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Nutrient Deficiency Stress and Relation with Plant Growth and Development

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12.1 Introduction

Plants need an adequate supply of nutrients for physiological functions to run as usual and growth to flourish. Nutrients are absorbed through roots and leaves (Singh et al. 2013; Bouain 2019) but most plants absorb various macro-nutrients and micro-nutrients via roots (Weisany et al. 2013). The nutrients have various functions such as to strengthen the structural components of the cell membrane and cell walls, participate as important components of organic metabolites, implement the role of co-factor in enzymatic reactions as well as to function as a component of the plant signalling system. Deficiency symptoms of these nutrients not fulfilling plant requirements will appear at the plant level (Table 12.1).

The macro-nutrients include nitrogen, phosphorus, potassium, calcium, magnesium, and sulphur, and these are required in more quantities for plant growth than are micro-nutrients like iron, boron, copper, manganese, zinc, molybdenum, nickel, and chlorine (Singh et al. 2015). These 14 macronutrients and micronutrients, along with carbon, oxygen, and hydrogen, are essential for plant physiological functions to happen without disturbance (Singh et al. 2015; Grusak Michael et al. 2016). Some trace minerals such as sodium, selenium, cobalt, silicon, and aluminium are also beneficial, if not essential, in some plants adapted to grow in a particular environment (Singh et al. 2013; Bloom 2015).

Mineral nutrients are present in low concentrations in the soil, and their availability is affected by different environmental factors, including soil pH, nutrient bio-physio-chemical processes, biogeo-chemical cycles, precipitation, climate, and soil organic matter (Maathuis and Diatloff 2013; Kalaji et al. 2018). Plants can absorb nutrients actively by releasing energy or passively without energy loss (Karthika et al. 2018), where plants' nutrient sufficiency range is described as important for normal growth and functioning of plants and nutrient deficiency or toxicity is said to occur when availability of a nutrient is either insufficient vis-à-vis need or surpasses the sufficiency range for normal plant physiological functioning to take place. Nutrient deficiency drastically affects plant overall health, and the characteristic symptoms can become visible at the level of the whole plant (Karthika et al. 2018). Therefore, a proper understanding of nutrients' roles in plants is vital for sustainable crop cultivation and healthy crop growth visible in: nutrient uptake, status of nutrition in soil, assimilation, nutrient deficiency symptoms, and their role in plant development.

12.2 Nutrient Classification

Nutrients are categorized into macro-nutrients and micro-nutrients on the basis of their functions in plant development and growth, and quantity needed by healthy plant tissues.

TABLE 12.1

Functions and Deficiency Symptoms of Macro- and Micro and Beneficial Nutrients in Plants

Element & Symbol	Class	Form Acquired	Functions	Deficiency Symptoms
Nitrogen (N)	Macronutrient	NH_4^+ , NO_3^-	Photosynthesis, Metabolites, structural	Chlorosis, wrinkled cereal grains
Potassium (K)	Macronutrient	K^+	Metabolism, CO_2 assimilation	Chlorosis, loss of apical dominance,
Phosphorus (P)	Macronutrient	$\text{H}_2\text{PO}_4^{4-}$	Metabolites, structural signalling	Chlorosis, necrosis, premature leaf fall
Calcium (Ca)	Macronutrient	Ca^{2+}	Structural signalling	Deformed chlorotic appearance, stunted growth
Magnesium (Mg)	Macronutrient	Mg^{2+}	Metabolism, photosynthesis	Interveinal chlorosis, necrosis in older leaves
Sulphur (S)	Macronutrient	SO_4^{2-}	Osmotic, metabolites, structural	Leaf defoliation, stunted growth
Iron (Fe)	Micronutrient	Fe^{2+} , Fe^{3+}	Redox, photosynthesis	Interveinal chlorosis, necrotic tips
Manganese (Mn)	Micronutrient	Mn^{2+}	Redox, cofactor	Impaired growth
Zinc (Zn)	Micronutrient	Zn^{2+}	Redox, structural,	Stunted root development
Copper (Cu)	Micronutrient	Cu^+ , Cu^{2+}	Electron transport chain, redox	Necrotic spots
Boron (B)	Micronutrient	$\text{B}(\text{OH})_3$	Structural,	Deformed leaves, deformed capitulum
Nickel (Ni)	Micronutrient	Ni^{2+}	Urease	Chlorosis, necrosis
Molybdenum (Mo)	Micronutrient	MoO_4^{2-}	Redox, N_2 fixation	Yellow leaf area
Chlorine (Cl)	Micronutrient	Cl^-	Electrochemical, enzyme component	Leaf curling, wilting
Sodium (Na)	beneficial	Na^+	Electrochemical,	—
Selenium	beneficial	SeO_4^{2-} , SeO_3^{2-}	Redox	—
Cobalt	beneficial	Co^{2+}	Symbiosis	—
Silicon	beneficial	$\text{Si}(\text{OH})_4$	Structural	—
Aluminium	beneficial	Al^{3+}	Structural	—

12.2.1 Macronutrient

Nutrients which plants require in large quantities to live a healthy life and consume in large quantities ranging from 0.2–4.0% dry matter weight basis in plant tissues are termed as macronutrients. Main macronutrients include C, H, O, N, P, K, Ca, Mg and S. The primary macronutrients needed in larger quantities include N, P, and K, whereas Ca, Mg, and S are required in moderate amounts and termed as secondary nutrients.

12.2.2 Micronutrients

The nutrients plants require in lesser amounts vis-à-vis that required by macro-nutrients, and which plants consume with an uptake ranging from 5–200 ppm or lesser than 0.02% of dry weight are characterized as micronutrients. These are either cationic (Fe, Mn, Zn, Cu, Ni,) or anionic (B, Mo, Cl).

12.2.3 Beneficial Elements

There are some elements that stimulate plant growth in some plants and are termed as beneficial elements: Sodium (Na), silicon (Si), cobalt (Co), selenium (Se), and aluminium (Al).

12.3 Nutrient Functions, Uptake, Transport, and Deficiency in relation to Plant Development

All plants must absorb mineral nutrients to ensure their normal growth and development. The role of mineral nutrients in plant development, mineral uptake, transport, and the impact of deficiency of certain elements in relation with plant development are discussed here.

12.3.1 Nitrogen

Nitrogen (N) is a valuable part of various plant components, and in combination with C, H, and O, it is the building block of proteins, amino acids, nucleic acids, phospholipids, and several secondary metabolites (Figure 12.1). Again, nitrogen is part of the ring structures of the purine and pyrimidine bases of nucleotide structures, the basis of nucleic acids, like DNA and RNA involved in the transfer of genetic code to the offspring (Virginia-Pérez et al. 2015; Pandey 2018). As an essential component of vitamins that help in metabolism, and of coenzymes that play a vital role in turgor generation as biochemistry analysis shows, nitrogen is the structural part of different alkaloids synthesized from the amino acids with names as diverse as tyrosine, arginine, tryptophan and lysine (Kováčik and Klejdus 2014). Plants with nitrate availability show more tolerance against photodamage. Given it can provide defence against oxidative stress, nitrogen improves defence system against stress by enhancing antioxidant systems and improving quantity of dry matter as a whole in plant tissues in crops (Kausar et al. 2017).

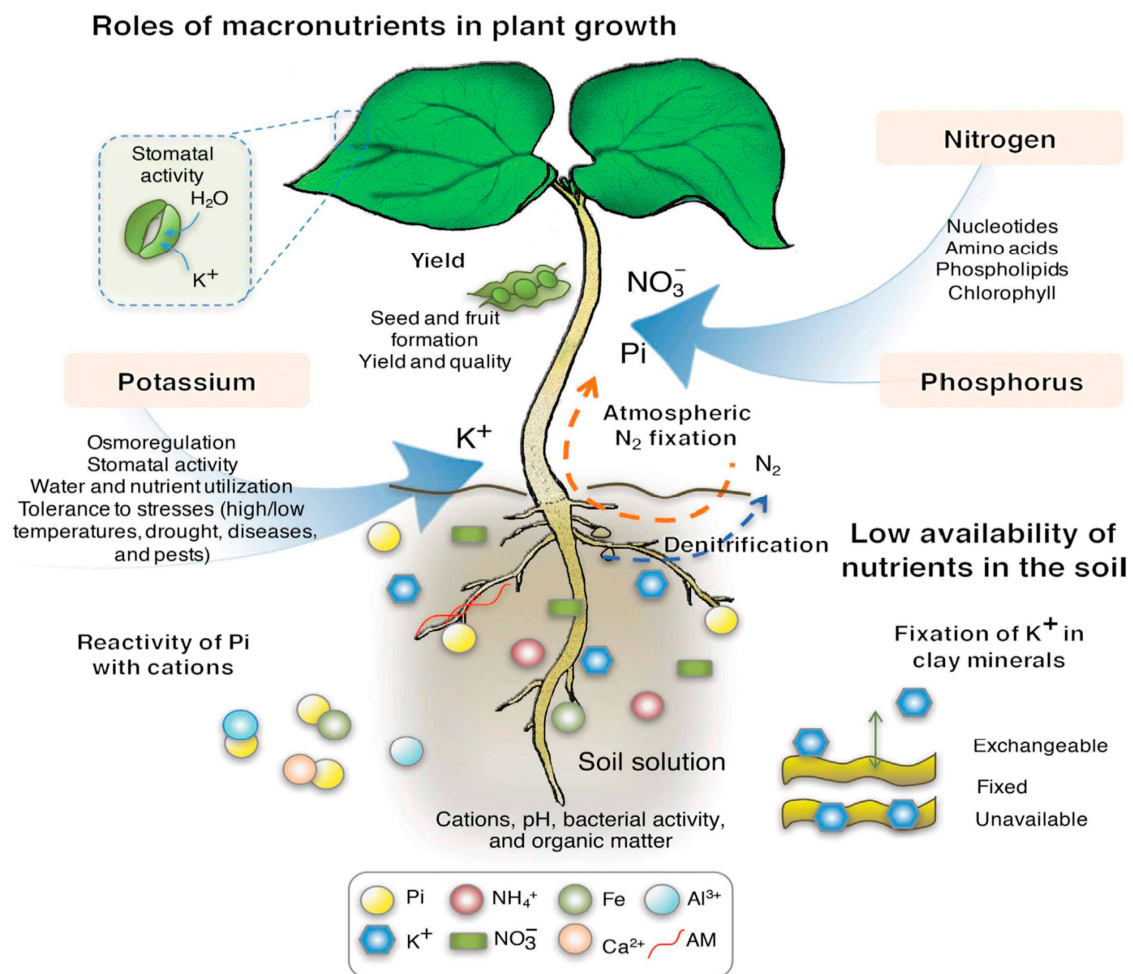


FIGURE 12.1 Role of macronutrient phosphorus, nitrogen, and potassium in plant and their bioavailability in soil. Plant uptake macronutrient in the form of phosphorus (Pi), nitrogen (NO_3^-), and K^+ which are essential structural components and plays different role in cellular processes. Their availability depends on several factors such pH, organic matter, and cations in the soil solution.

12.3.1.1 Nitrogen Uptake and Assimilation

Nitrogen is the most abundant gas present (80%) in atmosphere. However, its stable, atomic form (N_2) is not accessible to plants directly (Mahmud et al. 2020). After carbon, it's nitrogen that is required by plants in perceptively large amounts with a major source of N found to exist for plant roots to take up as ammonium (NH_4) and nitrate (NO_3). To become available to plants in this form, freely-living microorganisms and symbiotic ones fix atmospheric nitrogen into NH_4 or the nitrifying bacteria convert atmospheric nitrogen into NO_3 . For roots to absorb nitrate and ammonium, they are assisted by the transport system located on the plasma membrane of the epidermal and cortical roots cells of the plant (Rentsch et al. 2007). Various physiological transport systems exist which mediate nitrate or ammonium uptake and possess different affinities: A high affinity transport system (HATS) works at low concentrations of outer nitrate or ammonium; whereas, at high concentrations of the same, a low affinity transport system (LATS) participates in uptake permitting great influxes of substrate at high substrate accessibility (Karthika et al. 2018). The genes involved in nitrate or ammonium transporters are members of NRT, AMT, and CLC families. Nitrogen translocation in plants occurs when nitrate and amino acids travel across xylem in roots to upper plant parts, where high affinity H^+ -coupled symporters as members of NRT family process NO_3 uptake and MT transporters mediate NH_4 uptake in plants (Karthika et al. 2018; Tegeder and Masclaux-Daubresse 2018). In *Arabidopsis*, six transporters are found to exist: NRT1.1 and NRT1.2 operate under high nitrate resource while NRT2.1, NRT2.2, NRT2.4, and NRT2.5 work under nitrate starvation (Li et al. 2008; Kiba et al. 2012). Excess ammonium is noxious to plant cells and its uptake and assimilation are highly regulated, where high affinity ammonium transporters (AMTs) and low affinity uptake systems (aquaporins or cation channels) regulate ammonium transport in plants (Yuan et al. 2007; Ferreira et al. 2015).

12.3.1.2 Nitrogen Deficiency

Nitrogen is a mobile element, and during N deficiency, plants exhibit chlorosis in older leaves followed by necrosis symptoms which causes yellow leaves and leaf to fall off. Triggering slow and stunted growth in plants due to inhibition in cell division and dormancy in lateral buds (Kimura et al. 2016; Kathpalia and Bhatla 2018), nitrogen deficiency in some plants such as maize and tomato show symptoms of purple appearances and chlorosis symptoms on stems as well as on petioles and leaves (Lin et al. 2011). Plants exhibiting N-deficiency indicate smaller leaves and premature shedding of older leaves associated with adverse effects on the root (Costa et al. 2017; Karthika et al. 2018). Nitrogen starvation could increase flavonoids such as rutin, and if ferulic acid forms in excess amounts in plant parts, it can harm plant growth. In cereal crops, nitrogen deficiency causes reduction in amino acids Gln, proteins, and photosynthetic pigments which trigger decrease in tillering and in numbers of ears per unit area as well as small grain size due to decrease in carbohydrate levels in the grains. It was reported that N-deficiency causes excess anthocyanin production in plants that is usually associated with symptoms of purple leaves. Triggering 34%, or even 36%, decrease in plant chlorophyll and carotenoid contents in rice plants (Huang et al. 2004), nitrogen limitation is also associated with reduced enzyme activities during energy metabolism including during photosynthesis and respiration (Lin et al. 2011). The reduction in Rubisco activity in electron transport chain under nitrogen starvation has been reported by Evans and Terashima (1987), while deficiency of nitrogen can lead to excess electron flow possibly causing an increase in oxygen photoreduction in the chloroplast vis-à-vis the Mehler reaction following augmented levels of ROS production. All enzymatic and non-enzymatic antioxidants revealed the presence of primitive antioxidant systems in spinach, maize, barley, and *Arabidopsis* plants (Kandlbinder et al. 2004; Finkemeier et al. 2003; Tewari et al. 2006; Tewari et al. 2007). An increased level of abscisic acid and H_2O_2 in roots was reported in plants deficient in nitrogen (Shin et al. 2005; Zhao et al. 2007). The activities of ascorbate peroxidase, glutathione reductase, peroxidase, and catalase were recorded in rice plants (Lin et al. 2011). Whereas some studies have reported that nitrogen deficiency causes reduction in quantum yield of PSII and electron transport, others say it diminishes chloroplast pigments and production of several enzymes involved in Calvin cycle especially Rubisco. Moreover, N starvation could drastically affect Rubisco-related CO_2 assimilation and photorespiration in cassava plants (Cruz et al. 2003).

12.3.2 Phosphorus

Phosphorus (P), one of the major mineral nutrients that plants cannot do without, is the key component of many biological processes such as energy metabolism and synthesis of nucleic acids, cell membrane, phospholipids, and amino acids (Figure 12.1). Having a key role to play in the energy transmission of plant processes, phosphorus through pyrophosphate bonds in ATP, offers metabolic energy to a multitude of plant processes, like plant photosynthesis and respiration, via addition of phosphate group to different sugars (Taiz and Zeiger 2002). Involved in enzyme regulation and signal transduction through protein phosphorylation and dephosphorylation reactions, phosphorus is necessary for nucleoproteins and phosphorus-comprising compounds formation in young meristematic cells. In plants, phosphorus is available as *phosphate ester* which helps DNA and RNA carry out biosynthesis; and ester is an important structural constituent of phospholipids constituting the cell membranes. It also plays a key role in membrane biochemistry and is a key component of ATP, AMP, ADP, and pyrophosphate which are essential components of energy metabolism. Inositol triphosphate (IP₃) is a secondary messenger involved in signal transduction, whereas in many plants, phosphorus and nitrogen regulate plant growth and maturation (Zhang et al. 2014; Kanno et al. 2016). Playing an important role in seed formation and to enhance root diameter of plants to receive more water and nutrients, phosphorus increases plant tolerance against drought or other abiotic stresses and improves water use efficiency and yield efficacy (Shen et al. 2011). Rhizobium and nitrogen fixing legume's activity have been known to break into a sprint with sufficient phosphorus availability (Karthika et al. 2018).

12.3.2.1 Phosphorus Uptake and Transport in Plants

Most plants require phosphorus as an inorganic phosphate (Pi), and though phosphorus is present in enormous amounts in soil still high chemical fixation rate and low diffusion make it one of minimum available nutrients for plant growth (Wang et al. 2018). Plants acquire phosphorus as primary or secondary food as a monovalent H₂PO₄⁻ and a divalent HPO₄²⁻ present in low concentrations in the soil solution. Most cations form insoluble salts with phosphorus like in a soil rich in iron and aluminium, phosphorus can react with these minerals to form insoluble salts and, thus, become unavailable to plants (Fang et al. 2009; Wang et al. 2018). Phosphorus is readily absorbed by plants as the monovalent H₂PO₄⁻ and least absorbed as the divalent HPO₄²⁻. Either roots can take Pi from soil or plant organs rely on various transport systems like H₂PO₄⁻ symporters PHT family or other phosphate transporters (Młodzińska and Zboińska 2016) to receive its daily ration of phosphorus. Various studies reported proteins with phosphate transport include PHT family and it involves Pi uptake from soil; on the other hand, SPX-EXS subfamily PHO1 and homologous genes are responsible for Pi translocation from root to shoots (Rausch and Bucher 2002; Wang et al. 2018).

12.3.2.2 Phosphorus Deficiency

Phosphorus is an essential nutrient forming a structural component of nucleic acids, plays a role in signal transduction, and takes part in various biological functions in plant development. Being the primary source of nutrition for plant development, any lack of phosphorus will cause plants to respond with symptoms of P deficiency, particularly when P concentration falls below 0.1%. Affecting plant growth and development, with first symptoms affecting older leaves (Takizawa et al. 2008), phosphorus deficiency causes anthocyanin pigment production to occur with high concentration in plants which gives purple colour to plant leaves and triggers necrotic spots on the leaves. With symptoms detected in dark greenish purple coloured and malformed leaves (Ramaekers et al. 2010), P deficiency triggers 4-fold decrease in leaf tissue when Pi reduces to 20 to 40 in chloroplast; furthermore, reduction in ATP synthase causes decreased growth (Muneer and Jeong 2015). It's also observed that the NADP⁺ levels working as substrate for NADPH synthesis is significantly decreased in P deficient plants. Causing decreased ATP synthase which limits the export of proton to the chloroplast stroma, and thus acidifying the thylakoid lumen (Goltsev et al. 2016; Karlsson et al. 2015), P deficiency in plants causes leaf expansion to be disrupted with reduced leaf area and slowed down overall growth of plants. Scarcity in phosphorus causes disruption in shoots and flower development in fruit trees, and is also a reason for reduced tillering in cereal crops (Karthika et al. 2018), while other symptoms include premature drying and shedding of leaves, and debilitated growth of fronds in coconut palms, with drastic P

deficiency possibly causing leaf etiolation with leaves turning yellow. Young plants require more P as compared to mature plants, and a low P environment, for young plants, causes reduced cell division and cell enlargement so that plant development is stunted with dark green leaves as well as reduced leaf surface area (Malhotra et al. 2018). Phosphorus deficiency causes upward curling from base to tip of leaves and tilting of leaves associated with delayed maturity in crops under P limitation (Carstensen et al. 2018). The reduced leaf area triggers decline in photosynthetic efficiency in white clover plants (Schulze et al. 2006); and, in targeted metabolic profiles, phosphorus deficiency has been known to result in amino acids disturbing the nitrogen metabolites and to repress nitrogen fixation in common bean plants. *Arabidopsis* plants deprived of requisite phosphorus have shown altered Ca and Fe availability and increased ROS production, with hampered root development (Matthus et al. 2019).

12.3.3 Potassium

Potassium (K) is the third most essential macronutrient and a richly absorbed cation that performs a major role in plant growth, metabolism, and development (Figure 12.1) (Prajapati and Modi 2012; Karthika et al. 2018). As a crucial nutrient for meristematic development and in carrying out functions such as gas exchange and water regulation in plants, protein synthesis, enzyme activations, photosynthesis, and carbohydrate transport (Pandey and Mahiwal 2020), potassium also neutralizes different organic anions and compounds inside the plants to help stabilize tissue pH between 7 and 8 which is considered +optimal for most enzymes. With major effects on nucleic acid, protein, and vitamin metabolism that facilitate carbon movements and CO₂ assimilation activities (Wang and Wu 2017; Pandey and Mahiwal 2020), this mineral facilitates cell extension, plant development via management of turgor, and gas exchange through stomatal aperture control (Koch et al. 2019). As the element loading into phloem helping long distance nutrient transport via pressure driven flow, it maintains electrochemical gradient through cell membrane, and contributes to the translocation solutes (Karthika et al. 2018; Pandey 2018; Liu and Martinoia 2020). A potassium constituent uptake by cells of 50% by equal weight and in quantities more significant than other nutrients, except nitrogen, is suitable for plant growth (Pandey, 2018). It constitutes 80 mM to 200 mM concentration in cytoplasm and varies in subcellular compartments. The plants' young and active parts, especially buds and young root tips and leaves, contain rich amounts of potassium (Koch et al. 2019), and it is mainly used in its catalytic and regulatory roles while having a say in activation of 60 enzymes involved in photosynthesis and respiration, such as starch synthase and pyruvate kinase. Potassium is significant in maintaining crop growth improving disease resistance and enhancing shelf life of vegetable and fruits (Lei 2019; Koch et al. 2019).

12.3.3.1 Potassium Uptake and Transport in plants

Potassium is absorbed by plant roots in cationic form (K⁺) where root epidermal and cortical cells are responsible for K uptake where the concentration of potassium varies from 1 to 5% in healthy plant tissues (Pandey and Mahiwal 2020). Membranes identified as transport proteins facilitate K⁺ transport inside the plant cell as the lipid bilayer cell membrane is impervious to ions (Becker et al. 2004; Chao et al. 2016) with potassium uptake following biphasic kinetics, and high affinity potassium transport facilitated by H⁺/K⁺ symporters (active) as well as low affinity K⁺ transporters, mediated by channels (Pandey and Mahiwal 2020). The translocation of K from soil to plant tissues involves different channels and transporters. Potassium is a mobile element and can travel from absorption site to the place it's needed, where the three main transporter families which contribute to K transport are TRK/HKT family, HAK, KT, and KUP family, and (CPA) cation/proton antiporter family. It is reported that in *Arabidopsis thaliana* plant, there are 15 genes encoding potassium channels and three transporter families (Rawat et al. 2016; Pandey and Mahiwal 2020).

12.3.3.2 Potassium Deficiency

Scavenged from older plant parts and travelling to where it is needed, potassium (K) is a mobile element with potassium deficiency symptoms observed in older leaves, having multiplier effects in the form of:

Decreased nitrogen availability affecting protein synthesis it is associated with (Figure 12.2) (Chérel and Gaillard 2019); loss of amino acid, amides, and nitrate buildup being the precursor of decreased protein synthesis where visual symptoms are not immediately perceptible for following up, and, with the visible symptoms of K^+ deficiency signing in as chlorosis in older leaves followed by leaf curling and wrinkle advances; and plants appearing with shorter and weak internodes. In soybeans, leaf tissues are damaged, leaf edges become ruptured and ragged with delayed maturity and less uniform beans. Under potassium deficiency, cotton leaves turn yellowish green around margins and veins followed by leaf etiolation where leaves turn brownish and can die prematurely with leaf shedding (Ashley et al. 2006; Karthika et al. 2018). It has been observed that under K deficiency, in apple plants, yellowish green curl along entire leaf and ragged, poorly formed edges, and the shedding of fruits early are most visible symptoms (Yadav and Sidhu 2016). Necrotic spots occur on the older leaf tips and subsequently on younger leaves related to chlorophyll degradation which impedes carbon flow and disrupts the water status of plants. Potassium-deficient plants develop poor root system, and stalks become weak followed by lodging of crops such as corn and legumes. Fruits and vegetables deteriorate early when shipped and have a short shelf life when plucked from potassium deficient plants (Jaiswal et al. 2016). While poor root development, damaged nodal tissues, chaffy ears, and stalk lodging are common symptoms in corn plants (Karthika et al. 2018; Koch et al. 2019), in areca palms, K deficiency causes shrunk trunk diameter and canopy size while in K^+ starved coconut palm, growth with reduced trunk and shorter leaf with decreased number of inflorescences and nuts per branch are the most common symptoms (Prajapati and Modi 2012).

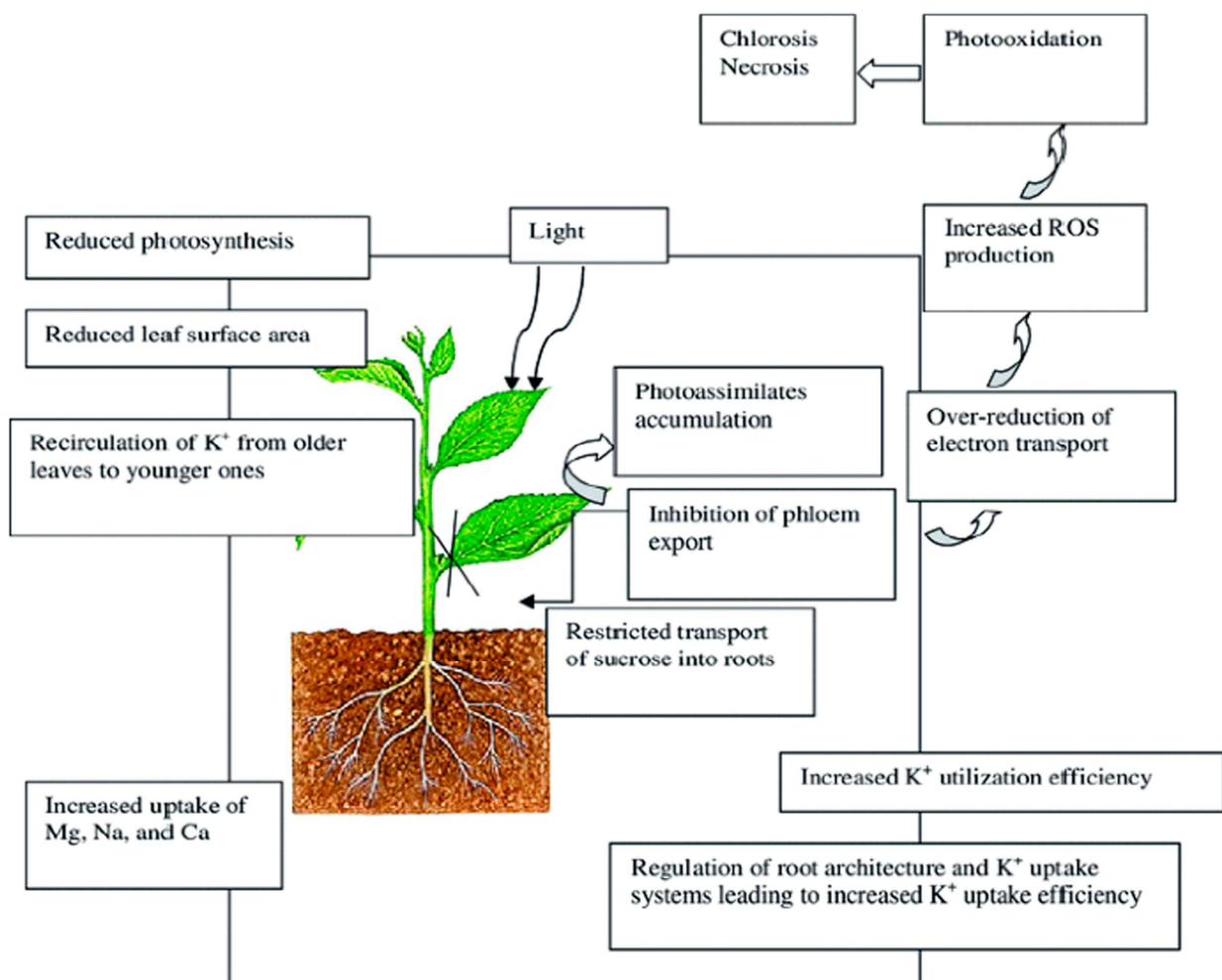


FIGURE 12.2 Potassium deficiency effects on different plant processes. Potassium deficiency triggers decrease in photosynthetic activity and causes oxidative stress leading to severe harmful effects on plant growth while plant develop various defence strategies to enhance potassium uptake and utilization (Hafsi et al. 2014).

12.3.4 Calcium

Calcium (Ca) available to plants in high concentration in the soil system is an essential nutrient for plant growth and development. Ca required by plants works as a secondary messenger of shock during stress events and stabilizes normal functioning of cell membranes, where concentration of free Ca is maintained in the cytoplasm at sub-micromolar levels to facilitate intracellular signalling (Karthika et al. 2018). Calcium plays a vital role in meristematic growth and, in plants, Ca levels range between 0.1% and 0.2%. Acting against hormonal and environment stress in plants, Ca forms calcium complex with calmodulin protein known as calmodulin calcium complex which regulates several key metabolic processes (Demidchik and Shabala 2018). While calcium pectate maintains cell elongation, as well as cell division, and plays a key role in sustaining the structure of chromosome (Karthika et al. 2018; Pandey 2018), high levels of Ca supply are required for symbiotic leguminous plants prone to infection by *Rhizobia* bacteria. Calcium is also involved in enzyme activation such as activation of arginine kinase, phospholipase, amylase, and ATPase. With a large ion range, calcium helps during ion dehydration by subsequently binding to different anionic substances (Makavitskaya et al. 2018). With a strong influence on cell wall strength and cell pH, calcium can help plant cells stick together due to its cation effect on cell medium. Calcium has the ability to influence the synthesis of cell wall polysaccharides including 1,3, β glucan that acts like a glue in cell walls. Calcium is reported to have high binding capacity which makes it an important signalling molecule in the cytosol (Karthika et al. 2018; Huang et al. 2017). Besides, calcium plays an important role in cytosolic signal transduction pathway responsible in activating proteins, kinase, and phospholipases which regulate cellular response to different biotic and abiotic stresses. Protecting root cells when there is imbalance of nutrient in soil, calcium helps to maintain cell membrane integrity (Karthika et al. 2018). Mitochondrial enzymes such as glutamate dehydrogenase are also activated by calcium (Gong et al. 2016).

12.3.4.1 Calcium Uptake and Transport

Calcium is taken up by plant roots as divalent cations (Ca^{2+}) by calcium selective channels and then must be diffused through the plant in the absence of pumps or channels through lipid bilayers (Kathpalia and Bhatla 2018; Pandey 2018). In plants, apoplastic and symplastic pathways are available for calcium movement with the need for calcium to be in the micromolar range to guarantee the cell to generate Ca^{2+} signal (Thor 2019). Calcium enters root xylem at the apical region of the root tip where root endodermis is differentiated and, then, distributed within the plant in its free form or by making a complex with organic acid (Kathpalia and Bhatla 2018; Karthika et al. 2018). The process of Ca uptake requires the help of members of CAX $\text{H}^+/\text{Ca}^{2+}$ antiporter family ATP driven P-ATPase (Gao et al. 2019). Higher concentration of Ca is toxic to plant growth, so, its movement through the phloem is slow replenishing older leaves containing more Ca after supply to younger leaves is done (Karthika et al. 2018). Higher concentration of Ca (0.1–1.0 mM) is required to maintain the functional and structural integrity of plasma membrane (McAinsh and Pittman 2009).

12.3.4.2 Calcium Deficiency

Calcium is the fifth most abundant element in the environment and constitute around 3.5% of the earth's crust, with plants requiring a stable supply of 1–10 mM for its everyday normal functioning (De Freitas et al. 2016). Calcium deficiency triggers stunted growth of middle lamella in cell expansion, and membrane structure can collapse and molecular weights of solutes show solute leakages (Tian et al. 2016; Karthika et al. 2018). In flowering plants with Ca-low condition, pollen tube growth and direction of pollen tubes are disrupted, and younger leaves exhibit deformed, small, and chlorotic appearance, with leaf etiolation causing leaves to change from flourish to cup-shaped appearances; even as terminal buds deteriorate with collapse of petioles, and the stem is nourished by a weakened root system leading to brownish small branches (Liu et al. 2019). The most common Ca deficiency symptoms are nasty pit in apples, black heart in celery, and blossom end rot in tomatoes (Huang et al. 2017; Karthika et al. 2018). In Ca starved tomato plants, deficiency symptoms usually appear during fruiting where the Ca deficiency condition was named as blossom end rot (BER) (Hermans et al. 2013). Water soaked tissues in the blossom's expanse that later become brown with necrotic spots developing in plants at later stages of Ca deficiency are also common. In vegetables, Ca

deficiency causes low transpiration rate in young leaves characterized by stunted growth and brownish spots associated with necrosis due to phenol oxidation of younger leaf tips and meristematic cell in cauliflower plants. In artichoke plants, lack of calcium is known as tip burn, which is characterized by discoloration and immature flower buds (Taiz and Zeiger 2002; Pandey 2018; Karthika et al. 2018).

12.3.5 Magnesium

Magnesium (Mg) in green leafy plants is one mineral plants cannot do without because of its role in chlorophyll production and its functions as an activator of many plant enzymes (Hermans et al. 2013). As a mobile element, magnesium performs diverse functions in plants; and with the central magnesium atom of the chlorophyll molecule with the nitrogen atoms of four pyrrole rings, chlorophyll has a porphyrin like composition (Gransee and Führs 2013; Hermans et al. 2013). Small amounts of Mg^{2+} is essential for different functions to run in cytoplasm, and for functions to be carried out such as counterions for vacuolic organic acid anions and inorganic anions in the middle lamella of plant cell walls (Karthika et al. 2018). Magnesium is essential for pH stabilization and maintenance of ionic balance in plants, while helping sustain the structural integrity of cellular ribosome and attaching ribosomal aggregates to tRNA, a method important for biosynthesis of proteins (Liang et al. 2009; Guo et al. 2016). Magnesium activates not only several key enzymes along with K but also involved in phosphate or carboxyl group enzyme catalase transfer and, in some cases, it freely functions as a dissociable cofactor (Deng et al. 2006; Karthika et al. 2018). With a role in ATP synthesis in plants, Mg is an essential component in all nucleoside triphosphates forming magnesium complexes. Important for the enzyme RNA polymerase to function, magnesium is essential for RNA synthesis. The enzyme RuBP carboxylase and fructose 1,6 diphosphate involve Mg as does higher pH levels for optimum activity (Hermans et al. 2004; Marschner 2012). Magnesium is an important nutrient given 75% of leaf Mg is involved in protein synthesis, and 15–20% of total Mg is linked with chlorophyll pigments (Kathpalia and Bhatla 2018). Counted among the basic components of polyribosome for protein synthesis, Mg levels determine gene transcription and translation in plants (Guo et al. 2016).

12.3.5.1 Magnesium Uptake and Transport

The Mg uptake from soil solution is lower than K though it is present in higher concentrations in soil, with translocation of Mg facilitated by potassium towards fruits and storage tissues. It has been reported that Mg being a mobile element can be transferred from older to younger leaves as need (Mengutay et al. 2013). The Mg uptake is facilitated by MGT family which is similar to bacterial CorA mg transporters. In recent years, Mg homeostasis has been explained with the discovery of *Arabidopsis* Mg^{2+} transporters (Chen et al. 2009; Guo et al. 2016). Recently, an AtMRS2/AtMGT gene family which encodes Mg transport proteins has been identified (Li et al. 2008; Chen et al. 2009; Mao et al. 2014). Ten Cor A family AtMGT genes clustered into high affinity genes (AtMGT1 and AtMGT10), low affinity genes (AtMGT3, AtMGT7, AtMGT9), and dual affinity genes (AtMGT5) was considered as the primary Mg transporter, and is responsible for uptaking, circulation, and homeostasis in plants (Luo et al. 2006; Gilliham and Conn 2010; Conn et al. 2011).

12.3.5.2 Magnesium Deficiency

Magnesium deficient leaves accumulate sugars in source leaves in high quantities caused by restricted loading of phloem which may trigger feedback and disruption of Rubisco carboxylase activity and change to oxygenase activity (Tewari et al. 2006; Guo et al. 2016). Magnesium-starved plants show chlorosis associated with high sugar buildup, whereas severe Mg deficiency can cause reduction in photosynthetic electron transport in PSI and PSII recorded in pine and beat plants (Kathpalia and Bhatla 2018). Even with the possibility of magnesium deficiency triggering ROS production which causes oxidative damage to plants, there are reports of activation of antioxidant defence system in different plants under Mg deficiency stress (Gruber et al. 2013). Oxidative damage caused by Mg deficiency increases malondialdehyde (MDA) and H_2O_2 synthesis (Pandey 2018). Further, magnesium is the central atom in the chlorophyll molecule and its deficiency causes premature leaf abscission in plants associated with interveinal chlorosis and with leaf margins turning reddish purple (Guo et al. 2016). In different plants such as wheat, distinct mottling

associated with yellowish green patches are recorded, and in alfalfa plants leaf curls with reddish underside has been reported (Karthika et al. 2018; Pandey 2018). Leaves of Mg-starved sugar beet and potato plants turn stiff and brittle, while it is an established fact that depolymerization of ribosome leads to premature ageing of plants with Mg deficiency symptoms appearing first in older leaves and later extending to younger leaves resulting in drying of tissue and death. In Areca palms and cocoa plants, the symptoms of interveinal chlorosis, necrosis of older leaves, and leaf margins which curve upwards after prolonged Mg deficiency were recorded (Hermans et al. 2005; Guo et al. 2016). Photosynthetic CO₂ fixation impairment can trigger non-utilized accumulation of electrons in the chloroplast which causes ROS generation and photooxidative damage of chloroplast membrane lipids (Guo et al. 2016). Magnesium deficiency inhibits N reductase, glutamate synthase, urease, and glutamic oxaloacetic protease transaminase enzymes associated with reduction in nitrogen metabolism (Yang et al. 2012).

12.3.6 Sulphur

Sulphur (S), an important macronutrient, has for its most important source sulphate (SO₄²⁻) and plant roots are responsible for its uptake as divalent Sulphate anions and, then, the nutrients' transportation to xylem and phloem (Kathalia and Bhatla 2018). Aerial parts of plants can also absorb SO₂ from air; however, gaseous S needs to be transformed into Sulphate, and then reduced to sulphide before being incorporated into cysteine and amino acid which is important for metabolism. Essential for protein synthesis and with a role in chlorophyll synthesis, sulphur levels in plants fluctuate between 0.1% and 0.4%. Its need is most important for oilseed crops as they require more S concentration in the tissues than cereal crops do. Sulphur is an essential constituent of amino acids such as cysteine. Cysteine and methionine are also present in different coenzymes and vitamins needed for metabolism (Huang et al. 2019). Required for nodulation, sulphur is needed in flowering and for maintaining the quality of oil seed plants. An important component of tripeptide glutathione compounds involved in ROS detoxification, and the production of phytochelatins and metallothionein involved in metal detoxification (Karthika et al. 2018), sulphur provides root growth, seed production, and also facilitates plant resistance against cold. It is also present as an iron Sulphur protein complex such as ferredoxin in photosynthesis electron transport chain. Sulphur is a component of thiocyanates and isothiocyanates responsible for pungent flavour in cabbage, mustard, and turnips.

12.3.6.1 Sulphur Uptake and Transport

Sulphur is taken up by plant roots against electrochemical gradient generated at plasma membrane due to proton gradient caused by membrane H⁺-ATPase. The plants' sulphate uptake is a high affinity transport with expression of transporter genes, but low affinity sulphate transporters do cell-to-cell distribution across plasma membrane and storage of mobilization from vacuoles across cell tonoplast. Sulphite, molybdate, selenite, and chromate compete with sulphate for sulphate transport proteins binding (Huang et al. 2019). Electrochemical gradient favours sulphate transfer, and sulphate transfer across tonoplast follows sulphate-specific channels. Different transporters, that are present in plants roots with variable affinities for sulphate in *Arabidopsis* 14 genes, have been identified which facilitate sulphate transfer (Takahashi 2019). High affinity transporters SULTR1.1 and SULTR1.2 are present in root epidermis, while the four low affinity transporters SULTR1.3, SULTR 2.1, SULTR3.5, and SULTR2.2 have been identified in the vascular system (Sacchi and Nocito 2019; Takahashi 2019).

12.3.6.2 Sulphur Deficiency

Sulphur is an immobile element and its deficiency symptoms include leaf yellowing, anthocyanin accumulation, and stunted growth, with symptoms first appearing in younger leaves (Samborska et al. 2019), and triggering leaf defoliation and reduced nodulation associated with stunted root growth in tomato plants. While sulphur starvation in plants causes reduced stomatal degradation, root hydraulic conductivity, and improper photosynthesis, thus reducing leaf area and leaf numbers (Veliz et al. 2017), other symptoms as reported in wheat plants with sulphur deficiency are decrease in chlorophyll and protein levels of leaves (Sutar et al. 2017). S-containing amino acid methionine, under S deficient conditions, is disrupted from

functioning which causes reduction in protein synthesis followed by decreased chlorophyll concentrations. Causing enhanced amide content in plants, sulphur deficiency leads to proportions of amide content to be enhanced in relation to soluble N fractions (Karthika et al. 2018; Pandey 2018). In sulphur deficient plants, increased ROS production enhances the glutathione levels which generate hydrogen peroxidase H_2O_2 in barley leaves (Veliz et al. 2017; Qadeem et al. 2015), with sulphur deficient plants showing symptoms of small stems, that in the lateral stage causes the entire plant to become pale green (Karthika et al. 2018). Sulphur deficiency occurs in plants at less than 0.1 to 0.2% concentrations and deficiency symptoms are characterized by chlorosis. Decrease in plants' leaf numbers and leaf size in sulphur-deficient older palms have been reported, while in cocoa plants symptoms are reported as leaves turning pale yellow and older leaves having yellow blotches (Taiz and Zeiger 2002; Saha et al. 2016).

12.3.7 Iron

Iron (Fe) is an important micronutrient for plant growth required for multiple cellular processes, including chlorophyll biosynthesis, photosynthesis, and respiration (Figure 12.3) (Connorton et al. 2017). An essential component of different cofactors that participate in electron transfer or radical mediated modification, Fe assists in chemical transition such as hydroxylation. Iron cofactors participate in oxygen transport and regulate protein stabilization (Karthika et al. 2018). Leaf chloroplast contains iron sulphur (FeS) proteins i.e., ferredoxins, as do photosystem I and a range of different metabolic enzymes. Iron enzymes are essential

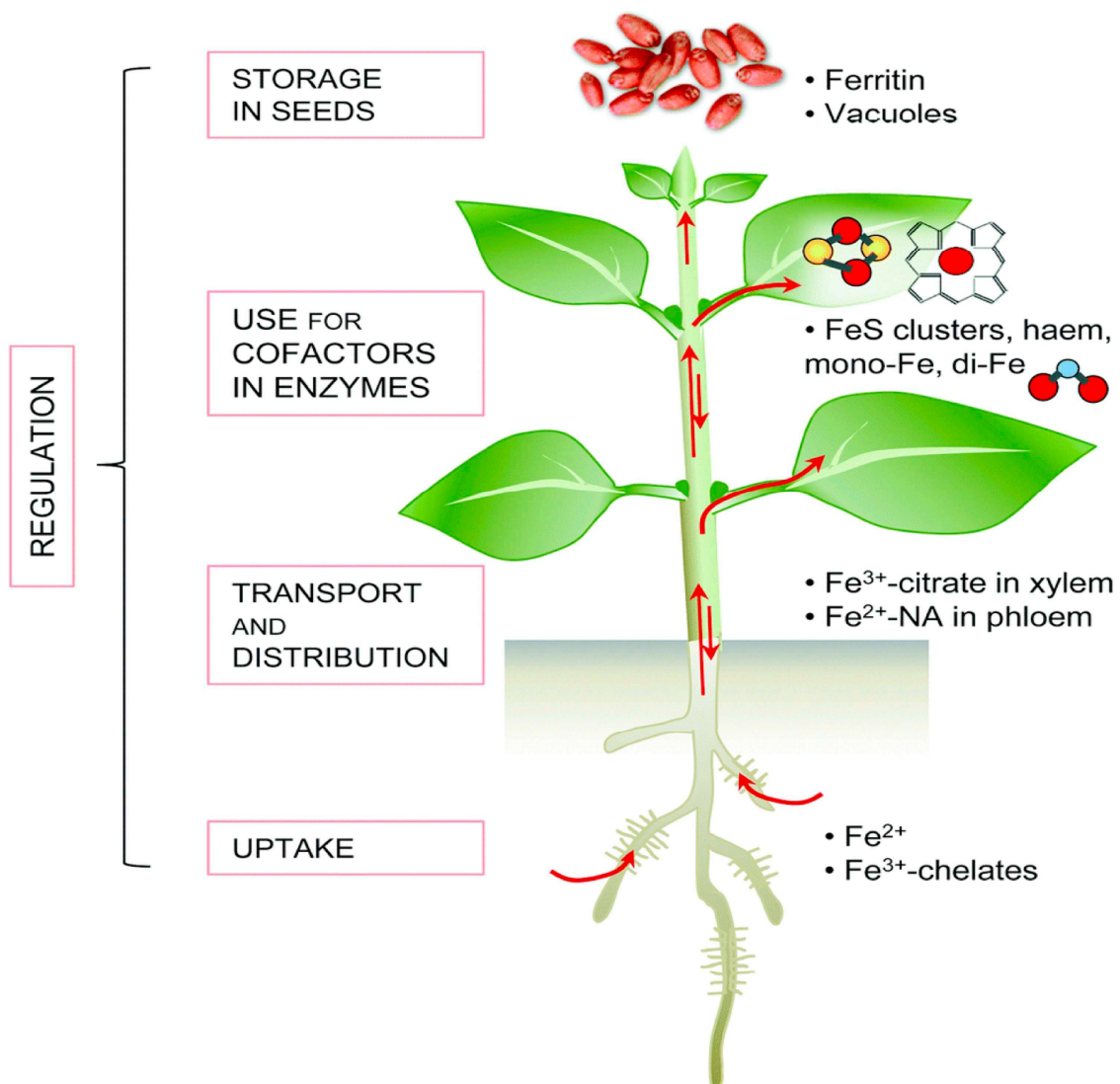


FIGURE 12.3 An overview of Fe homeostasis in plants facilitated by high affinity iron uptake systems; transport, distribution and storage mechanisms (Connorton et al. 2017).

components in respiratory complex comprising of Fe-S clusters, a combination of Fe-S and haem copper in the mitochondria. Involved in synthesis of gibberellic acid, jasmonic acid, and ethylene as well as osmolytes associated with scavenging of ROS under oxidative stress (Pandey 2018), iron as a component of cytochromes plays a role in electron transfer in redox reactions. Three groups of iron-comprising proteins such as ferredoxin work as electron carriers in electron transfer reactions (Gao et al. 2020), while iron plays a key role in nucleic acid metabolism, and chlorophyll synthesis, and is loaded in seeds vacuoles or in ferritin. Important for harvesting light energy, Fe is also known for transfer of electrons yielding from water splitting via photosystem II and I (Kroh and Pilon 2020).

12.3.7.1 Iron Uptake and Transport

Iron constitutes nearly 5% of earth's crust and is present as amorphous Fe (OH)₃ precipitate in soil which is a source of iron for plants. Availability depending on redox potential and soil pH (Figure 12.3), iron is absorbed by plant roots as Fe²⁺ via specific channels on the plasma membrane, given Fe²⁺ is closely related to Fe³⁺ reduction (Connorton et al. 2017). Iron (Fe³⁺) siderophores are transported by diffusion or mass flow to the root spaces which moves to plasmalemma bound Fe³⁺ reductase (Inoue et al. 2009; Connorton et al. 2017). The IRTs of ZIP family transporters (AtIRT1, AtIRT2; OsIRT1, OsIRT2) are associated with high affinity Fe uptake by roots. Second ABC transporters (ArBCB25, AtATM3) a mitochondrial transporter associated in Fe-S biogenesis clusters in different plants (Eide et al. 1996).

12.3.7.2 Iron Deficiency

Iron plays an important role in photosynthetic reactions. However, because iron is an important micronutrient for plant growth and development, its deficiency decreases chlorophyll levels and hampers chlorophyll synthesis characterized by interveinal chlorosis in young leaves and followed by entire leaf turning whitish yellow and which later leads to necrosis (McCauley et al. 2009). Iron deficiency is common in members of Rosaceae family with symptoms of leaves turning irregularly yellow and showing deformed growth (Karthika et al. 2018). Iron deficiency is relatively high in calcareous soils, and when concentrations are lower than 50 mg/kg, plants are considered as Fe deficient. In coconut plants, uniform chlorosis is associated with Fe deficiency where from top of the crown to the base the plant turns dark yellow or pale green (McCauley et al. 2009). Under severe Fe deficiency, newly germinated leaves show necrotic tips and, in later stages, can turn completely yellow (Taiz and Zeiger 2002; Karthika et al. 2018). Causing photodamage because electron transport requires Fe sulphur containing proteins, iron deficiency causes activities of enzymes involved in ROS scavenging to decrease.

12.3.8 Boron

Boron is an important micronutrient, and although required in low amounts, it serves essential metabolic processes in plants (Shah et al. 2017; Wu et al. 2018). Belonging to subgroup III metalloids, it has intermediate characteristics of both metals and non-metals, and its availability in irrigation water and soil is important for agriculture purpose (Archana and Verma 2017). Forming borate esters with apiose RG-II, boron, in the form of this complex, plays a key role in cell wall function and structure, and controls cell wall permeability (Shireen et al. 2018). Boric acids perform complexes with polyols and diols such as uranic acids and sugar alcohols which are important for binding of cell wall polymers. Being a component of haem proteins, which contain Fe porphyrin complexes (i.e., cytochrome, catalase) and iron sulphur proteins (ferredoxins, superoxide dismutase, and aconitase), boron is involved in chlorophyll synthesis and photosynthetic processes (Landi et al. 2019; Lewis 2020). With an important role to play in pollen tube elongation and nutrient use efficiency, boron has a secondary use in its role in cell division, sugar transport, and enzyme synthesis (Brdar-Jokanović 2020; Moghadam et al. 2020).

12.3.8.1 Boron Uptake and Transfer

Boron (B) is present in several forms in soil but the commonest form is as the undissociated boric acid (H_3BO_3). Depending on the availability, plants uptake of boron happens in three different molecular mechanisms: (i) passive diffusion through lipid bilayer (ii) facilitated transport by intrinsic proteins MIP, and (iii) energy supported high affinity transport facilitated by BOR transporters (Karthika et al. 2018; Moghadam et al. 2020). In *Arabidopsis*, a boric acid channel (ArNIO5;1) that belongs to nodulin 24 intrinsic protein (NIP) which is the subfamily of MIPs family has been identified. The AtNIP5;1 expression in B deficient plants is upregulated which suggests its importance as required B uptake under boron starved environments (Archana and Verma 2017; Moghadam et al. 2020).

12.3.8.2 Boron Deficiency

Boron deficiency is the most widespread phenomenon among all the deficiency phenomena involving micronutrient shortfall in plants, and said to take effect from the tropical regions to the temperate zones (Shah et al. 2017). Boron deficiency symptoms are known as corky core, sickness of tobacco, internal cork, water core of turnip, yellows of alfalfa, heart rot of sugar beet, and hollow stem of broccoli and cauliflower (Moghadam et al. 2020). Appearing in terminal shoots in the form of deformed, small leaves, boron deficiency shows symptoms like growth of apical meristem having a stunted look and necrotic spots with axillary branches eventually causing necrosis (Princi et al. 2016; Archana and Verma 2017). Symptoms in the sunflower petiole and stem appear as longitudinal splits and deformed capitulum, with poor seed set results and weak root system (Archana and Verma 2017). Boron deficient onion plants show brittle leaves and blue green colour associated with necrosis, while leaves of cauliflower and cabbage show bluish appearance (Wu et al. 2018). In higher plants, deficiency symptoms show up in stunted root elongation in the lateral roots and, in leaves, malformed growths, while in the case of severe boron deficiency, the whole plant growth appears stunted (Lewis 2020; Landi et al. 2019). In boron-starved plants, nitrogen fixation and nitrate assimilation are adversely affected (Karthika et al. 2018). Citrus fruits, like pears, grow lumpy with uneven thickness of the peel under boron deficiency. Under drought stress, a boron deficient plant appears to have aggravated symptoms, and with internal tissues of roots appearing to take on a darkened tint and referred to as black heart (Shah et al. 2017; Gracia et al. 2020).

12.3.9 Copper

Copper (Cu), an important micronutrient in plant growth, is considered optimal for plant tissues when it is found in the range 5–30 mg/kg. An essential component of the electron transport chain, it is involved in lignin biosynthesis (Kumar et al. 2020). As the basic component of cytochrome oxidase enzymes and plastocyanin, copper facilitates root metabolism and utilization of proteins. Copper is involved in cell wall lignification, ethylene perception, and carbohydrate metabolism (Karthika et al. 2018), and is one of the components of proteins grouped in three types which includes blue proteins, non-blue protein, and multicopper protein. Copper imparts resistance to plants against different stresses, enhances fertility in male flowers, and functions as oxidizing and reducing agents in biochemical reactions (Pandey 2018).

12.3.9.1 Copper Uptake and Transport

Plants uptake copper as the divalent cupric Cu^{2+} ion in aerated soil or will absorb copper as monovalent Cu^+ ion from wet soil with pH below 7.0. Copper concentration in plant tissues ranges between 1–5 $\mu g g^{-1}$ of dry weight and 5–20 $\mu g g^{-1}$ in leaves (Bernal et al. 2012; Kumar et al. 2020). A wide range of copper transporter proteins (COPT), P-type ATPases, and YSL transporters are involved in Cu homeostasis (Yruela 2009). In *Arabidopsis*, copper uptake is regulated by expression of ZIP family transporters through ZIP2 and ZIP2 (Kavitha et al. 2015; Kumar et al. 2020).

12.3.9.2 Copper Deficiency

Copper deficiency in many crops has been reported to cause delayed flowering and reduced number of flowers at a time, delayed hormone signalling, and decrease in photosynthesis reactions. Plastocyanin activity, which is involved in cyclic electron transport coupled to ATPs, decreases photosynthetic activity and disrupts PSII/PSI rate in Cu deficient plants (Kumar et al. 2020; Arshad et al. 2016). Copper-starved plants show lower chloroplast activity and reduced chlorophyll levels, and CO₂ assimilation while necrosis spots starting at the leaf tip and extending down along the margins towards the leaf base (Karthika et al. 2018). Copper deficiency delays senescence and the most common deficiency symptoms include necrosis, white tips, and reclamation disease (Taiz and Zeiger 2002).

12.3.10 Manganese

Manganese (Mn) was described as the essential nutrient for plants in 1922 and is involved in different metabolic processes (Li et al. 2016a, 2016b; Arafat et al. 2016). With an essential role in oxygen evolving photosynthetic apparatus, manganese catalyzes water splitting process in photosystem II (PSII). While carrying out activation of more than 30 enzymes, manganese is counted among the nutrients found in different enzymes such as Mn superoxide dismutase (SOD) (Corpas et al. 2017). Manganese functions as cofactor for many enzymes such as glutamine synthase, arginase, and pyruvate carboxylase (Köllner et al. 2008), and is required in small quantities in plants and is the essential element metalloenzymes cluster of the oxygen evolving complex (OEC) in photosystem II. Interchangeable with different divalent cations i.e., cobalt, copper, Mn is involved in ROS detoxification in plants (Bloom 2019). Oxalate oxidase is an Mn dependent enzyme which catalyzes oxalate oxidation to CO₂ coupled with O₂ reduction to H₂O₂, and facilitates plant defence against pathogens. Being the essential cofactor of enzymes, Mn is involved in isoprenoid biosynthesis and participates with Mg in terpene synthase (Basu et al. 2015; Alejandro et al. 2017). Manganese is considered to play an important role in deposition of waxes in leaves and essential in protein glycosylation and pectin biosynthesis in plants (Venkidasamy et al. 2019).

12.3.10.1 Manganese Uptake and Transport

Manganese (Mn) uptake has been considered to be facilitated by plasma membrane Ca²⁺ transport channels which are permeable to Mn²⁺. In *Arabidopsis* plants, Mn²⁺ absorption is mediated by AtNRAMP1 transporter localized in plasma membrane of root epidermis and root cortex (Edmond et al. 2009; Alejandro et al. 2020). In addition, Mn²⁺ is facilitated by ZIP transporter AtRT1 which is considered as Fe uptake transporter (Gao et al. 2018). Furthermore, two ZIP transporters facilitate root-to-shoot Mn translocation in *Arabidopsis*, which are: AtZIP1 localized to the tonoplast involved in Mn²⁺ remobilization from vacuoles to cytosol in roots cells; whereas, AtZIP1 localized to plasma membrane mediated by Mn²⁺ uptake to root stele in plants. In barley plants, HvIRT1 plasma membrane transporter is considered to facilitate Mn uptake and transport (Fu et al. 2017; Gao et al. 2018).

12.3.10.2 Manganese Deficiency

Manganese deficiency in plants often occurs with significant, clear symptoms and Mn concentration below 10–20 mg/kg dry weight is considered lethal in plant survival. Manganese-starved plants show impaired growth and reduced biomass caused by lower chloroplast levels and photosynthetic efficiency rate (Hebborn et al. 2009; Schmidt et al. 2016), while there is decreased tolerance to drought and low temperatures, as well as the number of Mn-complexes in photosystem II, and triggering of disintegration and destabilization of PSII complexes which lowers photosynthetic efficiency in plants (Alejandro et al. 2017; Alejandro et al. 2020). Photosystem disruption initiates chlorophyll degradation and leads to interveinal leaf chlorosis development under Mn deficiency (Broadley 2012; Li et al. 2017), with reports that Mn deficient plants show necrotic spots as a consequence of enhanced free oxygen radicals, decreased MnSOD activity, and damaged chloroplast (Broadley 2012; Alejandro et al. 2020). Interveinal chlorosis in different plants such as cherry, peas, apple, onion, and raspberry with small leaf vein has been observed in Mn deficient plants (Shao et al., 2017; Karthika et al. 2018; Alejandro et al. 2020).

12.3.11 Zinc

Zinc (Zn) is the essential plant micronutrient which is involved in many different physiological and metabolic processes, as well as acts as cofactor in more than 300 proteins, RNA polymerase, and DNA polymerase (Gupta et al. 2016). Involved in the activation of enzymes for protein synthesis, carbohydrate metabolism, auxin regulation, and maintaining the functional integrity of cellular membrane (Karthika et al. 2018), zinc is involved in regulation of gene expression needed for combatting environmental stresses in plants, in tryptophan biosynthesis which is the auxin precursor molecule (Rudani et al. 2018), and is essential for maintaining cellular membrane integrity to hasten the structural adjustment of macromolecules and ion transfer system. Zinc involvement with phospholipids and sulfhydryl clusters of membrane proteins promotes maintenance of membrane (Kathpalia and Bhatla 2018). The Zinc-Cu-SOD plays a role in protecting the proteins and lipids of membrane from oxidation by detoxification of superoxide radicals. This nutrient is required for seed development and promotes cytochrome C synthesis (Karthika et al. 2018).

12.3.11.1 Zinc Uptake and Transport

Zinc is taken up by plant roots as divalent cation Zn^{2+} through mass flow and diffusion. However, organic-ligand-Zn complexes' uptake by plants roots is also known to occur. Important families of zinc transporter proteins involved in zinc transport are ZIP permease family ZRT-IRT, the HMA heavy metal ATPases, and the MTP metal tolerance proteins family. The ZIP family facilitates Zn entry into cytosol while HMA participates in Zn efflux to the apoplast, and the MTP family facilitates Zn sequestration in cellular compartments such as vacuole (Gupta et al. 2016; Rudani et al. 2018; Karthika et al. 2018).

12.3.11.2 Zinc Deficiency

Zinc deficiency triggers decrease in protein synthesis and inhibits root development (Karthika et al. 2018). Showing symptoms of disturbed water and nutrient uptake from soil resulting in stunted growth and yield, zinc deficient plants display interveinal chlorosis and inhibited growth in maize, beans, and sorghum leaves (Rudani et al. 2018). Zinc-starved leaves show malformed bushy roseate appearance and delayed maturity leading to crop reduction, with common deficiency symptoms being white maize bud, little leaf of cotton, khaira disease in rice, and mottled leaf or crown choking in areca nut (Cabot et al. 2019). The deficiency of this nutrient causes decreased shoot growth photosynthesis, which leads to decreased biomass accumulation in wheat plants (Kaznina and Titov 2017).

12.3.12 Molybdenum

Molybdenum (Mo) is absorbed by plant roots as molybdate anion (MoO_4^{2-}) soluble form present in soil. The common component in over 30 enzymes which facilitate oxidation reduction reactions, Mo is essential for symbiotic nitrogen fixation in legume and non-leguminous plants (Padhi and Mishra 2019), and it acts as the cofactor of nitrate reductase assimilation and ureide metabolism in plants. With a significant part played in plant reproductive structure growth and seed yield (Manuel et al. 2018), molybdenum is involved in pollen formation and Mo-containing enzyme aldehyde oxidase which is engaged in the final step of catalytic reactions. This nutrient is a component of sulphur oxidase which helps plants combat damaging effects of sulphite after acid rain (Karthika et al. 2018).

12.3.12.1 Molybdenum Uptake and Transport

Molybdenum is present in soil for plants to uptake, and given the total Mo level in the soil depends on soil pH concentration of adsorbing oxides, it is important that there is an interface with organic compound found in soil colloids (Manuel et al. 2018). Molybdenum is absorbed and stored in vacuoles as MoO_4^{2-} under neutral to mild alkaline conditions. Plant proteins facilitating Mo transport belong to high affinity MOT1, and MOT2 family, specifically for MoO_4^{2-} transport in higher plants (Manuel et al. 2018).

12.3.12.2 Molybdenum Deficiency

Molybdenum is a mobile element and deficiency symptoms appear on the whole plant in the form of stunted growth with pale green or yellow area on the leaf edges. In Mo deficient plants, necrosis around leaf edges and veins due to plant's inability to assimilate nitrate and to convert it to proteins is common. The deficiency symptom of 'whiptail' in cauliflower occurs when leaf tissue fails to develop surrounding mid leaf vein. Due to insufficient N supply in legumes, growth stunting, and yellowing have been seen in Mo deficient plants (Padhi and Mishra 2019), while in broccoli plants, twisting of young leaves which die later is reported. Furthermore, interveinal necrosis associated with enhanced nitrate concentration showing lack of nitrate reductase activity has been reported in plants. Deficiency symptoms include flaccid, grey tinting and mottling of plant's leaves at seedling stage (Karthika et al. 2018; Kathpalia and Bhatla 2018).

12.3.13 Nickel

Nickle (Ni) is a micronutrient which was discovered in year 1987 and is required in a low quantities amounting to <0.5 mg/kg and is taken up as Ni^{2+} . Nickel exists in three oxidation states such as I, II, III in plants and is the key component in particular enzymes involved in N metabolism and biological nitrogen fixation, such as urease. Important is N metabolism, nickel also acts as cofactor in urease facilitating substrate hydrolysis to CO_2 and ammonia. Nickel is required in the growth of legume root nodules and hydrogenase enzyme activation (Liu et al. 2011). Beneficial effects of Ni have been reported like increasing the growth of wheat, oats, and tomato crops (Karthika et al. 2018).

12.3.13.1 Nickle Uptake and Transport

Ni comprises about 3% of the earth's crust and is available to plants from soil with alkalinity above pH 6.7. Studies have shown that AtIRT1 iron regulated transporter 1 member of ZIP family is possibly involved in Ni transport in *Arabidopsis* plants (Nishida et al. 2011).

12.3.13.2 Nickle Deficiency

Nickel deficiency has not been studied to the extent needed which affects understanding how urease hydrolysis to carbon dioxide and ammonia happens. In nickel deficient plants, symptoms can include decrease in dry matter weight, amino acid content, and nitrate accumulation. Necrosis of leaf tips, and leaf necrosis and chlorosis are major symptoms of Ni deficiency (De Macedo et al. 2016). Delay in leaf expansion, rosette bronzing, and chlorosis are common symptoms of Ni deficiency (Liu et al. 2011).

12.3.14 Chlorine

Chlorine (Cl) is a halogen element which occurs in plants as free anion Cl^- bound to chlorinated organic compound at exchange site. A structural component of Mn oxygen evolving complex associated with charge accumulation and water oxidation by PSI (Ali et al. 2020), chlorine plays an important role in maintaining turgor and osmoregulation. Furthermore, the osmoregulatory role of chlorine involves turgor driven cell growth and stomatal functions. Chlorine exists in high concentration in shoot and root apices, and functions in turgor-induced growth of cells (Shrivastav et al. 2020). Involved in regulating activities of certain enzymes such as asparagine synthase, chlorine is known to be involved in glutamate dependent asparagine synthesis. This nutrient is important for its role in inducing plant resistance against stem rot, sheath blight in rice, root rot in barley, stalk rot in corn, common root rot in wheat, downy mildew in millet, coconut grey leaf spot, and brown centre in potatoes (Karthika et al. 2018; Ali et al. 2020).

12.3.14.1 Chlorine Uptake and Transport

Chlorine is absorbed by plants as Cl⁻ ions and concentration ranges from 100–500 mg kg of dry matter in healthy plants. It is a mobile element and its uptake is mediated by Cl⁻/H⁺ cotransport through plasmalemma.

12.3.14.2 Chlorine Deficiency

Plants are considered chlorine deficient when chlorine concentrations are less than 100mg/kg in plants. Deficiency symptoms of chlorine consist of leaf curling, leaf chlorosis, decreased leaf surface area, restricted root branching, and plant wilting (Karthika et al. 2018). Other Cl deficiency symptoms involve leaf wilting near the margins as transpiration is disrupted with chlorine deficiency and followed by plants becoming chlorotic. Chlorine deficiency symptoms are cultivar-specific and causes wilting, swelling, or root tips and leaf change colour to bronze (Kathpalia and Bhatla 2018).

12.4 Conclusion

The chapter emphasizes the physio-biochemical roles of mineral nutrients associated with plant growth and development. The manifestations include macro-nutrient roles and micro-nutrient roles, uptake, and transport. The availability of nutrients fluctuates as plant faces various biotic and abiotic stresses resulting in nutrient deficiency. Nutrient deficiencies cause different physiological disorders identified in the plant displaying deficiency symptoms which causes disrupted growth and yield losses in plants. Present review would help to understand nutrient homeostasis in plants, and to identify deficiency symptoms in relation to plant development which will be beneficial for yield improvement. Molecular approaches and defence mechanisms against nutritional deficiency in plants languishing under different stress conditions should be studied in the future to help understand how to cope with low nutrient availability and leading to improved crop productivity and yield to meet the global food demands.

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