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Review Article

Managing the Nutrition of Plants and People

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One definition of food security is having sufficient, safe, and nutritious food to meet dietary needs. This paper highlights the role of plant mineral nutrition in food production, delivering of essential mineral elements to the human diet, and preventing harmful mineral elements entering the food chain. To maximise crop production, the gap between actual and potential yield must be addressed. This gap is 15–95% of potential yield, depending on the crop and agricultural system. Current research in plant mineral nutrition aims to develop appropriate agronomy and improved genotypes, for both infertile and productive soils, that allow inorganic and organic fertilisers to be utilised more efficiently. Mineral malnutrition affects two-thirds of the world's population. It can be addressed by the application of fertilisers, soil amelioration, and the development of genotypes that accumulate greater concentrations of mineral elements lacking in human diets in their edible tissues. Excessive concentrations of harmful mineral elements also compromise crop production and human health. To reduce the entry of these elements into the food chain, strict quality requirements for fertilisers might be enforced, agronomic strategies employed to reduce their phytoavailability, and crop genotypes developed that do not accumulate high concentrations of these elements in edible tissues.

1. Introduction

Food security can be defined as having sufficient, safe, and nutritious food to meet the dietary needs of an active and healthy life [1]. This paper discusses the role of plant mineral nutrition in crop production, the delivery of mineral elements required for human wellbeing, and the prevention of toxic mineral elements entering the human food chain.

Crop production is predicated on the phytoavailability of sufficient quantities of the 14 essential mineral elements required for plant growth and fecundity (Table 1; [2, 3]). These are the macronutrients, nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and sulphur (S), which are required in large amounts by crops, and the micronutrients chlorine (Cl), boron (B), iron (Fe), manganese (Mn), copper (Cu), zinc (Zn), nickel (Ni), and molybdenum (Mo), which are required in smaller amounts [4]. Deficiency in any one of these elements restricts plant growth and reduces crop yields. In geographical areas of low phytoavailability, these mineral elements are often applied to crops as inorganic or organic fertilisers to increase crop production [2, 3]. However, the application of fertilisers incurs both economic and environmental costs. In some regions, especially those remote from the origin of manufacture, the cost of inorganic fertilisers can constitute a high proportion of total production costs, and vagaries and uncertainties in the price of inorganic fertilisers can prohibit their use [5, 6]. The manufacture of inorganic fertilisers is energy intensive and depletes natural resources, and fertiliser applications that exceed crop requirements can reduce land, water, and air quality through leaching and runoff, eutrophication, and gaseous emissions [7, 8]. Current research in plant mineral nutrition is directed towards developing (1) agronomic strategies that improve the efficiency of fertiliser use by crops and (2) genetic strategies to develop crops with greater acquisition and physiological utilisation of mineral elements [3, 4]. These efforts contribute both to food security and to the economic and environmental sustainability of agriculture.

Humans require sufficient intakes of many mineral elements for their wellbeing [4, 11–13]. In addition to the 14

Table 1: The main chemical forms in which mineral elements are acquired from the soil solution by roots, and the critical leaf concentrations for their sufficiency and toxicity in nontolerant crop plants. 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%. 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. Data are compiled from references [4, 9, 10].

Element	Form acquired	Critical leaf concentrations (mg g^{-1} DM)	
		Sufficiency	Toxicity
Nitrogen (N)	NH_4^+, NO_3^-	15–40	
Potassium (K)	K^+	5–40	>50
Phosphorus (P)	$H_2PO_4^-$	2–5	>10
Calcium (Ca)	Ca^{2+}	0.5–10	>100
Magnesium (Mg)	Mg^{2+}	1.5–3.5	>15
Sulphur (S)	SO_4^{2-}	1.0–5.0	
Chlorine (Cl)	Cl^-	0.1–6.0	4.0–7.0
Boron (B)	$B(OH)_3$	$5–100 \times 10^{-3}$	0.1–1.0
Iron (Fe)	Fe^{2+} Fe^{3+}-chelates	$50–150 \times 10^{-3}$	>0.5
Manganese (Mn)	Mn^{2+} Mn-chelates	$10–20 \times 10^{-3}$	0.2–5.3
Copper (Cu)	Cu^+, Cu^{2+} Cu-chelates	$1–5 \times 10^{-3}$	$15–30 \times 10^{-3}$
Zinc (Zn)	Zn^{2+} Zn-chelates	$15–30 \times 10^{-3}$	$100–300 \times 10^{-3}$
Nickel (Ni)	Ni^{2+} Ni-chelates	0.1×10^{-3}	$20–30 \times 10^{-3}$
Molybdenum (Mo)	MoO_4^{2-}	$0.1–1.0 \times 10^{-3}$	>1
Sodium (Na)	Na^+	—	2–5
Aluminium (Al)	Al^{3+}	—	$40–200 \times 10^{-3}$
Cobalt (Co)	Co^{2+}	—	$10–20 \times 10^{-3}$
Lead (Pb)	Pb^{2+}	—	$10–20 \times 10^{-3}$
Cadmium (Cd)	Cd^{2+} Cd-chelates	—	$5–10 \times 10^{-3}$
Mercury (Hg)	Hg^{2+}	—	$2–5 \times 10^{-3}$
Arsenic (As)	$H_2AsO_4^-$, H_3AsO_3	—	$1–20 \times 10^{-3}$
Chromium (Cr)	Cr^{3+}, CrO_4^{2-}, $Cr_2O_7^{2-}$	—	$1\text{-}2 \times 10^{-3}$

elements that are essential for plants, humans require significant amounts of sodium (Na), selenium (Se), cobalt (Co) and iodine (I) in their diet and possibly small amounts of fluorine (F), lithium (Li), lead (Pb), arsenic (As), vanadium (V), chromium (Cr), and silicon (Si) also. Ultimately, plant products provide humans with the majority of these mineral elements. Unfortunately, the diets of over two-thirds of the world's population lack one or more of these essential mineral elements [13–15]. In particular, over 60% of the world's 6 billion people are Fe deficient, over 30% are Zn deficient, almost 30% are I deficient, and about 15% are Se deficient. In addition, dietary deficiencies of Ca, Mg and Cu occur in many developed and developing countries. Mineral malnutrition is attributed to either crop production on soils with low phytoavailability of mineral elements essential to human nutrition or consumption of staple crops, such as cereals, or phloem-fed tissues, such as fruit, seeds, and tubers, that have inherently low tissue concentrations of certain mineral elements [14, 16], compounded by a lack of fish or animal products in the diet. Soils with low phytoavailability of mineral elements include (1) alkaline and calcareous soils that have low phytoavailabilities of Fe, Zn, and Cu, and comprise 25–30% of all agricultural land [10, 14, 17–21], (2) coarse-textured, calcareous, or strongly acidic soils that have low Mg content [22], (3) midcontinental regions that have low I content [23, 24], and (4) soils derived mostly from igneous rocks that have low Se content [25, 26]. Currently, mineral malnutrition is considered to be amongst the most serious global challenges to humankind and is avoidable [13–15, 27].

The presence of excessive concentrations of potentially harmful mineral elements also compromises both crop production (Table 1) and human health. On acid soils, toxicities of Mn and aluminium (Al) limit crop production [3, 4, 10, 28]. Soil acidity occurs on about 40% of the world's agricultural land [29, 30]. Additionally, Na, B, and Cl toxicities reduce crop production on sodic or saline soils, which comprise 5–15% of the world's potential agricultural land [31] and toxicities of Mn and Fe can arise in waterlogged or flooded soils [10]. Excessive concentrations of Ni, Co, Cr, and Se can limit growth of plants on soils derived from specific geological formations [10, 32, 33]. In addition, imbalances of Ca, Mg, and K can occur in irrigated agriculture and toxic concentrations of Zn, Cu, Pb, As, cadmium (Cd) and mercury (Hg) have accumulated in agricultural soils in some areas due to human activities [10, 34–36]. Mineral imbalances of Ca, Mg, and K in forage can have serious consequences for the nutrition and health of ruminant animals [14]. Toxic elements contained in produce can accumulate in the food chain with detrimental consequences for animal and human health.

This paper describes how the application of current knowledge of soil science, agronomy, plant physiology, and crop genetics can underpin the production of edible crops that contribute sufficient mineral elements for adequate animal and human nutrition, whilst limiting the entry of toxic elements to the human food chain.

2. Increasing Food Production

The successes of the "Green Revolution" have enabled food production to keep pace with the growth of human populations through the development of semidwarf crops resistant to pests and pathogens, whose yields are maintained through the application of agrochemicals to control weeds, pests, and diseases, mineral fertilisers, and irrigation [3, 37, 38]. It is widely believed that the world currently produces sufficient food for its population, and it is often assumed that food security can be achieved by better distribution and access, driven principally by open markets [39, 40]. In this context, it is often stated that about one-sixth of the world's population are obese, whilst another sixth are starving. The immediate social imperative is, therefore, to redistribute food according to need and, in the future, to maintain food production at rates equal to, or greater than, population growth. The world's population is increasing at a rate of 80 million people a year, and many of these people will live in developing countries [6, 38, 41]. Feeding these people will necessitate significant infrastructural development.

Recent estimates suggest that less than 20% of the increased crop production required in the next two decades could come from the cultivation of new land and about 10% from increased cropping intensity [6, 42]. Thus, food security for the world must be achieved by increasing yields per hectare on the same land area farmed today. It was suggested that average cereal yields needed to increase by about 25% from 3.23 t ha^{-1} in 2005/07 to 4.34 t ha^{-1} in 2050 to feed the world's population [41]. This is a challenging task. The production of food crops is further challenged by increasing demands for animal feeds, fibres, timber, biofuels, landscape amenities, biological conservation, and urban development [6, 38–45]. It is estimated that almost half the world's food production is directly supported by manufactured N-fertilisers and that this reliance will increase as the population of the world grows [8, 12, 46].

2.1. Reducing the Yield Gap. The "yield gap" is the difference between actual and potential crop production. Potential crop production is defined as an idealised state in which an adapted crop variety grows without losses to pests or pathogens and experiences no biophysical limitation other than uncontrollable factors, such as solar radiation, air temperature, and water supply [47, 48]. Yield gaps can range from 15 to 95% of yield potential, depending on the crop grown and the agricultural system employed [38, 47–50]. Irrigated crops often approach 80% of potential yield, whilst rainfed systems deliver a lower percentage of potential yield [47]. Higher inputs realise greater yields and reduce yield gaps [47]. Global aggregated yield gaps are currently estimated to be about 60% for maize, 47% for rice, and 43% for wheat [48]. Agricultural systems can be categorised as either "intensive" or "extensive". Intensive agricultural systems utilise high inputs of fertilisers, agrochemicals, and water, together with effective mechanization, to produce high yields per unit area. Extensive agriculture is associated generally with smallholder farming. It has low inputs of capital and labour and, often, low yields per unit area. Yield gaps are greatest for extensive agricultural systems, which have, therefore, the greatest potential for increased crop production. Extensive agriculture occupies >40% of the world's agricultural land and sustains about 40% of its population [49]. Major contributors to yield gaps include (1) biophysical factors, such as soil texture, pH and mineral composition, drought, flooding, and land topology, (2) biotic factors, such as weed pressures, which can reduce global yields of major crops by 20–40%, and losses to pests and diseases, which can reduce global yields of major crops by 25–50% [51], (3) poor husbandry, such as inferior seed, suboptimal planting rates, inappropriate fertiliser applications, and occurrence of lodging, and (4) socioeconomic factors, such as profit maximization, risk aversion, market influences, lack of capital, infrastructure or labour, and lack of information [38, 39, 47, 48]. Thus, reducing yield gaps will depend on the implementation of improved technologies that address water availability, soil conditions, mineral nutrition, crop protection, and crop husbandry [47].

2.2. Alleviating Constraints on Infertile Soils. Major constraints to crop production occur on alkaline, acid, saline, and sodic soils [4]. These constraints can be addressed by both agronomic measures and by the cultivation of adapted genotypes.

The major constraints to crop production in acid soils are Al and Mn toxicities. Liming, especially with dolomitic lime ($CaMg(CO_3)_2$), is an effective way to raise soil pH to avoid Al and Mn toxicities, and also to avoid Ca and Mg deficiencies [10, 21, 28]. The primary constraint is often Al toxicity, and cultivating Al-excluding or Al-tolerant crops allows agricultural production on acid soils. Plant roots can reduce Al uptake (1) by secretion of organic acids or mucilage from the root to chelate Al in the rhizosphere, (2) by raising rhizosphere pH to reduce the concentration of Al^{3+}, which is the phytotoxic Al species, and (3) by binding Al to cell wall components [28, 52–54]. Aluminium entering plant cells can be rendered nontoxic by sequestration in the vacuole as a complex with organic acids [28, 52, 53]. Crop genotypes with these attributes can be selected in breeding programmes or created by genetic modification (GM) of elite germplasm [3, 54]. Likewise, there are large differences both between and within plant species in their exclusion and tolerance of Mn, which can be exploited to improve crop production on acid soils [28].

The major constraint to crop production on calcareous or alkaline soils is often the low phytoavailability of Fe, Zn, Mn, or Cu [10, 17, 19, 21, 27, 34]. This can be remedied by supplying these elements as soil or foliar fertilisers. The application of acidifying fertilisers, such as urea, ammonium nitrate, ammonium sulphate, ammonium phosphates, or elemental S, can address soil alkalinity, whilst the introduction of appropriate microorganisms and companion plants, either through intercropping or inclusion in rotations, that increase the phytoavailability of Fe, Zn, Mn, and Cu can increase the yields of crops susceptible to their deficiencies [10, 12, 14, 21]. In addition, since the total concentrations of Fe, Zn, Mn, and Cu in many soils would be sufficient for crop nutrition if they were phytoavailable, cultivating genotypes with greater acquisition or physiological utilisation of these elements can increase crop yields [10, 12, 19, 27, 55]. There is considerable genetic variation both between and within plant species in their growth responses to the phytoavailability of Fe, Zn, Cu, and Mn, in their ability to acquire these mineral elements, and in their physiological utilisation of these elements to produce yield [19, 21, 55–58].

Sodium toxicity is thought to affect 5–15% of potential agricultural land [31]. Crop production on this land can be increased by management practices that reduce the concentration of Na^+ in the soil solution [59]. Traditionally, saline soils are remediated by leaching soluble salts from the soil profile by irrigation with fresh water, and sodic soils are remediated through the application of Ca^{2+}, often as gypsum, followed by flushing the soil with fresh water [59]. These management practices also remove Cl and B (depending on soil pH) from saline and sodic soils. These management strategies can be augmented by growing crops or varieties that have greater exclusion or tolerance of Na, Cl, or B. There is considerable genetic variation both between and within plant species for growth in soils with high Na, Cl and B concentrations that can be utilised for crop selection or breeding [31, 60–62]. In addition, knowledge of plant transport processes has allowed transgenic plants to be created that have greater yields on saline and sodic soils. For example, the overexpression of orthologues of HKT1 that retrieve of Na^+ from the xylem restricts shoot Na concentrations and confers Na tolerance to transgenic plants [31, 63], and increased expression of genes encoding transport proteins that catalyse B efflux from cells (BORs) increases tolerance to high B concentrations in the soil solution [62, 64].

2.3. Optimising Fertiliser Applications for Sustainable Intensification. In many agricultural soils, there is insufficient phytoavailable N, P, or K for the rapid growth of crop plants [3, 8, 65, 66]. To increase crop yields, these elements are, therefore, supplied as inorganic fertilisers, manures, composts, or miscellaneous “waste” materials including industrial biproducts, such as blood and bones, winery, brewery, and distillery residues, residues from sugar production, plasterboard, and paper crumble, and fly ash [8, 67–70]. To increase food production in the future, sustainable intensification will be required. High crop yields might be achieved and sustained through appropriate management of multiple sources of mineral input, both inorganic and organic, to remove nutritional constraints to crop production, supported by suitable amendments to address other soil constraints such as acidity or alkalinity [3, 67].

There are many agronomic strategies to improve efficiencies in the use of inorganic and organic fertilisers by crops. These include the use of (1) fertiliser recommendations informed by field response trials and based on soil or plant analyses [67, 71], (2) model-based decision support systems to inform fertiliser recommendations [72, 73], (3) fertiliser placement and other precision application technologies [66, 67, 73–75], (4) foliar fertilisation through insecticide and herbicide spraying programmes to allow fertiliser applications when crops are growing at maximal rates, and (5) crop residues, composts, or animal manures to improve soil quality [21, 67, 76, 77]. The introduction of legumes into rotations improves their N-economies and can increase crop yields in extensive, N-limited agricultural systems [67, 78].

These agronomic strategies can be complemented by the development of crop varieties that acquire and utilise fertilisers more efficiently to produce a commercial yield. The literature contains many definitions relating to the efficient use of fertilisers in agriculture [79]. The agronomic use efficiency of a mineral element (MUE) supplied in a fertiliser is generally defined as crop dry matter (DM) yield per unit of mineral element available (M_a) in the soil (g DM g^{-1} M_a). This is numerically equivalent to the product of the plant mineral content (M_p) per unit of available mineral element (g M_p g^{-1} M_a), which is often referred to as plant mineral uptake efficiency (MUpE), and the yield per unit plant mineral content (g DM g^{-1} M_p), which is often referred to as the mineral utilisation efficiency (MUtE) of the plant. There is considerable genetic variation, both between and within crop species, in all these measures for mineral elements supplied in fertilisers, including N, P, and K [21, 80–84].

Nitrogen utilisation efficiency (NUtE) often contributes more than N uptake efficiency (NUpE) to agronomic N use efficiency (NUE) when plants are grown with a low N supply [21, 85–87]. Historical improvements in NUtE are attributed to a greater partitioning of dry matter to the grain (i.e., increased harvest index), and NUtE is often positively correlated with yield. In crops, such as cereals and oilseed rape, that require continued N uptake by the root system following anthesis, NUpE also contributes significantly to NUE [87, 88].

In contrast, differences between genotypes in their yield responses to P fertilisation are often correlated with P uptake efficiency (PUpE) but not P utilisation efficiency (PUtE) within the plant [79, 82]. The trait of PUpE has been attributed to improved root architectures, particularly greater production of lateral roots, topsoil foraging characteristics, the production of root hairs, and the exudation of organic acids and phosphatases into the rhizosphere [65, 79, 82, 89, 90].

Chromosomal loci (QTL) influencing aspects of PUE have been reported in rice [91–96], wheat [97, 98], maize [99–101], bean [102–105], soybean [106–108], *Brassica rapa* [109, 110], *Brassica oleracea* [89], and *Brassica napus* [111, 112]. This genetic knowledge will accelerate breeding for PUE in crops.

Plant species vary considerably in their responses to K-fertiliser and in their abilities to acquire and utilise K for growth [21, 113, 114]. Although there is genetic variation in both K uptake efficiency (KUpE) and K utilisation efficiency (KUtE) within crop species [21, 81, 84, 113, 115], agronomic K use efficiency (KUE) is often correlated with KUpE and rarely with KUtE [84]. Greater KUpE has been attributed to: (1) increased exudation of compounds that release more nonexchangeable K^+ into the soil solution, (2) increased K^+ uptake capacity of root cells, which accelerates K^+ diffusion to the root surface, (3) proliferation of roots into the soil volume, which decreases the distance for K^+ diffusion to the root and increases the root surface area available for K^+ uptake, and (4) higher transpiration rates, which accelerates the mass flow of the soil solution to the root surface [114].

3. Biofortification of Edible Crops for Human Nutrition

In principle, two complementary strategies can be employed to increase mineral concentrations in edible crops [11, 12, 14, 15, 27, 116–119]. The first strategy, termed "agronomic" biofortification, employs the use of fertilisers containing the mineral elements lacking in human diets, principally Zn, Cu, Fe, I, Se, Mg, and Ca, in conjunction with (1) appropriate soil amendments, such as composts and manures to increase soil concentrations of essential elements, (2) acidifying fertilisers, such as urea, ammonium nitrate, ammonium sulphate, ammonium phosphates, or elemental S, to rectify soil alkalinity or lime to rectify soil acidity, and (3) appropriate crop rotations, intercropping, or the introduction of beneficial soil microorganisms to increase the phytoavailability of mineral elements [10, 14, 21, 55, 120]. Where mineral elements, such as Fe or Zn, become rapidly unavailable to roots, the use of foliar fertilisers, rather than soil fertilisers, is recommended [3, 10]. The application of N fertilisers, can be used to increase Zn concentrations in leaves and phloem-fed tissues [121–125]. The second strategy, termed "genetic" biofortification, employs crop genotypes with increased abilities to acquire mineral elements and accumulate them in edible tissues. There is sufficient natural genetic variation in the concentrations of mineral elements commonly lacking in human diets in the edible tissues of most crop species to breed for increased concentrations of mineral elements in edible tissues [14, 27, 118, 126] and also scope for targeted GM of crops [14, 125–127].

Agronomic strategies are most effective where appropriate infrastructures for the production, distribution, and application of inorganic fertilisers are available and are the only feasible strategies in regions where soils have insufficient concentrations of mineral elements required for human nutrition to support mineral-dense crops [12, 14, 20, 116]. Several authors have reviewed appropriate methods, infrastructural requirements, and practical benefits for food production, economic sustainability, and human health of agronomic biofortification of edible crops [12, 14, 20, 116]. Examples of the successful use of agronomic strategies include (1) the application of Se-fertilisers to increase dietary Se intakes in Finland, New Zealand, and elsewhere [25, 26, 128], (2) the iodinisation of irrigation water to increase dietary intakes of I in Xinjiang, China [23, 129], and (3) the use of compound fertilisers containing Zn to increase crop production, dietary Zn intakes, and human health in Anatolia, Turkey [20, 116]. Rational approaches to select areas that would benefit most from agronomic biofortification have also been developed [130].

Genetic strategies can be considered in regions where the total concentrations of mineral elements required for human nutrition are sufficient to support mineral-dense crops, but the accumulation of these elements is limited by their phytoavailability and acquisition by plant roots [14]. This strategy is particularly relevant in areas lacking the infrastructures required for fertiliser distribution [14, 15]. It is considered cost effective and beneficial to the 40% of the world's population who rely primarily on their own food for sustenance [14, 15]. It has been observed that there is sufficient genetic variation within germplasm collections of all major crops to breed varieties that accumulate greater concentrations of mineral elements in their edible portions [14, 15, 27, 118, 125]. Such breeding strategies can be facilitated by the development of molecular markers associated with the accumulation of essential mineral elements in edible portions of crop plants. Recent research has, therefore, been directed to the identification of chromosomal loci (QTL) associated with these traits (Table 2). For example, QTL affecting the accumulation of essential mineral elements commonly lacking in human diets in edible portions have been identified in rice [131–136], wheat [131–140], barley [141, 142], maize [143, 144], bean [145–152], soybean [153], brassicas [154–158], and potato [159]. This knowledge will facilitate conventional breeding of mineral-dense crops.

Strategies employing GM of crop plants are also being developed to increase the acquisition of mineral elements essential for human nutrition and their accumulation in edible tissues [14, 125, 160–162]. These strategies are primarily focussed on the biofortification of edible produce with Fe and Zn. In nongraminaceous plants, Fe uptake can be increased by overexpressing genes encoding Fe(III) reductases [163], and in graminaceous plants the acquisition of Fe and Zn can be increased by greater exudation of phytosiderophores [164]. The overexpression of genes encoding transporters catalysing Fe^{2+} or Zn^{2+} influx to root cells, sequestration in the vacuole, or delivery to the xylem have met with some success in the biofortification of roots and leaves of crop plants with Fe and Zn, but rarely in the biofortification of fruit, seeds, or tubers [14, 125, 127]. By contrast, the overexpression of genes encoding nicotianamine synthase (NAS) often leads to increased concentrations of Fe, Zn, and Mn both in leaves and in seeds [14, 125, 161]. In addition, targeted overexpression of genes encoding metal-binding proteins, such as ferritin and lactoferrin, have increased Fe, Zn, and Cu concentrations

Table 2: Studies in which chromosomal loci (QTL) have been identified in crop plants that affect the concentrations of essential mineral elements most commonly lacking in human diets.

Crop species	Tissue	Elements	References
Rice (*Oryza sativa*)	Grain	Fe	Gregorio et al. [131]
	Grain	Fe, Zn, Mn	Stangoulis et al. [132]
	Grain	Fe, Zn, Mn, Cu, Ca	Lu et al. [133]
	Grain	Fe, Zn, Mn, Cu, Ca, Mg	Garcia-Oliveira et al. [134]
	Grain	Fe, Zn, Mn, Cu, Mg, Se	Norton et al. [135]
	Grain	Zn	Zhang et al. [136]
Wheat (*Triticum* spp.)	Grain	Fe, Zn, Mn	Distelfeld et al. [137]
	Grain	Zn	Shi et al. [138]
	Grain	Fe, Zn	Genc et al. [139]
	Grain	Fe, Zn, Mn, Cu, Ca, Mg	Peleg et al. [140]
Barley (*Hordeum vulgare*)	Grain	Zn	Lonergan et al. [141]
	Grain	Zn	Sadeghzadeh et al. [142]
Maize (*Zea mays*)	Kernel	Fe	Lung'aho et al. [143]
	Kernel	Fe, Zn, Mg	Šimić et al. [144]
Bean (*Phaseolus vulgaris*)	Seed	Fe, Zn	Beebe et al. [145]
	Seed	Fe, Zn, Ca	Guzmán-Maldonado et al. [146]
	Seed	Zn	Cichy et al. [147]
	Seed	Fe, Zn, Ca	Gelin et al. [148]
	Seed	Fe, Zn	Blair et al. [149]
	Seed	Fe, Zn	Cichy et al. [150]
	Seed	Fe, Zn	Blair et al. [151]
	Seed	Fe, Zn	Blair et al. [152]
Soybean (*Glycine max*)	Seed	Ca	Zhang et al. [153]
Oilseed Rape (*Brassica napus*)	Seed	Fe, Zn, Mn, Cu, Ca, Mg	Ding et al. [154]
Brassica oleracea	Leaf	Ca, Mg	Broadley et al. [155]
	Leaf	Zn	Broadley et al. [156]
Brassica rapa	Leaf	Fe, Zn, Mn, Mg	Wu et al. [157]
	Leaf	Ca, Mg	Broadley et al. [158]
Potato (*Solanum tuberosum*)	Tuber	Fe, Zn, Cu, Ca, Mg	Subramanian [159]

in rice grain [160, 165, 166] and Fe concentrations in maize seeds [167], lettuce leaves [168], tomato fruits, and potato tubers [169]. In wheat, the expression of a functional NAC transcription factor (*NAM-B1*) increases grain Fe and Zn concentrations by accelerating senescence and increasing the remobilisation of these elements from leaves to developing grain [170]. Successful biofortification of edible produce with Ca has been achieved through the overexpression of genes encoding the vacuolar Ca^{2+}/H^{+}-antiporters AtCAX1 lacking its autoinhibitory domain (*sCAX1*), a modified AtCAX2 (*sCAX2*) or AtCAX4 in appropriate tissues [171–174].

4. Reducing the Entry of Toxic Elements to the Human Food Chain

Some natural soils can contain high concentrations of mineral elements that are potentially toxic to plants and animals [4]. For example, acid soils have excessive Al and Mn phytoavailability, serpentine soils can have excessive Ni, Co or Cr concentrations, and seleniferous soils contain excessive Se concentrations [10, 28, 33, 59]. Industrial activities have also contaminated agricultural soils with, for example, Pb, Cd, Ni, Zn, and Cu from the mining and refining of metal ores [10, 34, 59] and radioisotopes from intentional or accidental discharges [175, 176]. Other human activities, such as the burning of fossil fuels and various wastes, have also contributed to the atmospheric deposition of potentially toxic elements onto agricultural soils, and the application of Cu pesticides in agriculture has increased soil Cu concentrations [10, 34, 177, 178].

Soil amendments, including inorganic fertilisers, manures, sewage sludges, and urban wastes, can also contain high concentrations of potentially toxic mineral elements and radioisotopes [10, 34, 66–68, 178–181], and the recycling of agricultural and municipal wastes can also result in the accumulation of harmful, and persistent, organic compounds [68]. Some manufactured phosphate fertilisers can contain high concentrations of, in particular, Cd, Cr, Hg, Pb and radioisotopes of uranium (U), and radium (Ra), but

Table 3: Statutory maximum annual metal loading rates (kg ha^{-1} y^{-1}) over a ten-year period for agricultural soils in the United Kingdom [190] and the European Communities [191], statutory maximum cumulative metal loading rates (kg ha^{-1}) for agricultural soils in the United States of America [192], and critical soil concentrations (kg ha^{-1}) considered to be phytotoxic calculated assuming a soil bulk density of 1200 kg m^{-3} and a depth of 0.10 m [193].

Element	UK (kg ha^{-1} y^{-1})	EC (kg ha^{-1} y^{-1})	USA (kg ha^{-1})	Critical (kg ha^{-1})
Cd	0.15	0.15	39	6.0
Hg	0.1	0.1	17	3.7
Ni	3	3	420	120
Cu	7.5	12	1500	120
Cr	15	3	—	113
Pb	15	15	300	150
Zn	15	30	2800	390
Mo	0.2	—	—	8.1
Se	0.15	—	100	11
As	0.7	—	41	38

the concentrations of these elements vary widely depending upon the source of rock phosphate [2, 66, 67]. Animal manures and slurries can contain significant quantities of Cd, Cr, Pb, Co, Zn, Mn, Cu, and Mo [67, 178, 182]. Similarly, sewage sludges can contain high concentrations of Pb, Cd, Cr, Se, Co, Ni, Zn, Mn, and Cu, and also human pathogens [67, 178, 181, 183–186]. Composted municipal solid waste is frequently applied at high application rates (e.g., 200 Mg ha^{-1}), which can result in large amounts of Pb, Cd, Cr, As, Hg, Se, Co, Ni, Zn, Mn, Cu and Mo entering soils [67, 68, 185, 187]. Fortunately, the phytoavailability of many of these potentially toxic elements from municipal composts is relatively low [68, 185]. Industrial wastes such as food wastes, paper sludge, and fly ash can also contain significant amounts of potentially toxic elements [178, 188]. In many countries, legislation limits the quantities of heavy metals applied to soils on which edible crops are grown for human consumption (Table 3; [68, 178, 184, 187, 189–193]). It is important that these limits are followed to maintain both crop production and human health.

There are particular concerns about As concentrations in paddy rice, especially in South Asia in countries such as Bangladesh, India, and China [36]. Flooded paddy conditions lead to the mobilisation of arsenite, which is taken up efficiently by rice roots through the silicon transport pathway [36]. Growing rice for longer periods under aerobic soil conditions, by midseason draining of water or cultivation in raised soil beds, has been proposed as an effective way to reduce As uptake by rice, and Si-fertilisers can also be employed to restrict As uptake [36]. In addition to these agronomic strategies, varieties of rice are being identified that accumulate lower concentrations of As, and other potentially toxic elements, in grain and QTL associated with these traits are being identified for breeding safer crops [137, 194, 195]. Similarly, genotypes of other crops that accumulate lower concentrations of potentially toxic mineral elements in their edible portions are being developed through conventional breeding and GM approaches [10, 36, 126, 196].

The continued replenishment of mineral elements in the soil is essential to maintain future food production. Sustainable sources of mineral elements must be sought through recycling through the food chain. Crop residues, animal manures, sewage sludges, municipal composts, and industrial wastes can all contribute to the delivery of the mineral elements required for plant growth. However, their use can also increase inputs of potentially toxic elements and organic pollutants to agricultural soils. Legal limits to their use must be followed to prevent toxicities to plants and animals, and it is generally recommended that they are used in combination with inorganic fertilisers through integrated nutrient management to avoid threats to human health and the wider environment [67]. In particular, animal manures can contribute significantly to the input of potentially toxic elements to agricultural soils [68, 186]. To reduce the entry of potentially toxic elements to the human food chain from this source, feed regimes can be adopted that result in lower concentrations of such elements in animal manures. When municipal composts are applied to agricultural land, these should conform to good quality criteria [67, 68, 185]. The concentrations of potentially toxic elements in some sewage sludges can be unacceptably high [184, 186]. Thus, controls on discharges to sewers and treatment of sewage effluents to remove potentially toxic elements should be actioned [183]. Furthermore, it is not recommended that municipal composts are mixed with sewage sludge, since this practice can increase the phytoavailability of potentially toxic elements [68]. Finally, phytoextraction strategies can be employed to remediate contaminated land, and the plant material generated might be used as biofuels [32, 126, 197].

5. Conclusion

This paper has described how managing plant mineral nutrition might contribute to future food security. It has highlighted roles for both agronomy and plant breeding in delivering sufficient, safe, and nutritious food to meet the dietary needs of an increasing human population. It has noted that the problems of mineral deficiencies and toxicities must be addressed to maximise crop production in both intensive and extensive agricultural systems. The chemical constraints to crop production on alkaline, acid, saline, and sodic soils can be addressed through agronomy or the development of tolerant genotypes. In intensive agricultural systems it is likely that inorganic fertilisers will continue to be required to maintain yields. However, their use might be reduced by agronomic strategies that improve fertiliser use efficiencies, by replacement with organic fertilisers, and by judicious choice of genotypes that acquire and utilise mineral elements better in producing commercial yields. In extensive agricultural systems integrated fertiliser management strategies using biological N_2 fixation, nonacidifying inorganic fertilisers, and organic fertilisers and amendments to develop soil fertility can be usefully adopted. To increase the dietary delivery of mineral elements essential to human wellbeing, agronomic strategies to increase the phytoavailability of these elements combined with the cultivation of crops that acquire and accumulate greater concentrations of these elements in their edible tissues can be pursued where there is sufficiency of these elements present in the soil to support mineral-dense crops. However, where these essential elements are not present in the soil, the application of fertilisers containing these elements is required to increase their amounts in human diets, if diets remain unchanged. To reduce the entry of toxic elements into the human food chain, strict quality requirements for inorganic and organic fertilisers might be enforced, agronomic strategies could be used to reduce the phytoavailability of these elements, and crop genotypes can be developed that do not accumulate toxic concentrations of mineral elements in their edible tissues. Thus, ongoing interdisciplinary research in plant mineral nutrition, soil science, agronomy, and crop breeding is required for future food security to improve soil quality, optimise fertiliser applications for sustainable crop production, and develop strategies for the biofortification of edible crops with essential mineral elements to address mineral malnutrition in humans and other animals.

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