOR* genes in barley and wheat has been associated with an increased tolerance to high B concentrations in the environment (Reid, 2010). Thus, transgenic strategies based on expression of B transporters might enable the engineering of crops with greater yields in soils with low or high B phytoavailability.

## FERTILIZER MANAGEMENT FOR OPTIMAL PRODUCTIVITY AND SUSTAINABILITY

Crops require a sufficient, but not excessive, supply of essential mineral elements for optimal productivity. An insufficient supply of mineral elements required in large quantities and/or mineral elements with low phytoavailability in soils often limits crop production. In many agricultural soils, there is rarely sufficient phytoavailable N, P or K to supply enough of these elements for the rapid growth of crop plants during their early growth. Hence, these elements are supplied as fertilizers in both intensive and extensive agricultural systems. In addition, in areas where mineral deficiencies occur in animals and/or humans, fertilizers are applied not only to increase crop production but also to increase concentrations of essential mineral elements in edible portions. However, there are both financial and environmental costs to the use of mineral fertilizers (Lægreid *et al.*, 1999; Galloway *et al.*, 2008; Conley *et al.*, 2009; Ju *et al.*, 2009). It is therefore important to optimize the efficiency with which fertilizers are used in crop production. Increased fertilizer use efficiency can be achieved agronomically, through improved fertilizer-management practices, and/or genetically, by cultivating crops that acquire and/or utilize mineral elements more effectively (Hirel *et al.*, 2007; Rengel and Damon, 2008; White and Hammond, 2008; Fageria, 2009; Ju *et al.*, 2009). The latter can be addressed through conventional breeding and/or modern biotechnological approaches. Ultimately, sustainable crop production is achieved when stable levels of food production and quality are maintained without compromising economic profitability or the environment.

Agronomic mineral use efficiency (MUE) is generally defined as crop dry matter (DM) yield per unit of mineral element available (Ma) in the soil (g DM $g^{-1}$ Ma), which is equivalent to the product of the plant mineral content (Mp) per unit of available mineral (g Mp $g^{-1}$ Ma), often referred to as plant mineral uptake efficiency (MUpE), and the yield per unit plant mineral content (g DM $g^{-1}$ Mp), often referred to as the mineral utilization efficiency (MUtE). Considerable within-species genetic variation has been observed in all these measures for the mineral elements frequently supplied in fertilizers, including N, P and K (see reviews by Hirel *et al.*, 2007; Rengel and Damon, 2008; White and Hammond, 2008; Fageria, 2009; Sylvester-Bradley and Kindred, 2009). Several articles in this Special Issue explore the phenotypic traits and genetic factors affecting nitrogen use efficiency, phosphorus use efficiency and potassium use efficiency by crops.

Masclaux-Daubresse *et al.* (2010) review our current understanding of the physiology, metabolism and genetics of nitrogen uptake, assimilation and remobilization by plants, and discuss how misexpression of genes encoding transport proteins, metabolic enzymes and transcription factors have been manipulated in attempts to improve agronomic nitrogen use efficiency (NUE) in crops. They observe that the over-expression of genes encoding nitrate transporters, nitrate reductases or nitrite reductases rarely has any effect on NUE. However, the over-expression of genes encoding glutamine synthases, asparagine synthases or glutamate synthases (GOGAT) often increases the yield of transgenic plants and, concomitantly, improves NUE. They also observe that the over-expression of alanine aminotransferase can increase the nitrogen uptake efficiency (NUpE) and yields of plants grown with a low N supply, and that ectopic expression of *Dof1*, a transcription factor that regulates the expression of genes involved in organic acid metabolism, increases the accumulation of amino acids in transgenic *A. thaliana*. These observations are broadly consistent with reports that genes encoding glutamine synthases or the NAC transcription factor NAM-B1, which accelerates leaf senescence and the remobilization of nutrients to seeds, occur in quantitative trait loci (QTL) controlling NUE in various plant species (Hirel *et al.*, 2007; Masclaux-Daubresse *et al.*, 2010). They also provide a context for the papers by Couturier *et al.* (2010), who describe the processes of N remobilization from leaves to stem during autumn senescence in poplar (*Populus*

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*trichocarpa*), and Beatty *et al.* (2010), who consider the physiology of NUE in spring barley (*Hordeum vulgare*).

Forest soils have extremely low N availability and woody plants show characteristic adaptations to cope with seasonal N demand for growth (Cooke and Weih, 2005). In autumn, deciduous trees remobilize N from their senescing leaves for storage in woody tissues over winter. Couturier *et al.* (2010) observe that glutamine accumulates in senescing leaves of poplar, whereas arginine concentrations increase dramatically in the stem. They also observe that the expression of *Pt-CAT11*, which encodes a cationic amino acid transporter, increases in the phloem of senescing leaves, noting that the abundance of *Pt-CAT11* transcripts was strongly correlated with leaf glutamine concentrations, and demonstrate that Pt-CAT11 transports glutamine. Simultaneously with the increased expression of *Pt-CAT11*, they observe an increase in the expression of arginine biosynthesis genes in the stem. Thus, they speculate that leaf proteins are converted to glutamine in senescing leaves, which is then loaded into the phloem by Pt-CAT11 and transported to the stem, where it is converted first to arginine and then to Bark Storage Proteins for winter storage.

Beatty *et al.* (2010) compare the morphological characteristics and seed yield of spring barley genotypes grown both in the field and in compost or hydroponics in growth chambers with low and high N supply to determine the efficiencies of N uptake (NUpE), N utilization (NUtE) and agronomic NUE in these two environments. The rank order of genotypes in these efficiency characteristics was consistent between environments, suggesting that trials scored in controlled environments can be used to identify phenotypic and genetic targets for improving NUE in spring barley. In addition, they observed that, in their experiments, NUtE contributed more than NUpE to NUE when plants were grown with a low N supply. This has also been observed for other crops grown in low N environments (Fageria, 2009). Beatty *et al.* (2010) also note significant differences in tissue amino acid profiles between spring barley genotypes, which might be related to their NUtE.

The phytoavailability of P limits crop production worldwide and crop genotypes with better P-fertilizer use efficiencies are being sought (Vance *et al.*, 2003; White and Hammond, 2008). Extensive screening of germplasm collections has indicated that differences between genotypes in their yield responses to P fertilization are often correlated with P acquisition efficiency (PUpE) but not P utilization efficiency (PUtE) within the plant (White and Hammond, 2008). Plant roots acquire P as phosphate. Because phosphate is present at exceedingly low concentrations in the soil solution, plant roots must forage for this element (White and Hammond, 2008). Strategies that improve PUpE include the exudation of protons, metabolites and enzymes into the rhizosphere to increase P availability and changes in root morphology and/or associations with microorganisms to explore the soil more effectively (Lynch, 2007; White and Hammond, 2008; Hammond *et al.*, 2009; Hinsinger *et al.*, 2009).

In this Special Issue, Devau *et al.* (2010) describe the use of a mechanistic model based on the adsorption of cations and anions to soil constituents to investigate the effects of root-induced chemical changes on P acquisition by durum wheat (*Triticum durum* Desf.). They reveal that, in addition to rhizosphere acidification, Ca uptake by roots can increase phosphate availability in the rhizosphere and therefore P acquisition by plants. They also observed that the effect of Ca uptake on P availability increased with increasing pH. Tian *et al.* (2009) have described the cloning of two genes encoding small purple acid phosphatases (*PvPAP3*, *PvPAP4*) from common bean, expression of which in both leaves and roots is increased by P-starvation and correlates well with both P acquisition and growth of progeny derived from a cross between P-efficient (G19833) and P-inefficient (DOR364) lines reported in a previous field experiment conducted with a low P supply (Liao *et al.*, 2004). These enzymes are thought to hydrolyse extracellular organic phosphates.

It has been proposed that breeding crops that acquire and/or utilize K more effectively can reduce the use of expensive K fertilizers in agriculture (Rengel and Damon, 2008; Fageria, 2009). In this Special Issue, White *et al.* (2010) report over two-fold variation in shoot K concentration ($[K]_{shoot}$) in a collection of *Brassica oleracea* L. genotypes thought to contain most of common allelic variation in this species when grown in the glasshouse. They also identify chromosomal loci (QTL) affecting K utilization efficiency (KUtE), defined as the reciprocal of shoot K concentration ($1/[K]_{shoot}$), and K acquisition efficiency (KUpE), defined as shoot K content, using a genetic mapping population grown in the glasshouse and field. They observe that shoot biomass is correlated with KUpE but not KUtE and that, although there is sufficient genetic variation in *B. oleracea* to breed for KUpE or KUtE, QTL associated with these traits differed between glasshouse and field environments. Hence, marker-assisted breeding programmes addressing KUE must consider carefully the conditions under which the crop will be grown.

## PLANT NUTRITION FOR HUMAN HEALTH

Humans are likely to require at least 25 mineral elements for their well-being (Table 1; Graham *et al.*, 2007; Stein, 2010). The dietary source of most of these elements is plants. Regrettably, mineral malnutrition is prevalent in both developed and developing countries and it is estimated that up to two-thirds of the world's population might be at risk of deficiency in one or more essential mineral element (White and Broadley, 2009; Stein, 2010). This is considered to be one of the most serious challenges to humankind (Copenhagen Consensus 2008, http://www.copenhagenconsensus.com/Home.aspx). The mineral elements most commonly lacking in human diets are Fe, Zn, I, Se, Ca, Mg and Cu (White and Broadley, 2009; Stein, 2010).

Edible plant tissues can contain low concentrations of mineral elements for a variety of reasons: some plant species have inherently low concentrations of particular mineral elements – for example, the Poales have inherently low concentrations of Ca and Mg (Broadley *et al.*, 2004; Watanabe *et al.*, 2007); crops might be grown in areas with low mineral phytoavailability, such as occur throughout the world for Fe, Zn and Cu in calcareous or alkaline soils (Frossard *et al.*, 2000; Rengel, 2001; Cakmak, 2004, 2008; Broadley *et al.*, 2007), for Mg in coarse-textured, calcareous or strongly acidic soils (Wilkinson *et al.*, 1990), for I in mid-continental regions (Lyons *et al.*, 2004; Risher and Keith,

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2009) and for Se in soils derived mostly from igneous rocks (Hartikainen, 2005; Broadley *et al.*, 2006); or edible portions could be consumed that have intrinsically low concentrations of mineral elements with restricted phloem mobility, such as fruits, seeds and tubers (Karley and White, 2009; White and Broadley, 2009).

To address the occurrence of mineral deficiencies in human populations, plant scientists are devising methods of applying fertilizers and/or using plant breeding strategies to increase the concentrations and/or bioavailability of mineral elements in agricultural produce (Cakmak, 2004, 2008; Graham *et al.*, 2007; Pfeiffer and McClafferty, 2007; White and Broadley, 2009). These approaches are termed 'agronomic' and 'genetic' biofortification, respectively. Agronomic strategies to increase the concentrations of mineral elements in edible portions of major crops have been reviewed recently by various authors in the contexts of both sustainable economic development and global health (Cakmak, 2004, 2008; Graham *et al.*, 2007; White and Broadley, 2009). These have included reviews of appropriate methods, infrastructural requirements and practical benefits for food production, economic sustainability and human health, of agronomic biofortification of edible crops with Fe and Zn (Cakmak, 2004; Graham *et al.*, 2007; White and Broadley, 2009), the successful use of inorganic Se fertilizers to increase dietary Se intakes in Finland, New Zealand and elsewhere (Hartikainen, 2005; Broadley *et al.*, 2006; Ekholm *et al.*, 2007), and the iodinization of irrigation water to increase dietary intakes of I in China (Jiang *et al.*, 1997; Lyons *et al.*, 2004).

Similarly, researchers are investigating genetic variation in mineral concentrations in edible portions of major crops, the interactions between genotype and environment, and the potential for breeding for increased concentrations of mineral elements in produce (Pfeiffer and McClafferty, 2007; Cakmak, 2008; White and Broadley, 2009). Although the total concentrations of Fe, Zn and Cu in most soils are sufficient to support mineral-dense crops, the accumulation of these mineral elements is often limited by their phytoavailability and acquisition by plant roots. White and Broadley (2009) have provided a detailed overview of genetic factors influencing the concentrations of essential mineral elements in edible tissues of common crops, and Pfeiffer and McClafferty (2007) have described the research undertaken by the HarvestPlus programme to increase concentrations of Fe and Zn in staple foods.

Recently, several authors have addressed sociological and economic aspects of genetic biofortification strategies, concluding that biofortification is an appropriate, achievable and cost-effective strategy to alleviate mineral malnutrition (Nestel *et al.*, 2006; Graham *et al.*, 2007; White and Broadley, 2009; Stein, 2010). In this Special Issue, Chatzav *et al.* (2010) report the genetic variation in concentrations of mineral elements in grain of wild emmer wheat (*Triticum turgidum* ssp. *dicoccoides* (Körn.) Thell.) and discuss the potential to exploit favourable alleles to increase the concentrations of mineral elements in domesticated wheats (*Triticum aestivum*; *Triticum durum*). Similarly, Ding *et al.* (2010) report chromosomal loci (QTL) affecting the concentrations of mineral elements in seed of oilseed rape (*Brassica napus*) grown in the field in two seasons with contrasting P-fertilization regimes. They discuss the likelihood that common QTL control seed concentrations of diverse mineral elements, but suggest that the lack of environmental robustness could compromise the use of these QTLs in breeding programmes to increase the concentrations of mineral elements in seed of *B. napus*.

## SUMMARY

The articles in this Special Issue of the *Annals of Botany* provide examples of how knowledge of plant mineral nutrition is contributing to sustainable crop production and to human health.

Crop production is often limited by low phytoavailability of essential mineral elements and/or the presence of excessive concentrations of potentially toxic mineral elements in the soil. This can be addressed partially by traditional agronomic strategies and through the development of novel crop genotypes. In recent years, researchers have contributed to future breeding strategies by identifying traits and genes that can increase yields on soils with restricted phytoavailablity of essential mineral elements and soils compromised by excessive concentrations of mineral elements. Examples of this are presented in this Special Issue. In particular, authors have targeted improved use efficiencies of N, P and K fertilizers (Beatty *et al.*, 2010; Couturier *et al.*, 2010; Devau *et al.*, 2010; Masclaux-Daubresse *et al.*, 2010; White *et al.*, 2010) and tolerance of sodic, acidic or waterlogged soils (Eticha *et al.*, 2010; Führs *et al.*, 2010; Kobayashi *et al.*, 2010; Miwa and Fujiwara, 2010).

The essential mineral elements required by humans and other animals enter the food chain primarily through plants. The concentrations of mineral elements in edible plant tissues are therefore of fundamental importance to human nutrition. It is estimated that up to two-thirds of the world's population might be at risk of deficiency in one or more essential mineral element, with deficiencies of Fe and Zn being most common (White and Broadley, 2009; Stein, 2010). The concentrations of mineral elements in edible crops can be increased by the judicious application of mineral fertilizers and/or by cultivating genotypes with higher concentrations. The bioavailability of mineral elements can also be increased through crop husbandry, breeding or genetic manipulation (White and Broadley, 2009). In this Special Issue, Conn and Gilliham (2010) describe how transport processes and cell-specific accumulation affect the concentrations of mineral elements in edible tissues and Chatzav *et al.* (2010) and Ding *et al.* (2010) assess the potential for increasing the concentrations of essential mineral elements in wheat and brassica crops.

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