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Molecular Mechanisms of Nutrient Deficiency Stress Tolerance in Legumes

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Abstract

Legumes, which are an essential source of plant proteins and dietary fibre, are the most valued diet for humans after cereals. Globally, legume is commonly grown in the arid and semi-arid tropics. Legumes play an important role in the effective management of fertilisers and improve soil fertility, thereby sustaining agriculture. Improved nutrient absorption, translocation, and cellular homeostasis are essential for optimum plant growth and development. Legumes have evolved strategies to adapt to nutritional deprivation at both physiological and molecular levels. High-throughput sequencing as well as other recent advancements in molecular biology techniques have allowed researchers to investigate the molecular basis of nutrient deficiency tolerance in legume crops. In this chapter, we attempt to present various physiological and molecular mechanisms, specific to legumes wherever available, assisting in adaptation to nutrient-deficient conditions. However, increased efforts are needed on food and feed legumes in the area of mineral nutrition covering physiology and molecular aspects.

Keywords

Legume · Mineral nutrients · Transporters · Nutrient stress · miRNA

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P. Muthu Arjuna Samy et al. (eds.), *Legumes: Physiology and Molecular Biology of Abiotic Stress Tolerance*, https://doi.org/10.1007/978-981-19-5817-5_12

12.1 Introduction

Legumes, belonging to the Fabaceae family, consist of more than 700 genera, including 20,000 species that comprise the second major group of food and fodder crops cultivated globally (Iantcheva et al. 2013). Around 250 Mt of grain and legumes are produced annually accounting for 27% of the global primary food output and 33% of human dietary protein requirements (Hussain et al. 2018). Global malnutrition is a serious threat to nutritional security that leads to a high mortality rate due to the emerging non-communicable diseases (Roorkiwal et al. 2021). Legumes are considered an economical source of nutrition with a high percentage of protein (20–25%) and fibre (8–27%) and a low glycaemic index (Sánchez-Chino et al. 2015). A cup of cooked dried legume contains 6–8 g of fibre and 14–16 g of protein. The majority of legume grains are storage protein, which consists primarily of globulin (70%), albumin (10–20%), and glutelins (10–20%) (Sharif et al. 2018). Protein quality is determined by its amino acid composition, and a protein containing all the essential amino acids (EAA) is called a 'complete protein'. Most of the proteins in legumes are deficient in EAA and considered 'incomplete proteins', whereas proteins from eggs, meat, and milk products are categorised as 'complete proteins'. Usually, legumes contain low fat (<5%) except for soybean (*Glycine max*), lupin (*Lupinus albus*), and chickpea (*Cicer arietinum*) (15–47%). Besides, legumes also contain substantial amounts of nutritionally important minerals as well as vitamins (B1, B2, B3, B6, and B9) (Rebello et al. 2013; Roorkiwal et al. 2021).

Legumes constitute a major part of sustainable agriculture as it improves soil fertility through symbiotic association with beneficial rhizobia and mycorrhizal fungi (Abdelrahman et al. 2018). The interaction of plant roots with soil and water influences nutrient availability in soil and their uptake, leading to a significant role in the growth and productivity of plants. Plants require 17 nutrients for completing their life cycle, which is grouped as macro- and micronutrients based on the quantity required by plants. The macronutrients include carbon (C), hydrogen (H), oxygen (O), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and sulphur (S). Out of these, C, H, and O constitute 90–95% of the total biomass and are available to plants from carbon dioxide and water. Other macronutrients which make up 0.2–4.0% of plant dry weight are divided into two categories: primary (N, P, K) and secondary (Ca, Mg, S). Micronutrients, although required in very less amounts, constitute only 0.002% of the total plant dry weight, but they are indispensable for plant growth. Micronutrients are divided into two groups: positively charged (iron (Fe), copper (Cu), manganese (Mn), zinc (Zn), and nickel (Ni)) and negatively charged (boron (B), chlorine (Cl), and molybdenum (Mo)) (Singh et al. 2013).

The root of legume crops forms two types of symbiotic association with soil microorganisms: rhizobial symbiosis, responsible for atmospheric N fixation, and arbuscular mycorrhizal (AM) symbiosis, which enhances plant P uptake (Püschel et al. 2017). The AM fungi colonise roots, and its hyphae spread over the surrounding soil, forming enormous mycelium networks, which enhance P and Zn uptake by improving root-soil interaction (Kiers et al. 2011; Püschel et al. 2017).

This chapter deals with the physiological and biochemical adaptation strategies with a focus on molecular mechanisms that allow legumes to tolerate nutritional deprivation.

12.2 Physiological Tolerance Mechanisms to Nutrient Deficiency in Legumes

The atmospheric N_2-fixing ability not only benefits the legume crop but is also useful for succeeding crops or main crops with the former as an intercrop. However, several factors influence the process of symbiotic N_2 fixation, including crop growth stage, soil water status, soil temperature, N concentration in the rhizosphere, and presence of other nutrients in the soil (Garg and Geetanjali 2006). In legumes, N deficiency is less common, and the mechanism of symbiotic N_2 fixation is another vast topic and therefore not covered in this chapter. The biological role and the physiological tolerance mechanisms specific to legumes for different nutrients' stress are summarised in Table 12.1. Under low-P conditions, legumes adopt many physiological strategies for mitigating P starvation by adjusting their external and internal P demand. The first strategy involves an improved root-soil interaction by increasing root surface area through alteration in root architecture like an increased number of secondary roots with more root hairs and nodules (Lazali and Bargaz 2017; Meena et al. 2021; Ramtekey et al. 2021; Reddy et al. 2020; Richardson et al. 2011). In addition to altered root morphology, other changes include rhizosphere acidification, root exudation of low-molecular-weight organic acids and acid phosphatase, and symbiotic association with microorganisms including fungi and bacteria (Meena et al. 2021; Singh and Pandey 2003; Smith and Read 2010; Vengavasi et al. 2016; Vengavasi and Pandey 2018). K plays a vital role in CO_2 assimilation, and under its deficiency, the rate of photosynthesis drastically reduces due to a reduction in the leaf size, leaf number, leaf sunlight interception, stomatal conductance, increased mesophyll resistance, and reduced Rubisco (ribulose 1,5-*bis*phosphate carboxylase/ oxygenase) activity in plants (Liu et al. 2008; Pettigrew 2008; Zhao et al. 2001). The physiological influence of S starvation is a reduction in root hydraulic conductivity, which is the first response that signals nutrient hunger through root to shoot (Hawkesford and De Kok 2006). Availability of S in soil determines the relative status of reduced sulphate pools as a means of mobilising S within the plant. If vacuolar sulphate pools are small due to S starvation, the involvement of reduced S compounds translocated through phloem increases dramatically and plays an important role in delivering sulphur to sink tissues like developing seed (Hawkesford and De Kok 2006). The most common adaptation of plants under Mg starvation is starch accumulation in chloroplast at the source leaves. The de-chelating of Mg^{2+} ion from chlorophyll molecules during chlorophyll catabolism is a defence strategy of plants experiencing Mg starvation. Mg is relatively a phloem-mobile element; thus, the regenerated Mg is transported in favour of growth of young tissues (Ceppi et al. 2012; Yang et al. 2012). In legumes, during the early stage of infection in nodule development process, the rhizobia invade plants through a transcellular tunnel and

Table 12.1 A summary of biological roles and physiological tolerance mechanisms developed by legumes in response to various nutritional stresses

Nutrient	Biological roles in plants	Physiological tolerance mechanisms	References
Phosphorus	Constituents of ATP, phospholipids, and nucleic acids, important for root growth and nodule development	Improved root-soil interaction by improved root surface area; exudation of low-molecular-weight organic acids and acid phosphatase	Lazali and Bargaz (2017), Meena et al. (2021)
Potassium	Osmoregulator and involved in ROS detoxification	Increased mesophyll resistance; lowered the Rubisco activity in leaf; altered root gravitropic behaviour	Pettigrew (2008)
Sulphur	Major constituent of cysteine (C) and methionine (M) and vitamins like biotin and thiamine, promotes nodule formation in legumes	Reduction in root hydraulic conductivity; reduces translocation of S towards seeds	Afzal et al. (2015)
Magnesium	Central atom of chlorophyll molecule, involved in protein synthesis, N uptake, and assimilation	Starch accumulation in chloroplast; increased mobilization of photosynthates towards root for nodule development	Peng et al. (2018, 2020), Yang et al. (2012)
Calcium	Secondary messenger; involved in cell division and cell wall strengthening	Reduces the passive flow of monovalent ions, which decreases membrane fluidity	De Freitas et al. (2016)
Iron	Cofactor, structural constituent of many antioxidative enzymes, involved in lipid peroxidation	Improved root growth, root-tip swelling, increased ferric reductase activity in the root, release of phyto-siderophore	Hindt and Guerinot (2012), Sharma et al. (2019)
Zinc	Regulates activities of all six classes of enzymes, involved in transcriptional control of the Ros-type regulator MucR in legumes	Increased length and number of root hairs; release of phyto-siderophore	Lurthy et al. (2020)
Manganese	Acts as a cofactor, component of antioxidant enzyme, oxygen-evolving complex of photosystem II	Lignin concentration decreased in the root	Socha and Guerinot (2014)

embed in the plant matrix glycoprotein (MGP), secreted by host plants. Ca with B plays an essential role in these stages to modulate plant-rhizobia interaction at the cell surface. The degree of attachment and cell invasion by *Rhizobium* in the root is regulated by both Ca and B nutrition, so the deficiency of both elements reduces the induction capability of *nod* genes (Redondo-Nieto et al. 2003).

Plants respond to Fe deficiency by exhibiting morphological changes, including increased root surface area, enhanced root hair development and branching, root-tip swelling, and increased lateral root formation for Fe reduction and uptake (Hindt and Guerinot 2012; Muller and Schmidt 2004). Previous studies on legumes showed that increased Fe^{3+} reductase activity in the root of soybean (*Glycine max*) and lotus (*Lotus japonicus*) provided higher tolerance to cope with Fe deficiency (Klein et al. 2012; Li et al. 2011). To manage Zn deficiency, a tightly regulated network of coordinated expression of Zn transporters for acquisition from the soil, translocation between tissues, and intracellular sequestration has been evolved in plants (Kabir et al. 2017). The cellular utilisation of Zn is considered as a potential Zn efficiency mechanism (Rengel and Graham 1995). Importantly, the activity of carbonic anhydrase, a metallo-enzyme that catalyses the conversion of CO_2 to HCO_3^-, is associated with cellular Zn concentration. In black gram (*Vigna mungo*), the activity of carbonic anhydrase and Cu/ZnSOD enzymes significantly correlated with Zn supply, which can be used as a marker for Zn deficiency (Pandey et al. 2002). Under Mn deficiency, Mg replaces Mn, which could have a detrimental effect on the cellular process such as lignin synthesis that involves Mg. The lignin concentration was found to decrease significantly in root tissue under Mn deficiency because Mn is a cofactor of phenylalanine ammonia lyase (PAL) enzyme, which is involved in the phenylpropanoid pathway to produce monolignols (Socha and Guerinot 2014).

12.3 Molecular Basis of Nutrient Uptake Under Starvation Conditions

All efforts have been made to present the information available up to date with particular reference to legumes wherever available for each nutrient element in the subsequent paragraphs. The transporters characterised for each nutrient element and their regulation are presented briefly in Table 12.2.

12.3.1 Phosphorus

12.3.1.1 Uptake and Transport

Plant roots absorb inorganic P (Pi) from the soil as $H_2PO_4^-$ or HPO_4^{2-} ions depending on soil pH; however, these ionic forms are present in the soil solution at very low concentrations, usually at micromolar (<10 μM) levels (Hinsinger 2001). Phosphate transporters (PTs) are localised in the plasma membrane of root cells and play a major role in the acquisition of soluble Pi from the soil solution against the concentration gradient. Plants possess two nutrient transport systems: (1) high-affinity transport system (HATS), regulated by P concentration in the media, and (2) low-affinity transport system (LATS) which is constitutively expressed. The plants' internal Pi status adjusts their P uptake, especially by raising I_{max} (maximum influx), while changes in K_m are insignificant in this process (Muchhal and Raghothama 1999; Pandey et al. 2018). According to the protein sequence, location, and structure, plants have a wide variety of Pi transporter families such as *Pht1*, *Pht2*, *Pht3*, *Pht4*, and *Pht5* (Guo et al. 2008; Liu et al.

Table 12.2 List of transporter and regulatory genes involved in the uptake and homeostasis of different nutrient elements in legume crops

Nutrients	Crop	Transporter/ regulatory gene	Description	References
Phosphorus	*Phaseolus vulgaris*	*PvPHR1*, *PvmiR399*	Positive regulator of genes implicated in P transport, remobilization, and homeostasis	Valdés-López et al. (2008)
	Medicago truncatula	*MtPT1*, *MtPT2*, *MtPT3*	Low-affinity P uptake	Cao et al. (2021), Liu et al. (2008)
		MtPT5	High-affinity P uptake	Liu et al. (2008)
	Glycine max	*GmPT5*	High-affinity P uptake and homeostasis	Qin et al. (2012)
	Cicer arietinum	Putative *CaPHO1*, *CaPHO2*, *CaPHT1;4*, *CaPAP17*, *CaPPase4*, CaDGD1	P uptake, transport, and mobilization from roots and leaves to nodules	Esfahani et al. (2016)
Potassium	*Lotus japonicus*	*LjKUP*	K transport across plasma membrane	Desbrosses et al. (2004)
	Glycine max	*GmKEA2* to *6*	Cation/proton antiporter involved in K accumulations	Chen et al. (2015)
	Cicer arietinum	K^+ efflux antiporter (KEA)	Accumulation of K	Azeem et al. (2018)
Calcium	*Medicago truncatula*	*MCA8*	Involved in calcium signalling during symbiotic contacts	Capoen et al. (2011)
	Medicago, *Lupinus luteus*, *Vicia faba*	Ca^{2+}/ATPases	Ca absorption into symbiosomes	Andreev et al. (1997, 1998), Benedito et al. (2010), Kataoka et al. (2004)
Sulphur	*Lotus japonicus*	Homolog of *AtSultr3.5*	Essential for S supply to the bacteroides	Kataoka et al. (2004)
	Medicago truncatula	*MtSULTR*	High-affinity sulphate transporter	Casieri et al. (2012)
	Glycine max	*GmSULTR1;2b*	High-affinity sulphate transporter	Ding et al. (2016)
Iron	*Phaseolus vulgaris*	Phvul.005G130500/ FIT1-like, Phvul.002G099700/ IRT1-like	Fe uptake	Castro-Guerrero et al. (2016)
		Phvul.003G086500/ OPT3-like	Fe signalling	Castro-Guerrero et al. (2016)

(continued)

Table 12.2 (continued)

Nutrients	Crop	Transporter/ regulatory gene	Description	References
	Melilotus japonicus	*MtIRT* and *MtFRD3*	Fe uptake and transport	Li et al. (2014)
	Medicago truncatula	*MtNRAMP1*	Fe uptake and transport, expressed in roots and nodules	Tejada-Jiménez et al. (2015)
	Glycine max, *Medicago*	*DMT1* (divalent metal transporter1)	Ferrous transporter in symbiosome membrane	Benedito et al. (2010), Kaiser et al. (2003)
	Glycine max	Glyma03g28610, Glyma03g28630	Fe acquisition	Peiffer et al. (2012)
Zinc	*Glycine max*	*GmZIP1*	Zn uptake and transport	Moreau et al. (2002)
	Phaseolus vulgaris	*PvZIP12*, *PvZIP13*, *PvZIP16*, *PvbZIP1*	Zn uptake and transport	Astudillo et al. (2013)
	Medicago truncatula	*MtZIP1*, *MtZIP3*, *MtZIP4*, *MtZIP5*, *MtZIP6*, *MtZIP7*	Zn uptake and transport	Lopez-Millan et al. (2004)
	Arachis hypogaea	*AhNRAMP1*	Zn, Fe, and Mn transport	Wang et al. (2019), Xiong et al. (2012)
Manganese	*Medicago truncatula*	*MtZIP4*, *MtZIP7*	Mn uptake and transport	Socha and Guerinot (2014)
	Pisum sativum	*PsIRT1*	Mn uptake and transport	Socha and Guerinot (2014)
Molybdenum	*Medicago truncatula*	*MtMOT1.3*	Mo transport to nodule cells	Tejada-Jiménez et al. (2015)
	Lotus japonicus	*LjMOT1*	Mo uptake and translocation to shoots	Gao et al. (2016)

2011; Qin et al. 2012; Raghothama 1999; Rausch and Bucher 2002; Schachtman et al. 1998). The *Pht1* family belonging to HATS is responsible for P absorption from rhizospheres and its transport to the xylem (Gu et al. 2016), while the families of *Pht2*, *Pht3*, *Pht4*, and *Pht5* are organelle transporters responsible for the transport of P across the plastid (*Pht2/4*), mitochondrial (*Pht3*), Golgi membrane (*Pht4*), and vacuole (*Pht5*) (Huang et al. 2019; Liu et al. 2016). The *Pht1* family has received utmost attention among the Pi transporter families, and the members of *Pht1* were identified and functionally validated from a wide range of plant species including *Arabidopsis*, tomato (*Lycopersicum esculentum*), rice (*Oryza sativa*), maize (*Zea mays*), soybean, *Medicago truncatula*, and lotus (Bulgarelli et al. 2020; Liu et al. 2008, 2011; Maeda et al. 2006; Nagy et al. 2006; Paszkowski et al. 2002). All the members of *Pht1* family are $H_2PO_4^-/H^+$ symporters with a similar structure containing 12 membrane-spanning domains with hydrophilic N- and C-terminals. A putative glycosylation site is present in transmembrane domain 10, while a hydrophilic loop is located between transmembrane domains six and seven (Karandashov and Bucher 2005; Smith and Read 2010).

Major transcripts of high-affinity transporter are strongly induced by P starvation and are preferentially expressed in the epidermal cells of root hairs and cortical cells, while a few are expressed in various aerial parts like stems, leaves, flowers, and grains (Ai et al. 2009; Qin et al. 2012). In soybean, 14 members of *Pht1* family, namely *GmPht1;1–14*, as well as one pseudogene (Glyma13g18420) have been identified. *GmPht1* transporters are distributed unevenly on soybean chromosomes ($2n = 20$); however, these transporters are located only on 8 chromosomes out of 20. Among 14 *GmPht1* transporters, maximum four (*GmPht1;4* to *GmPht1;7*) are located on chromosome 10, three (*GmPht1;12* to *GmPht1;14*) are on chromosome 20, two (*GmPht1;9* and *GmPht1;10*) on chromosome 14, while *GmPht1;1*, *2*, *3*, *8*, and *11* are located on chromosomes 2, 3, 7, 13, and 19, respectively (Qin et al. 2012). Except for *GmPht1;8*, which is located in the endoplasmic reticulum, all other *GmPht1* transporters are located in the plasma membrane (Fan et al. 2013). Similar to other Pi transporters, *GmPht1* transporters were significantly upregulated by P deficiency, with the exception of *GmPht1;10*. Among *GmPht1* transporters, seven, including *GmPht1;1*, *2*, *3*, *4*, *7*, *8*, and *12*, are expressed only in root tissues. *GmPht1;9* and *GmPht1;13* were strongly induced in roots and stems as well as in immature leaves and roots, while flowers and stems were the primary sites for the expression of *GmPht1;5* and *GmPht1;14* (Gu et al. 2016; Qin et al. 2012). The β-glucuronidase staining of transgenic soybean roots showed expression of *GmPht1;5* predominantly in the junction region of roots and young nodules as well as in nodule vascular bundles, suggesting its function in Pi transport from root vascular system into nodules. In *M. truncatula*, four *Pht1* members, *MtPT1*, *MtPT2*, *MtPT3*, and *MtPT5*, were identified which showed significant expression in root tissue under P starvation (Cao et al. 2021; Liu et al. 1998, 2008).

12.3.1.2 Regulation of Pi Transporters

The Pi trafficking across the plasma membrane is coordinated among different cellular organelles and regulated by cytosolic Pi homeostasis (Pratt et al. 2009). Under P deficiency, the expression of genes involved in C metabolism (glyceraldehyde 3-phosphate dehydrogenase), N assimilation (glutamine synthetase and glutamate synthase), phospholipid biosynthesis (phosphoethanolamine *N*-methyl transferase), photosynthesis, and mitochondrial electron transport (ferredoxin NADPH reductase) is suppressed in response to cytosolic P and maintains cytosolic Pi homeostasis (Misson et al. 2005; Valdés-López et al. 2008). Proteins containing SPX domain at the N-terminal have been linked to Pi sensing and transport. The SPX-domain proteins (SPX1 and SPX2) function as intracellular Pi sensors and, when bound to PHR1 (PHOSPHORUS STARVATION RESPONSE1), suppress P starvation response under P-depleted condition (for details, see Wang et al. 2021). Inositol polyphosphate (InsP) is an intracellular P signalling molecule that binds with the SPX domain affecting the PHR1-SPX1 interaction. Inactivating the redundant genes, *VIH1* (*VIP1 HOMOLOG1*) and *VIH2*, which encode *PPIP5K* (diphosphoinositol pentakisphosphate kinase), limits InsP8 production and induces the expression of *PHT1* genes causing excessive Pi accumulation (Yan Wang et al. 2021; Zhu et al. 2019). Several genes with consensus *cis*-acting DNA sequences such as W-box, G(E)-box, TATA-box, P1BS (PHR1-binding sequence), MBS (MYB-binding site), helix-loop-helix, and PHO have been associated to the responsiveness of Pi transporters and other P starvation-responsive genes (details in Gu et al. 2016; He et al. 2019). The expression of most of the Pi transporter genes was induced by P starvation, while some of them are controlled by P starvation response transcriptional factors (TFs) such as MYB-coiled coil (MYB-CC), WRKY, and C2H2-type zinc finger protein. The transcription factor belonging to MYB-CC family regulates the transcription of P starvation-induced (PSI) genes by binding to their proximal promoter regions with the imperfect palindromic sequences (GNATATNC) (Baek et al. 2017; Bustos et al. 2010; Gu et al. 2016; Guo et al. 2015). The members of WRKY (WRKY6, WRKY42, WRKY45, and WRKY75) and C2H2 (ZAT6) families are involved in Pi starvation signalling in *Arabidopsis*, bean (*Phaseolus vulgaris*), soybean, *Medicago*, and lupin (Devaiah et al. 2007a, b; Graham et al. 2006). These TFs are localised in the nucleus and overexpressed under P starvation to regulate root architectural modifications. The WRKY75 recognises W-box ((T)TGAC(C/T)), DNA *cis*-regulatory elements, and a region of genes involved in P homeostasis and remobilisation, while ZAT6 regulates the expression of several genes of WRKY75 pathway (Devaiah et al. 2007a, b; Su et al. 2015; Valdés-López et al. 2008). Recently, two new transcriptional factors, namely, OsbHLH6 (He et al. 2021) and RLI1/HINGE1 (Zhang et al. 2021), were identified in rice, which regulates the expression of PHT1 family genes.

The regulation of Pi transporter genes at post-transcriptional level has been reported in plants. Small regulatory RNAs, microRNAs (miRNA), and small interfering RNAs (siRNAs) are considered the most ubiquitous molecules that regulate post-transcriptional gene expression (Bartel 2004). The expression profiles of various miRNAs in legumes under P starvation have been reported earlier. In lupin and soybean, 167 and 57 miRNAs, respectively, showed significant alteration in their expression (Zeng et al. 2010; Zhu et al. 2010). The role of miR399 during P deficiency is well characterised in plants; however, P deprivation alters the expression of some other miRNAs such as miR827, miR2111, miR778, miR169, and miR395 (Franco-Zorrilla et al. 2007; Fujii et al. 2005; Hsieh et al. 2009; Pant et al. 2008). In *Arabidopsis*, miR399 binds to the five complementary bases of the PHOSPHATE OVER ACCUMULATOR2 (PHO2) transcripts and inhibits internal Pi mobilisation from older to new leaves (Chiou et al. 2006; Fujii et al. 2005). miR399 also influences the PSI signalling in the roots of *Phaseolus vulgaris* and phloem sap of *Brassica napus* and *Cucurbita moschata* (Pant et al. 2008; Ramírez et al. 2013; Valdés-López et al. 2008). miR211 accumulates in the phloem sap only under low-P conditions, targets the F-box protein in soybean and *Arabidopsis*, and regulates the protein abundance under P starvation (Hsieh et al. 2009; Xu et al. 2013). Besides miRNAs, long non-coding RNAs (lncRNAs) are also expressed in response to P starvation, which plays a significant role in the regulation of P uptake. The well-studied *IPS1* (induced by P starvation1) acts as a ribo-regulator rather than the target of miR399 and functions as an endogenous target mimic (eTM) of *PHO2* in *Arabidopsis* (for details, see Franco-Zorrilla et al. 2007). The ribo-regulators *At4* and *Mt4* were induced by *IPS1* in *Arabidopsis* and *Medicago*, respectively. Further, in *Medicago*, three PHOSPHORUS DEFICIENCY INDUCED lncRNAs (*PDILs*) were characterised under P starvation, out of which *PDIL1* suppresses the degradation of *MtPHO2* transcripts (Wang et al. 2017). Borah et al. (2018) identified putative lncRNAs for nitrogen and P starvation in soybean and *Arabidopsis*, respectively, which can act as eTMs. They showed computationally that miR827 (P starvation induced) and miR169 (N starvation induced) could be sponged by two and three eTMs, respectively, thereby regulating nutrient uptake through the regulatory module of ‘eTM-miRNA-mRNA’.

12.3.1.3 Regulation of Pi Transporters by Arbuscular Mycorrhizal Fungi

Legumes establish root symbiosis not only with rhizobia but also with AM fungi, which significantly influences the expression of Pi transporters. Only *Pht1*, high-affinity H^+/Pi symporters, have been identified which are involved in mycorrhizal driven P acquisition among different Pi transporter families. The mycorrhiza-specific *Pht1* transporters are grouped into two subgroups, namely, subfamilies I and III. During AM symbiosis, most of the subfamily I transporters are expressed only in the arbuscule-containing cortical cells, while subfamily III *Pht1* genes are expressed in plant roots but specifically induced in cortical cells (Bucher 2007; Harrison et al. 2002; Javot et al. 2007). The upregulation of AM-inducible Pi transporter generally suppresses the expression of other Pi transporters, specifically those involved in direct P uptake from the rhizosphere. This interaction between *Pht1* transporters could indicate the association between mycorrhizal and direct Pi uptake routes. However, it is still unclear whether the downregulation of other Pi transporters is caused by a direct plant response to symbiosis or is caused by an enhancement in Pi acquisition (Garcia-Brugger et al. 2006; Paszkowski et al. 2002). The AM symbiosis-inducible *PHT1* subfamily I transporters were identified in a few plant species such as *M. truncatula* (*MtPT4*), rice (*OsPT11*), and *Astragalus sinicus* (*AsPT4*) (Breuillin-Sessoms et al. 2015; Xie et al. 2013; Yang et al. 2012). Generally, P starvation induced the expression of most of the *Pht1* family transporters in soybean, but AM symbiosis suppressed the expression of *GmPht1;6*, *7*, and *10* in root tissues, while the expression of *GmPht1;1*, *7*, and *11* was significantly induced (Bulgarelli et al. 2020; Tamura et al. 2012).

12.3.2 Potassium

12.3.2.1 K Uptake and Transport

Plant roots acquire potassium ion (K^+) from soil solution, which is derived from several sources such as potassium chloride (KCl), potassium nitrate (KNO_3), potassium carbonate (K_2CO_3), and potassium sulphate (K_2SO_4) present in soil or applied as chemical fertilisers. A wide variety of K transporters and channels are involved in the uptake of K by roots and its mobilisation throughout the plant. The transporter proteins have a high affinity for K^+ and are active at low K concentrations, whereas the channels have a low affinity for K and are active only at high K concentrations (>300 μM external K) (Wang and Wu 2013). The K transporters are grouped into five different classes: (1) shakers/voltage-gated channels, (2) non-voltage-gated channels/tandem pores, (3) HAK/KT/KUP high-affinity transporter family, (4) HAT high-affinity family, and (5) KEA family of antiporter (Gomez-Porras et al. 2012; He et al. 2012; Rehman et al. 2017).

The members of the shaker family, which controls membrane conductance in most plant cell types, are further classified into three groups: *inwards-rectifying* (K_{in}), activated by membrane hyperpolarisation and mediates K uptake; *outward-rectifying* (K_{out}), activated by membrane depolarisation and facilitates K efflux; and *weakly-inward rectifying* (K_{weak}) that mediates K efflux and influx based on the electrochemical gradient due to K^+ (Shabala and Pottosin 2010; Véry et al. 2014; Yi Wang and Wu 2013). All the voltage-gated K^+ channels contained a conserved amino acid motif (TVGYGD) and were widely expressed in plant tissues, allowing a fast K distribution across various parts of the plant and cellular compartments (Kuang et al. 2015; Rehman et al. 2017). In soybean, 16 genes encode voltage-gated K^+ channels, and all of them have a highly conserved gene structure with varying lengths, 57, 98, and 185 bp exons (Rehman et al. 2017). According to Damiani et al. (2016), a candidate gene implicated in membrane repolarisation, movements of stomata, and K^+ extrusion into the xylem sap of *M. truncatula* belongs to this family. The non-voltage-gated K^+ channels, also known as tandem pore channels (TPKs), contained two pore loops per subunit and four transmembrane domains (TM domain). There are six members of the non-voltage-gated K^+ channel family, including a single subunit channel and five tandem pore channels. With the exception of TPK3 and TPK4, voltage-gated channels are located at the plasma membrane in plants, whereas non-voltage-gated channels are located on the endomembrane of several organelles (Pandey and Mahiwal 2020).

The HAK/KT/KUP family plays a critical role in K acquisition from soil and is assumed to function as H^+/K^+ symporters (Véry et al. 2014). The HAK/KT/KUP transporter families have a wide range of subcellular localisation, including the plasma membrane, tonoplast, and another endomembrane, while its transcript is expressed in diverse plant tissues such as guard cells, vascular tissues, root meristems, and fruits (Scherzer et al. 2015). A large number of HAK/KUP/KT genes have been found in different plant species such as 17 in *Vitis vinifera*, 13 in *Arabidopsis*, 20 in *Medicago*, and 29 in soybean and poplar (*Populus alba*) (Davies et al. 2006; Nieves-Cordones et al. 2016; Rehman et al. 2017). Among legumes, *LjKUP* was the first KUP family high-affinity K transporter and was identified in *L. japonicus* with maximum expression in nodules under K stress (Desbrosses et al. 2004). The transcriptomic profiling of soybean showed that 22 HAK/KUP/KT genes were differentially expressed during nodulation, wherein *GmHAK5*, *GmKUP8*, and *GmKUP8* recorded higher expression in root hairs during nodulation (Clarke et al. 2014; Rehman et al. 2017).

The HKT family belonging to the high-affinity K transporters has been widely studied after the cloning of *TaHKT2;1* from *Triticum aestivum*, the first member of HKT gene family (Schachtman et al. 1992). Based on the presence of Gly or Ser residue in P loop, the selectivity pore-forming area, the members of this family were categorised into two subfamilies: subfamily I has a Ser residue (SGGG type) in the P-loop region that is thought to be linked to the specialised Na^+ transport. The subfamily II has only Gly residues (GGGG-type) in the P loop, which mediate the transport of both K^+ and Na^+ (Horie et al. 2009; Huang et al. 2020; Platten et al. 2006). These transporters are still very poorly characterised in legumes; *GmHKT1* and *GmHKT1;4* are two soybean genes that have been identified and functionally validated as participating in salt tolerance (Chen et al. 2014). Only 4 out of 70 potential K^+ transporters identified in soybean belong to the HKT family (Rehman et al. 2017).

The KEA (K^+ efflux antiporter) belongs to the cation/proton antiporter family-2 (CPA2 family) and is responsible for the active accumulation of K in plants. The first KEA was identified in gram-negative bacteria involved in a mechanism for cytosol acidification as a defence against harmful electrophiles (Munro et al. 1991). In plants, KEAs are located in tonoplast, plasma membrane, and membranes of mitochondria and chloroplast (Sze et al. 2004; Walker et al. 1996). Till date, six KEA genes have been identified in *Arabidopsis* genome (*AtKEA1* to *6*). The mutation in *KEA1* and *KEA2* gene in *Arabidopsis* showed that they have diverse effects on leaf development and photosynthetic rate (Dana et al. 2016). Chen et al. (2015) identified 12 members of a novel KEA gene family in soybean, which was divided into five subgroups based on their similarity with the *Arabidopsis* KEA gene family as *GmKEA2* to *6*, whereas the *KEA1*-type gene was not found in the entire genome of soybean. Recently, 23 K channels and transporter genes were identified by genome-wide analysis in chickpea (Azeem et al. 2018). Among 23 genes, only 6 belonged to KEA family, while 2 and 15 genes belonged to HKT and KUP/HAK/KT family, respectively.

12.3.2.2 Regulation of K Transporters

In most of the plant species, transcriptional regulation of K transporter is a ubiquitous mechanism to cope with K starvation conditions (Wang and Wu 2013). When high concentration of K is available in soil solution, most channels are employed to transport K through the membrane along with the concentration gradient, while under K starvation conditions, an active or energy-driven transport system is required to pull K inside the cell (Ragel de la Torre 2019; Rubio et al. 2010). In a few higher plants, the activity of K transporter and channels is regulated by external NH_4^+ concentration. K absorption is competitively reduced by NH_4^+ uptake via these K transporters and channels at high NH_4^+ concentrations (Wang and Wu 2013). The sensitivity to NH_4^+ is a key feature of carrier protein-mediated K^+ uptake. Several NH_4^+-sensitive or -insensitive high-affinity K uptake systems have been found in plants such as *Arabidopsis* (Nieves-Cordones et al. 2007), rice (Chen et al. 2015), and barley (Santa-Marıa et al. 2000). The $NH4^+/K^+$ channels mediate the trafficking of K across the symbiosome membrane (SM) of soybean, faba bean (*Vicia faba*), and *L. japonicus*; however, the identity of these transporters is unknown (Andreev et al. 2005). The interaction of CBL (calcineurin B-like proteins, major Ca^{2+} sensor in plants) proteins with CIPK (CBL-interacting protein kinase) plays a key role in regulating K acquisition in plants in response to K-starved conditions (Xu et al. 2006). In *Arabidopsis*, 26 CIPK and 10 CBL proteins have been identified that control multiple signalling pathways in response to many abiotic stresses (see review Ragel de la Torre 2019; Wang and Wu 2013). In soybean, the upregulated expression of CBL1/9 (Glyma05g05580), CIPK23 (Glyma14g04430), and CDPKs (Glyma14g02680, Glyma04g38150, and Glyma14g00320) genes under K starvation revealed that they probably play a vital role in adaptation to low-K stress (Wang et al. 2012). Earlier studies found that the phosphorylation and dephosphorylation processes regulate the activity of K channels (Chérel et al. 2002; Hashimoto et al. 2012; Lee et al. 2007; Xu et al. 2006). Most of the K channels have cytoplasmic regulatory domains and therefore could be regulated by many cytoplasmic regulatory domains, viz. trafficking proteins (such as SYP121), 14-3-3 proteins (such as GF14-6), and K channel β-subunits (Honsbein et al. 2009; Sottocornola et al. 2006; Sutter et al. 2006). Another gene family possessing BURP-domain protein (a plant-specific protein with a conserved C-terminal domain named after four common members: *B*NM2, *U*SP, *R*D22, and *P*G1) might be significant for plants' responses to stresses. Wang et al. (2012) identified 23 members of BURP gene family in soybean, which exhibited an alteration in expression under K stress, implying that they are involved in K uptake. Further, the expression of a few jasmonic acid biosynthesis-related genes (allene oxide synthase, allene oxide cyclase, and lipoxygenase) was found to be significantly induced by K starvation, but K resupply downregulated their expression indicating that jasmonic acid plays a prominent role in K starvation signalling (Armengaud et al. 2004). Many transcription factor genes such as GATA transcription factors (Glyma11g04060, Glyma07g05960) of the MYB family are thought to have a role in low-K tolerance in soybean (Wang et al. 2012).

A few miRNAs have been characterised as post-transcriptional regulators in response to K starvation such as miR319 and miR396 in barley (Zeng et al. 2019), miR399 in rice (Hu et al. 2015), and miR168 in tomato (Zeng et al. 2019). A recent study on cotton showed that the expression of miR165, miR166, and miR390 was inhibited in cotton after 8 days of K starvation, leading to increased expression of their target genes (ADF3 and HD-Zip) indicating their probable role in the K deficiency-regulating mechanism (Fontana et al. 2020). However, studies related to the regulation of K transporters by non-coding RNA in legumes are lacking.

12.3.3 Sulphur

12.3.3.1 S Uptake and Transport

Sulphate (SO_4^{2-}) is the predominant inorganic S form acquired by roots from the soil solution. Sulphate content in the cytoplasm is relatively constant, and the excess sulphate is stored in the vacuole. Once inside the cytoplasm, it travels through plasmodesmata from cell to cell and reaches the distant leaf chloroplast, where it is converted from sulphate to sulphide and subsequently assimilated into amino acids or other metabolites (Mitra 2015). A large family of sulphate transporters

(SULTRs) are employed in sulphate absorption from the soil solutions. The majority of the SULTR proteins are expressed in the root cell plasma membrane and are made up of a polypeptide chain of ~70 kDa. Sulphate transport through the plasma membrane is most likely a pH-dependent H^+-linked cotransport including $3H^+/SO_4^{2-}$ stoichiometry (Hawkesford and De Kok 2006). According to their function and location, SULTRs are categorised into five groups. The transporters of Group 1 and Group 2 are located in the plasma membrane; the former includes high-affinity while the latter includes low-affinity S transporters. Group 1 SULTRs are predominantly expressed in root tissue, while Group 2 transporters are expressed in vascular tissues (Buchner et al. 2004; Smith et al. 1997). Group 1 SULTRs were first identified in *Stylosanthes hamata*, a tropical legume (Smith et al. 1995), followed by characterisation in the many other plant species such as rice (Godwin et al. 2003), chickpea (Tabe et al. 2003), *Arabidopsis*, *Brassica oleracea* (Buchner et al. 2004), *L. japonicus* (Krusell et al. 2005), *Zea mays* (Nocito et al. 2006), and *T. aestivum* (Shinmachi et al. 2010). Group 3 SULTRs are also localised in the plasma membrane and associated with heterodimer association with unknown function. In *Arabidopsis*, one isoform, *AtSultr3.5*, failed to mediate sulphate transport itself but, after forming heterodimer with *AtSultr2.1*, catalysed sulphate transportation. In *L. japonicus*, a homolog of *AtSultr3.5* was identified, which was localised on the symbiosome membrane of nodules and indispensable for S mobilisation to the bacteroides (Kataoka et al. 2004). The SULTRs belonging to Group 4 mediate the efflux of sulphate from the vacuole to cytoplasm. Group 5 SULTRs, like Group 4, are located in tonoplast and are thought to be important in the absorption of molybdenum (Mo) and selenium (Se) (Shinmachi et al. 2010). Group 5 SULTRs, similar to Group 4, are located in the tonoplast and are thought to be important in the absorption of molybdenum (Mo) and selenium (Se).

Some SULTRs mediate the mobilisation of sulphate from plant cells to rhizobia and play an essential role in the establishment of symbiotic association (Frendo et al. 2013). The *Sst1* gene in *L. japonicus* is expressed in the symbiosome membrane of root nodules and encodes a SULTR protein, which mediates the transport of sulphate from plant cytoplasm to bacteroides, thus playing a vital role in symbiotic N_2 fixation (Krusell et al. 2005). Casieri et al. (2012) identified eight putative *MtSULTR* genes in *M. truncatula* belonging to four SULTR groups, expressed differentially in leaves and root tissue, and their transcript levels were affected by S concentration. Although SULTR genes have been characterised in many crops, only a few were reported in soybean. Ding et al. (2016) isolated and characterised a high-affinity sulphate transporter gene (*GmSULTR1;2b*) from soybean that was extensively expressed in root tissues and induced by S starvation.

12.3.3.2 Regulation of S Transporter

The regulation of sulphate uptake is well coordinated with the transcript levels of the SULTRs, which are mostly higher under low S supply and are rapidly reduced after resupplying of sulphate to S-starved plants (Koralewska et al. 2009; Rouached et al. 2008; Smith et al. 1997). The transcript levels of *AtSULTR1;1*, *1;2*, *2;1*, *4;1*, and *4;2* were induced by S starvation in *Arabidopsis*, and the same was true for wheat, *Medicago*, and *Brassica* (Gigolashvili and Kopriva 2014). Uptake of nitrate influences the sulphate uptake; with low nitrate concentrations, sulphate acquisition was also suppressed (Kopriva et al. 2002). An intermediary metabolite, *O*-acetylserine (OAS), acts as a sulphate starvation regulatory signal, which accumulates under S starvation-induced expression of SULTR genes at low or even at sufficient S conditions (Hopkins et al. 2005). A *cis*-element characterised in *Arabidopsis*, known as S-responsive element (SURE), regulates the S response in plants under S starvation. SURE is a 16-base pair sequence found in the promoter region of several S starvation-inducible genes (Maruyama-Nakashita et al. 2006). SURE21A and SURE21B are present in the 3′-flanking region of *SULTR2;1* (low-affinity sulphate transporter), which is required for the transcriptional activation of these low-affinity SULTRs and is essential for enhancing the rate of root-to-shoot sulphate mobilisation under S starvation (Maruyama-Nakashita et al. 2006). Additionally, transcriptional regulator, Sulfur LIMitation1 (SLIM1), was found to induce the expression of many SULTRs under S starvation (Maruyama-Nakashita et al. 2006). SLIM1, also known as ETHYLENE-INSENSITIVE3-LIKE3 (EIL3), is a member of the transcription factor family that controls the ethylene response. It could be hypothesised that ethylene regulates sulphate absorption and metabolism; however, the effect of ethylene on S metabolism remains unknown (Takahashi 2019). The soybean embryo factors (SEFs) 3 and 4 are also known to be S-responsive factors that bind to the 235 bp region of β-conglycinin promoter (Awazuhara et al. 2002). A similar component has also been reported in the promoter region of serine acetyltransferase in *Citrullus vulgaris* (Saito et al. 1997).

The post-transcriptional regulation of SULTRs by microRNAs such as miR395 induced by a S starvation regulates several genes of sulphur assimilation pathway, including *SULTR2;1* and two chloroplast-localising ATP sulphurylases (*APS1* and *APS4*) (Jones-Rhoades and Bartel 2004; Kawashima et al. 2009). Furthermore, Kawashima et al. (2009) found that the transcription factor SLIM1 regulates the accumulation of miR395 in addition to directing the expression of protein-coding genes involved in sulphur metabolism. Li et al. (2017) identified five novel miRNAs and 27 conserved miRNAs whose accumulation was altered under S starvation in *Arabidopsis*. Among five novel miRNAs, two (miR66 and miR67) were upregulated, while the other three (miR14, miR20, and miR43) were downregulated under S starvation condition.

12.3.4 Magnesium

12.3.4.1 Mg Uptake and Transport

The Mg content in the soil is usually very low because it binds weakly with soil particles and could be leached out by rainwater. The Mg homeostasis in various plant tissues is maintained by a very efficient transporter system, which is involved in acquiring Mg^{2+} from the soil and their allocation throughout the plants. The majority of Mg transporters are members of a single protein family belonging to bacterial CorA Mg^{2+} transporter (MGTs) (Li et al. 2001). The first family of MGTs in the plant was reported in *Arabidopsis*, *AtMGT* and *AtMRS2* (Li et al. 2001). According to the cellular localisation and tissue of expression, ten members of MGT were identified in *Arabidopsis*. Their structural analysis revealed that they possessed two transmembrane domains with a conserved amino acid (GMN) motif (Tang and Luan 2017). The molecular mechanisms of Mg acquisition in plants are poorly understood, and members of the MGT family have been identified in only a few crops including rice (Chen and Ma 2013), *Brassica napus* (Zhang et al. 2019), and maize (Li et al. 2016). To the best of our knowledge, no Mg transporter has yet been identified and characterised in legume crops.

12.3.5 Calcium

12.3.5.1 Ca Uptake and Transport

Plants absorb Ca as a divalent cation (Ca^{2+}) from the soil solution and its uptake by roots against the electrochemical potential gradient. Inside the root cells, Ca can be mobilised via symplast or apoplast, thereby maintaining a low Ca concentration in root cells and preventing its toxicity in the shoot (Marschner 2011). Plastids, endoplasmic reticulum, and mitochondria have the ability to store Ca, but vacuoles serve as the principal Ca storage organelle with a concentration 10,000 times more than the cytoplasm. The cytosolic Ca concentration is almost 0.1 μM during the resting phase of cells, while it rises to 1 μM when Ca participates in any signalling process (Dodd et al. 2010). Ca channels are located in the plasma membrane, and according to their voltage dependence, they are classified into two groups: (1) voltage-dependent cation channels (VDCCs) and (2) voltage-independent cation channels (VICCs) (Sanders et al. 2002). The VDCCs are further divided into two subgroups: (a) *depolarisation-activated cation channels* (DACC), permeable to both mono- and divalent cations and contributing to only short and transient Ca influx, and (b) *hyperpolarisation-activated cation channels* (HACC), permeable for sustained Ca influx and playing a key role in stomatal closure under drought condition. VICCs located at the plasma membrane can be constitutively opened, so are permeable to both mono- and di-valent cations and play a vital role in maintaining cytosolic Ca level (González-Fontes et al. 2017; Tang and Luan 2017).

Ca^{2+}/ATPases and H^+/Ca^{2+} antiporters actively regulate the trafficking of Ca between cytosol and apoplast or vacuoles against the electrochemical potential gradient. Previous studies proposed that the Ca^{2+}/ATPases possessing a higher affinity ($K_m = 0.4–10$ μM) but lower Ca transport capacity are essential for maintaining cytosolic Ca homeostasis in resting cells (Hayter and Peterson 2004; Hirschi 2001). Two major families of Ca^{2+}/ATPases that are identified in plants include (a) P-type ATPase II A family and (b) P-type ATPase II B family (details in González-Fontes et al. 2017; Tuteja and Mahajan 2007). The H^+/Ca^{2+} antiporters have lower affinities ($K_m = 10–15$ μM) but a higher efficiency for Ca transport. They function to withdraw Ca from the cytosol during signalling events and control cytosolic Ca concentration fluctuations (Hirschi 2001; Pittman and Hirschi 2016; Shabala and Palmgren 2011; Sze et al. 2000).

The first H^+/Ca^{2+} antiporter was characterised in yeast followed by *Arabidopsis*, oat (*Avena sativa*), barley (*Hordeum vulgare*), maize, rice, mung bean, soybean, and *Medicago* (Chanson 1991; Charpentier et al. 2016; Cunningham and Fink 1996; DuPont et al. 1990; Hirschi et al. 1996; Schumaker and Sze 1986; Ueoka-Nakanishi et al. 1999; Zeng et al. 2020). In *Medicago*, the calcium ATPase (MCA8) was identified, which was localised in the nuclear envelope; however, in the endoplasmic reticulum, MCA8 was necessary for nuclear calcium signalling during symbiotic contacts (Capoen et al. 2011). A Ca^{2+}/ATPase-driven Ca absorption into symbiosomes has been reported in yellow lupin and broad bean (Andreev et al. 1997, 1998), while NH_4^+/K^+ channels mediate Ca transport in the symbiosome membrane of *L. japonicus*. Out of the 15 Ca^{2+}/ATPases characterised in *Medicago*, only one showed a >150-fold increase in expression during the late stages of nodule growth (Benedito et al. 2010).

12.3.5.2 Regulation of Ca Transporters

The perturbations in cytosolic Ca concentration in response to a specific environmental challenge or developmental signal are referred to as the 'Ca^{2+} signature' that is unique to each response. An increase in cytosolic Ca concentration measured by an array of Ca sensors is a common response to stress (Tuteja and Mahajan 2007). Calmodulin (CaMs), calmodulin-like proteins (CMLs), Ca-dependent protein kinase (CDPKs), and calcineurin B-like proteins (CBLs) are the major families of plant Ca sensors whose conformation or catalytic activity changes after Ca^{2+} binding (González-Fontes et al. 2017).

CaMs are usually located in the cytosol; however, they have also been found in the nucleus, endoplasmic reticulum, and plasma membrane. CaMs/Ca complex regulates the expression of genes for several plant responses through post-translational modification of transcription factors (Rudd and Franklin-Tong 2001). Members of the CAMTA (calmodulin-binding transcription activator), bZIP, CBP60, MYB, MADS-box, NAC, and WRKY transcription factor families bind to CaM and control gene expression in response to light, mechanical stress, heat shock, and osmotic stress in plants (Kim et al. 2009; Reddy et al. 2011). Wang et al. (2015) identified 15 CAMTA proteins in soybean, all expressed in root tissues and induced by several stresses (dehydration, cold, H_2O_2) and hormone signals (abscisic acid, methyl jasmonate, and salicylic acid). Although all *GmCAMTAs* express constitutively in root and leaf tissue, a recent study found that five of them (*GmCAMTA2*, *4*, *5*, *11*, and *12*) were upregulated under drought indicating their contribution to the drought tolerance of soybean (Noman et al. 2021). An increased Ca influx and Ca accumulation in cells enhanced phytase (PA) and acid phosphatase (PAP) activity by increasing the expression of *PA*, *PAP*, and alkaline phosphatase (ALP) gene in the mung bean sprouts (Zhou et al. 2018). The Ca signature was also triggered by a variety of elicitors (either a group of compounds secreted or constituents of pathogens) including protein, oligogalacturonides, β-heptaglucosans, lipopolysaccharides, and xylanases. The perception of elicitors significantly increases Ca influx through various Ca channels such as cyclic nucleotide-gated channels (CNGC) and activated multiple protein kinases (Garcia-Brugger et al.

2006; Reddy et al. 2011). Recently, a few miRNAs were identified that target the sites within putative Ca transporter genes (gma-miR156b target sites on *GmACA22*, gma-miR156b target sites on *GmMCA13* and *GmMCA14*, and gma-miR9750 target sites on *GmMCA3* and *GmMCA4*), indicating that miRNA may be involved in Ca homeostasis and signalling (Zeng et al. 2020).

12.3.6 Metal Divalent Cations: Fe, Zn, and Mn

12.3.6.1 Uptake, Transport, and Regulation of Metal Divalent Cations

The transport of metal divalent cations is mostly mediated by similar transporter families such as zinc-regulated transporter/iron-regulated transporter [ZRT/IRT1]-related protein (ZIP), natural resistance-associated macrophage protein (NRAMP), yellow stripe-like (YSL), P-type ATPases, and vacuolar iron transporter (VIT) (Guerinot 2000; Socha and Guerinot 2014). Plants have a limited number of 'Mn-only' transporter because most of the divalent cation (Fe and Zn) transporters such as NRAMP, YSL, zinc-regulated transporter/iron-regulated transporter-related protein (ZIP), and cation exchanger (CAX) are involved in Mn transport (for details, see review Socha and Guerinot 2014).

In legumes, Strategy I which is a reduction-based mechanism is operational to acquire insoluble Fe^{3+} from the rhizosphere into the root cells. The enzymes, iron-regulated transporter (IRT) and ferric chelate reductase (FCR), are required for the uptake of the reduced form of ferric by the roots (White 2012). The gene encoding IRT belongs to the ZIP family (ZRT-IRT-like protein), and the FCR enzyme belongs to the ferric reductase oxidase (FRO) family (Wu et al. 2005). The IRT is a major Fe importer expressed in the root tissue and located in the plasma membrane, which contains eight transmembrane domains. In soybean, homologs of *Arabidopsis* IRT (*AtIRT1*) and FRO (*AtFRO2*) were identified, which showed an increased transcript level under Fe starvation in root tissue (Stribe 2012). Later, *MtIRT* and *MtFRD3* genes from *Melilotus japonicus* (Li et al. 2014) and homologs of IRT and FRO genes were characterised from *L. japonicus* (Campestre et al. 2016), which showed enhanced expression under low-Fe conditions. Besides Strategy I, the NRAMP family is another Fe transporter family with a highly conserved domain that mediates the trafficking of a divalent metal ion such as Mn and Fe across cellular membranes (Thomine and Vert 2013). The members of NRAMP gene family have been characterised in several plant species such as *Arabidopsis*, barley, rice, and mustard (Qin et al. 2017; Yamaji et al. 2013). Recently, various NRAMP genes have been characterised in legumes. For example, the *AhNRAMP1* gene in groundnut (*Arachis hypogaea*) was expressed in roots and leaves (Xiong et al. 2012), while the *MtNRAMP1* in *M. truncatula* was expressed in roots and nodules under low-Fe stress (Tejada-Jiménez et al. 2015). Further, Qin et al. (2017) identified 17 NRAMP genes in soybean that are differentially regulated by deficiencies of several nutrient elements such as N, P, K, S, and Fe. In contrast to soil conditions where Fe is present in ferric form, the nodule cytosol maintains Fe in its reduced form; hence, the absorption of ferrous is faster than ferric in the nodules (Moreau et al. 1995). The members of NRAMP, vacuolar iron transporter (VIT), yellow stripe-like (YSL), and ZIP transporter family are overexpressed in nodules and thereby may be involved in iron transport across symbiotic membranes (Brear et al. 2013). A ferrous transporter, *GmDMT1* (divalent metal transporter 1), has been identified in soybean symbiosome membrane and showed maximum similarity with NRAMP transporter family (Kaiser et al. 2003). Similarly, the homologs of *GmDMT1* were identified in *Medicago*, which were expressed specifically in the nodules (Benedito et al. 2010). The release of citrate by *LjMATE1* (multidrug and toxic compound extrusion 1) increased Fe transport into rhizobia-infected cells of *L. japonicus*, resulting in enhanced leghaemoglobin concentration and nitrogenase activity in nodules (Takanashi et al. 2013).

The Zrt and Irt-like proteins (ZIP) and bZIP families of transporters are involved in Zn absorption, and its mobilisation to shoot, developing embryo and seeds (Eide et al. 1996). The ZIP family is highly conserved in prokaryotes and eukaryotes, and it is thought to have eight transmembrane domains with a histidine motif (Chen et al. 2008; Eng et al. 1998). Members of the ZIP family transporter have been identified in several plant species, including *Arabidopsis* (15 members), rice (17 members), and wheat (14 members), demonstrating a wide range of localisation and function (Evens et al. 2017; Milner et al. 2012). Moreau et al. (2002) discovered that a member of the ZIP family, *GmZIP1*, was highly selective for zinc uptake in soybean nodules. *VvZIP3*, a member of ZIP family, identified in *Vitis vinifera* showed higher expression in flower tissue under Zn deficiency (Gainza-Cortés et al. 2012). Lopez-Millan et al. (2004) identified six genes in *M. truncatula*, namely, *MtZIP1*, *3*, *4*, *5*, *6*, and *7*, all of which contained a conserved Zn motif with eight transmembrane domains. They showed that *MtZIP1*, *5*, and *6* transporters restored yeast growth in Zn-deficient media; *MtZIP3*, *5*, and *6* proteins restored yeast growth in Fe-limited media; while *MtZIP4* and *7* proteins restored yeast growth in Mn-deficient media. Astudillo et al. (2013) identified and characterised a large family of Zn transporters in *Phaseolus vulgaris*, 23 of which belonged to the Zip family and three to the bZIP family.

The regulation of uptake and translocation of most divalent cations and their deficiency responses are controlled by the master regulator, *FER* transcription factor, which belongs to the bHLH transcription factor family and was first cloned from tomato (Ling et al. 2002). Its homolog, *AtFIT* (FER-like iron deficiency-induced transcription factor), was later found in Arabidopsis (Colangelo and Guerinot 2004; Yuan et al. 2008). Similar to *IRT1* and *FRO2*, the expression of *FIT* is also induced by Fe starvation in root tissue, where it upregulates the expression of *IRT1* and *FRO2*. Two soybean genes, Glyma03g28610 and Glyma03g26830, showed homology with *AtFIT* and upregulated the Fe acquisition genes *IRT* and *FRO2* under Fe starvation (Yuan et al. 2008). Another member of bHLH family transcription factor, *POPEYE* (*PYR*), controls the internal mobilisation of Fe or Zn by regulating the activity of *FRO6*, *ZIF1* (zinc-induced facilitator 1), and *NAS4* (nicotianamine synthase 4) (Long et al. 2010). The impact of phytohormones on Fe uptake has also been studied; auxin and ethylene positively control the Fe starvation response (Romera et al. 2011; Zuchi et al. 2009), while cytokinin and jasmonate act as a negative regulator of Fe acquisition by decreasing the expression of FRO2 and IRT1 (for details, see review, Hindt and Guerinot 2012).

12.4 Conclusions

Protein calorie malnutrition is a prevalent nutritional disorder, especially among children, in underdeveloped nations. The lower income populations are particularly vulnerable because they cannot afford to buy conventional protein sources like milk and meat. The high protein content in legumes makes them a viable replacement for more energy-dense animal protein sources. The availability of several mineral nutrients may influence legume productivity and N_2 fixation. Due to symbiotic nitrogen fixation, the demand for other nutrients is higher for legumes as compared to other non-legume crops. Among nutrient elements, P is a common limiting factor for nodulation in legume crops because of the energy-intensive N_2-fixation reaction. Similarly, Ca is significantly important for early symbiotic activities. On the other hand, S and K are not a major bottleneck for nodulated legumes, but the K supplement for osmoadaptation is necessary for the development of legume crops. Due to the anaerobic and acidic environment inside the nodule, Fe is more or less deficient in legume crops even though the soil contains sufficient Fe concentration.

Available literature showed that the characterisation of transporters and identification of their regulatory genes in legumes have been accomplished for a few nutrient elements. However, such studies for the majority of essential nutrient elements in legumes are still in the primitive stage. This chapter has outlined the various physiological and molecular mechanisms which assist in the adaptation of legumes to nutrient-deficient conditions. Future efforts should be directed to determine the molecular basis of nutrient absorption, translocation, and cellular homeostasis in legume crops.

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