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Sensory Biology of Plants

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Nutrient Perception and Signaling in Plants

3

Dinesh Kumar Jaiswal and Nandula Raghuram

Abstract

Plants have developed mechanisms to sense the fluctuating availability of nutrients, water, carbon dioxide, oxygen, etc. for their adaptation and survival under constantly changing atmospheric and soil conditions. The biological interventions for crop improvement for nutrient use efficiency have long been limited by the lack of adequate understanding of the sensing and signaling of nutrients and the targets for their improvement. Moreover, nutrient fluctuations could contribute to or accentuate the effects of other abiotic stresses such as drought, flood, salt, extreme light, heat, cold, and wind velocity or biotic stresses due to pests and pathogens. The global warming due to increased atmospheric CO₂ emissions also affects drought, salt stress, and nutrient status in plants. This chapter highlights several developments in the last two decades that have improved our understanding of the molecular physiology of nutrient sensing, signaling pathways, and their crosstalk, revealing the nature of plant responses toward its survival. We deal with sensing at the levels of roots for a few nutrients and sensing at the level of shoots for oxygen and carbon dioxide and how a balance of all these factors ensures growth and development. The sensing of water and stress environment is covered separately in two chapters.

Keywords

Carbon dioxide · Nitrogen · Nutrients · Oxygen · Phosphorus · Potassium · Sensing · Signaling

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3.1 Introduction

The sensing of nutrient availability regulates the plants' growth and development. Plants require macronutrients viz., nitrogen (N), phosphorus (P), potassium (K), sulfur (S), magnesium (Mg), and calcium (Ca), and micronutrients such as copper (Cu), iron (Fe), nickel (Ni), zinc (Zn), boron (B), molybdenum (Mo) chlorine (Cl), and manganese (Mn). These nutrients play a significant role in various cellular pathways; however, deficiency of N, P, and K macronutrients significantly affects plant growth. Deficiency of these nutrients in the soil could be due to their non-availability in usable forms, physicochemical properties of soil, soil pH, less solubility/stability in water, and slow diffusion rate among others. Depending upon the developmental stage, plants are in constant need of nutrients. In cultivated plants, this is usually complemented with the exogenous application of various doses and forms of fertilizers to replenish nutrients in the soil or even directly to the plants through foliar sprays, etc. However, even in the best of circumstances such as precision farming with drip irrigation providing just the right amounts of water and nutrients on daily basis, the plants do not uptake and use all the nutrients. The losses can be far worse when farmers in most countries apply large amounts of fertilizers in a few divided doses in the entire cropping season. The unutilized fertilizers pollute the ground water and surface water bodies apart from air pollution by volatilization, posing serious threats to the environment, within and across national boundaries (Sutton et al. 2013). While slow-release fertilizers and crop management practices such as timing, dose, and method of application yield some agronomic benefits in the short term (Li et al. 2018a), the inherent inefficiency of the crop cultivar to use the available nutrients has to be tackled biologically. The problem of biological or genetic improvement of nutrient use efficiency (NutUE) of crops is compounded by the fact that many efficient genotypes may have even been selected out unintentionally during screening under high-nutrient input conditions in yield-centric crop improvement programs of the earlier decades. Finding them and bringing them back for low-nutrient input screening for NutUE are huge challenges because their phenotypes remain largely unknown. Fortunately, there has been some progress in the basic understanding of molecular mechanisms underlying nutrient sensing and signaling, at least with respect to the development of root system architecture (RSA), which is increasingly emerging as an important target for phenotype development and phenomics. *Arabidopsis* has been extensively used as a model system to study nutrient-responsive changes in RSA. Low dose of nitrate induces elongation of lateral root (LR), whereas high doses suppress LR elongation in *Arabidopsis* (Zhang and Forde 1998). A phenotypic screening of *Arabidopsis* natural population under controlled condition using different doses of nitrate showed the pronounced variation in RSA trait at low dose across different accessions (De Pessemier et al. 2013). Nitrate-induced ANR1 gene, which encodes a MADS box transcription factor, has been shown to control lateral root branching in *Arabidopsis* (Zhang and Forde 1998; Gan et al. 2012). The GS3 and DEP1, atypical heterotrimeric G-protein gamma subunits, interact with OsMADS1 in rice (Liu et al. 2018). Rice OsMADS1 transcription factor is encoded by grain yield-associated qLGY3 QTL (Liu et al. 2018)

and its NutUE function yet to be established. Molecular and genetic analyses have led to the identification of key components regulating nutrient uptake, transport, and assimilation inside cell and their biological role in growth and development of plants even under adverse agricultural climatic conditions. As case studies, we will discuss sensing mechanism of a few well-studied nutrients.

3.2 Sensing the Nutrients

3.2.1 Nitrogen Sensing

N is the integral component of biomolecules including nucleic acids and proteins. Plants cannot utilise atmospheric N_2 and depend on compounded forms such as nitrate or ammonium ions or urea. The cellular N level is known to regulate the shoot and root developmental processes, which in turn regulate nitrogen use efficiency (NUE) in plants (Wang et al. 2018a; Gent and Forde 2017). In most of the plants, the intracellular N level could be sensed by glutamine concentration, an amino acid and an end product of N assimilation (Chellamuthu et al. 2014). N-regulated long-distance signaling from shoot to root is possibly mediated via the phloem sap containing high amino acid contents. Therefore, understanding the role of glutamine in long-distance signaling would provide new insight for N-sensing in plants. Recently, the role of elongated hypocotyl 5 (Hy5) was identified as a phloem mobile signal for shoot to root mediated enhancement of nitrate uptake (Chen et al. 2016). It may be possible that the N status may be sensed by C/N ratio as shown for PII protein pathway in lower organism (Arcondeguy et al. 2001). PII proteins are evolutionarily conserved, but their signaling is more complex and diverse in higher organisms. Glutamine is known to bind PII proteins in plants. PII proteins are localized in the plastids of plants, and their interaction with NAGK (N-acetyl-L-glutamate kinase) regulates fatty acid metabolism (Sugiyama et al. 2004). This suggests that the N-sensing role of PII proteins is yet to be established in plants.

Among N, P, and K, only the function of N, especially nitrate, has been proved as a nutrient and signaling molecule affecting cell physiology in plants (Krouk et al. 2010). Genome-wide effect of N starvation and N sources and doses revealed a large-scale transcriptional reprogramming in plants (Shin et al. 2018; Sun et al. 2017, Wei et al. 2016; Yang et al. 2015; Misyura et al. 2014; Sharma et al., unpublished data). NO_3^- induces expression of associated transporters; however, no such sensing and signaling role is known for NH_4^+ in the activation of its own transporters (AMTs). Instead, NH_4^+ functions in the opposite way and inhibits the expression of many AMTs in most of the plant species. In case of rice, however, exogenous application of NH_4^+ has been reported to induce OsAMT1;1 and OsAMT1;2 expressions and inhibited by N starvation condition (von Wieren et al. 2000). The signaling role of urea is not well documented; however, urea induces the expression of urea transporter (AtDUR3) similar to nitrate transporter but repressed by NO_3^- and NH_4^+ in *Arabidopsis* (Kojima et al. 2007). This suggests that the transceptor function of urea transporters needs to be investigated.

Fluctuation in cellular N level and its demand enhances the perception of soil N, ammonium, nitrate, and urea, concentrations by root cells, which modulate the cellular acquisition, assimilation, and other processes in plants during optimal and adverse environmental condition (Tsay et al. 2011). NO_3^- concentration is much higher than NH_4^+ in soil, but the acquisition of both the ions is crucial as NH_4^+ significantly affects the activity of nitrate transporters in the root. Transport of urea occurs inside the cell in either a non-metabolized form or a metabolized form, CO_2 and ammonia, produced by bacterial urease activity (Wang et al. 2012). Influx and efflux rates control the acquisition processes in root cells via either high-affinity transport systems (HATS) or low-affinity transport systems (LATS) localized on the plasma membrane (Miller et al. 2007). HATS have been characterized for both NO_3^- and NH_4^+ whereas LATS for NO_3^- (Noguero and Lacombe 2016). Nitrate transporter 1/peptide transporter family (NPF), nitrate transporter 2 (NRT2), slow anion associated channel homologs (SLAC/SLAH), and chloride channel family (CLC) proteins are involved in nitrate acquisition and may play a role in the sensing mechanism as reported for NRT1.1/NPF6.3 transporter (O'Brien et al. 2016). NRT1.1/NPF6.3 acts as a transceptor and is phosphorylated by CIPK23, a calcineurin B-like interacting protein kinase 23, which alters its function for low-affinity or high-affinity state (Ho et al. 2009). NO_3^- induced local gene expression, and long-term feedback repression due to nitrate resupply is regulated by NRT1.1/NPF6.3 in *Arabidopsis*. A diverse set of transcriptional regulators have been implemented to regulate N-sensing/transport in plants (O'Brien et al. 2016). Nodule inception-like protein 7 (NLP7), a NIN family transcription factor, is a positive regulator of nitrate signaling as evidenced from nitrate-induced impaired expression of nitrate transporter (NRT2.1) and nitrate reductase (NR) genes in *nlp7* knockout mutants (Castaings et al. 2009). NLP7 works upstream of NRT1.1-dependent nitrate signaling in the presence of ammonium, whereas in the absence of ammonium, NLP7 functions in NRT1.1-independent signaling in *Arabidopsis* (Zhao et al. 2018). AMT, ammonium transporter/methylammonium permease/rhesus (AMT/MEP/Rh), family proteins are involved in root-mediated NH_4^+ transport along the electrochemical potential gradient in plants (Ludewig et al. 2007). Six AMT family members were reported in *Arabidopsis*, and most of them were expressed in the root. A total of ten AMT transporters were reported in rice, and three OsAMT1 genes, viz., OsAMT1;1, OsAMT1;2, and OsAMT1;3, were characterized for their expression and NH_4^+ transport function in yeast (Sonoda et al. 2003). Increased NH_4^+ influx was observed in the root of transgenic plants overexpressing OsAMT1;1 in rice (Hoque et al. 2006). In plants, two types of urea transporters were reported, namely, DUR3 orthologue and MIPs, i.e., major intrinsic proteins (Wang et al. 2012). MIPs belong to a low-affinity transporter group, whereas DUR3 is a high-affinity urea transporter. DUR3 orthologue has been reported in algae, fungi, mosses, and higher plants; DUR3 urea transporter activity was demonstrated in the root of *Arabidopsis* (Wang et al. 2012); however, its role in urea sensing and signaling, if any, is yet to be discovered.

Target of rapamycin (TOR) is an evolutionarily conserved protein kinase that regulates the nutrient sensing mechanism in yeast and mammals. Plants do not have all the homologs of TORC1 complex present in animals (Dobrenel et al. 2016). Diverse roles of TOR kinase including growth and development functions have been characterized in plants (Dobrenel et al. 2016). *Arabidopsis* mutants defective in TOR signaling components showed induction of genes associated with amino acid recycling and reduced expression of nitrate assimilatory genes (Ahn et al. 2011). Despite the important role of TOR complex, its N-sensing mechanism is unknown in plants. It has been shown that GCN2 or general amino acid control non-repressible 2 protein kinase maintains the cellular amino acid pool during N deficiency in yeast (Chantranupong et al. 2015). GCN2 protein kinase phosphorylates eukaryotic translation initiation factor (eIF2 α) and inhibits protein synthesis during N deprivation (Chantranupong et al. 2015). The GCN2 kinase and eIF2 α in plants have been implicated in seed germination and development and multiple stresses (Li et al. 2018b). It has been shown that GCN2 kinase phosphorylates eIF2 α in *Arabidopsis* under various conditions including amino acid starvation; however, in-depth analyses are required to enlighten the molecular aspect of GCN2 and eIF2 α in sensing N level in plants. Another important candidate for N sensing is glutamate-like receptors (GLRs) in plants. *Arabidopsis* genome codes for 20 GLRs showing homology with mammalian ionotropic glutamate receptor (iGluR) that act as glutamate-gated cation channels (Weiland et al. 2016). GLRs are localized in different membranous systems including plasma membrane (Weiland et al. 2016) and showed broad range specificity to amino acids (Tapken et al. 2013). Experiment with AtGLR1.1 knockdown mutants showed that specifically sucrose has an inhibitory effect on germination in an N-depleted medium, which was restored after exogenous NO₃⁻ supply to the medium (Kang and Turano 2003). However, the N-sensing role of GLRs is not known and needs more experimentation.

3.2.2 Phosphorus Sensing

Soil is often limited in the concentration of phosphorus (P), an essential macronutrient, and therefore plants have developed efficient mechanisms for phosphate uptake, remobilization, and recycling to maintain growth. P is an essential constituent of biomolecules such as lipids, proteins, and ATP among others, and phosphate deficiency in soil affects the agronomical performance of crops. Plant utilizes inorganic phosphate (orthophosphate, Pi) from soil, and Pi deficiency is due to slow diffusion rate and complex chemical fixation in soil (Raghothama 1999). Arbuscular mycorrhizal fungi (AMF) colonization with root does not involve indirect Pi acquisition; however, AMF enhances the uptake via mineralization of organic P and solubilization of insoluble inorganic P in plants (Smith et al. 2011). AMF-induced P uptake is mediated by the regulation of PSI, Pi starvation-inducible, genes including Pi transporters in plants (Yang et al. 2012; Xu et al. 2007). Pi deficiency also induces remobilization of P, between root and shoot involving phosphate transporters and purple

acid phosphatase among others. Insoluble P compounds are not usable by plants; therefore, secretion of acid phosphatases such as purple acid phosphatase and organic acids by roots solubilizes these compounds to expedite the efficient P acquisition in plants (Robinson et al. 2012). Membrane transporters associated with Pi uptake have been identified and characterized in many plant species (Wang et al. 2018b; Mlodzinska and Zboinska 2016). Phosphate transporter traffic facilitator 1 (PHF1) regulates the targeting of high- and low-affinity Pi transporters from ER to plasma membrane and therefore plays an important role in Pi uptake in plants (Bayle et al. 2011).

Cellular Pi homeostasis is regulated through the combinatorial effects of local and systemic sensing and signaling under Pi-deficient condition in plants. The Pi deficiency in soil is sensed by root cells, which transmit the signal to the shoot for activation of adaptive responses at whole plant level. Root tips perceive the Pi deficiency signal, and root cells activate Pi uptake either by membrane-localized receptors for soil Pi level or by intracellular receptors (Nagarajan and Smith 2012). Local as well as systemic Pi signaling is regulated through sugars, ABA, ethylene, cytokinins, and auxin, among others in plants (Chiou and Lin 2011).

During Pi deficiency, the plant enhances the Pi acquisition from soil and remobilization within plant systems. Phosphate stress responses (PSRs) are Pi deficiency-induced adaptive responses, which include changes in the root system architecture, viz., increased root hair and lateral root density; reduction in primary root length; enhanced PSI (phosphate starvation-induced) gene expression and high-affinity Pi transporter activities; change in root/shoot ratio; starch, sugar, and anthocyanin accumulation; and release of phosphatases and organic acids into the soil (Lynch 2011). Pi acquisition-efficient crops showed better growth response as compared to relatively less efficient genotypes due to shallower root growth angles in Pi-rich soil (Lynch 2011). Pi deficiency-induced PSR genes showed delayed induction in response to media lacking Pi, suggesting that internal Pi levels regulate the PSR expression in *Arabidopsis*. Reduced primary root growth was observed under Pi deficiency in many ecotypes with natural variation in *Arabidopsis* (Chevalier et al. 2003), whereas such responses were lagging in crops like maize and rice, suggesting that different adaptive mechanisms are involved to regulate RSA in Pi-deficient soil (Shimizu et al. 2004).

Transcriptomic and genetic analyses of different mutants to delineate the Pi sensing and signaling mechanism showed that the root tip senses the Pi deficiency in soil (O'Rourke et al. 2013; Lan et al. 2012; Thibaud et al. 2010). Transcriptomic analyses have provided in-depth information on the differential regulation of many genes associated with Pi deficiency-induced signaling cascades governing adaptive responses in plants. The differentially expressed genes were phosphate transporters, SPX domain-containing proteins, and acid phosphatases among others associated with Pi uptake, remobilization, and recycling in plants. The genes induced by Pi deficiency include early signaling event genes such as 14-3-3 proteins, CDPKs, MAPKs, WRKY, bHLH, NAC, MYB TFs, cytochrome P450, and peroxidases including those that belong to hormone- and stress-related pathways (Chiou and Lin 2011); among others were the transcriptional regulators also identified. Genes

associated with late signaling events were associated with the adaptive response pathways, viz., metabolic process, protein synthesis and degradation, and photosynthesis among others (O'Rourke et al. 2013; Thibaud et al. 2010).

Nitrate signaling has provided the evidence that plasma membrane-localized transporter, CHL1, can act as tranceptor i.e., transporter and receptor molecules in *Arabidopsis* (Ho et al. 2009). Yeast Pho84 works as a tranceptor in Pi sensing and transport mechanism (Popova et al. 2010). By analogy, PHT1 may work as a tranceptor to sense and transport Pi in plants. Regulation of Pi-induced signaling by inositol polyphosphates (IPs), ROS, and Ca²⁺ molecules is known in the plants (Chiou and Lin 2011). The IP signaling mutant, *atipk1*, showed a hypersensitive phenotype to Pi and was less responsive to the changes in Pi level. The *atipk1* mutant showed increased accumulation of internal Pi as compared to wild-type plants, confirming their role in Pi sensing pathways (Stevenson-Paulik et al. 2005). The spatial ROS distribution in the RSA is regulated by Pi deficiency in *Arabidopsis* (Tyburski et al. 2009). ROS accumulation was observed in the elongation zone and other parts of the root under high Pi concentration, whereas ROS accumulation was absent in the elongation zone under low Pi, highlighting the importance of ROS in Pi sensing mechanism (Chiou and Lin 2011). Pi deficiency induces the higher expression of Ca²⁺ transporter, suggesting its possible role in Pi-mediated signaling in plants. Pi deficiency-induced local signal generated in the root cells may transport to the shoot via the xylem to regulate the various responses associated with increased accumulation of sugar and anthocyanin, reduced photosynthesis, and shoot development among others (Bouain et al. 2016). Molecular mechanism involving systemic signaling and shoot-associated responses under Pi deficiency is yet to be discovered. Pi deficiency regulates the expression of auxin-responsive transcription factors, which corroborate the auxin-mediated increase in lateral root density and inhibition of primary root length (O'Rourke et al. 2013). The downregulation of gibberellin-responsive genes was observed in Pi deficiency condition (O'Rourke et al. 2013). The expression of genes associated with ethylene and cytokinin pathways were induced under Pi deficiency (O'Rourke et al. 2013).

Pi deficiency-mediated inhibition of primary root length was due to reduced cell division and cell elongation processes in *Arabidopsis* (Svistonoff et al. 2007). A PDR2 (phosphate deficiency response 2) gene encodes for P5-type ATPase, and the *pdr2* mutant showed a hypersensitive phenotype to Pi deficiency due to defectiveness in the viability of the meristem in root (Ticconi et al. 2009). Low-phosphate root 1 (LPR1), a protein localized in the endoplasmic reticulum, is a part of the quantitative trait loci (QTL) that affect the primary root growth and genetically interact with PDR2 to regulate meristem activity via SCARECROW (SCR) regulation (Ticconi et al. 2009). Both LPR1 and PDR2 proteins have been documented in sensing of extracellular Pi in soil (Ticconi et al. 2009). The SPX domain proteins (SPX) control the phosphate starvation response 1 (PHR1) activity in response to Pi level in rice and *Arabidopsis* (Zhou et al. 2015). Pi sensing role of SPX is yet to be established.

3.2.3 Potassium Sensing

Potassium (K^+) is the most abundant macronutrient involved in many biological processes including membrane transport, osmoregulation, and enzyme activation among others. Fluctuation in K^+ level affects many physiological processes such as transport and photosynthesis, which ultimately regulate the growth responses in plants (Hafsi et al. 2014). Due to limited concentration of K^+ in soil, plants have developed complex signaling network to sense the K^+ deficiency and activate the adaptive responses under adverse condition. Roots are the main organs to absorb K^+ from the soil; therefore, root cells are likely to play a K^+ sensing role in plants. Plant cells sense the reduction in cellular K^+ level and activate physiological, biochemical, and molecular changes to enhance K^+ uptake and K^+ homeostasis (Schachtman and Shin 2007). The concentration of K^+ regulates the membrane potential and hyperpolarization state of the membrane in root cells, which is the earliest known event during K^+ deficiency sensing (Nieves-Cordones et al. 2008). Plasma membrane-localized AHA proteins, i.e., H^+ -ATPases, are responsible for the hyperpolarization of the membrane (Falhof et al. 2016).

Transcriptomic analyses of nutrient deficiencies led to the identification of many genes involved in various biological processes including transcriptional regulators. Transcriptomic analyses under K^+ deficiency identified many genes involved in K^+ acquisition and assimilation, metabolism, and regulatory responses among others (Shen et al. 2017; Zhang et al. 2017; Ma et al. 2012). Transcriptomic studies under N and P deficiency have also identified many genes involved in K^+ sensing and signaling pathways. This overlapping signal transduction may be due to similar physiological changes and adaptive responses for efficient cellular ion homeostasis.

Plant genomes encode a number of K^+ transporters and channels, and among them many of the potential candidates showed differential selectivity and affinity to K^+ (Ward et al. 2009). Shaker family AKT1 subfamily and KUP/HAK/KT transporter HAK5 include most of the K^+ transports in the studied plants (Fuchs et al. 2005; Buschmann et al. 2000; Hartje et al. 2000). Despite the functional redundancy of these AKT1 transporters, there is significant variation in the K^+ acquisition and assimilation across plant species. Root cells sense the K^+ deficiency, and therefore, the plasma membrane-localized proteins could be potential K^+ sensors to sense the changes in the environmental condition. However, there is no report of K^+ sensors in plants till today. The AKT1 involved in the influx of K^+ could function as K^+ sensor similar to NO_3^- transporter, which not only senses the NO_3^- level but is also involved in acquisition in *Arabidopsis* (Ho et al. 2009). The possible reasons for AKT1 as a K^+ sensor are (1) detection of K^+ fluctuation and efficient functioning in high and low affinities, (2) plasma membrane localization in the epidermal cells of root, (3) *akt1* mutant phenotype similar to K^+ deficiency condition, (4) absence of K^+ deficiency-induced hyperpolarization of membrane in *akt1* mutant plants, and (5) CIPK23-mediated AKT1 phosphorylation, which affects K^+ transport (Xu et al. 2006). It has been shown that K^+ binds to H^+ -ATPase to regulate membrane polarization (Buch-Pedersen et al. 2006). Sensing of K^+ deficiency, possibly by AKT1, immediately slows down the ATP hydrolysis by inducing the uncoupling of plasma

membrane-localized H⁺-ATPase from ATP hydrolysis reaction and initiates the hyperpolarization state of membrane in root tissues.

It has been well documented that Ca²⁺ acts as a second messenger in stress signaling pathways. Stress conditions induce ROS production, which in turn enhances Ca²⁺ accumulation to activate downstream signaling cascades in plants. K⁺-deficient soil induces the accumulation of cytosolic Ca²⁺ (Allen et al. 2001), which activates the Ca²⁺ sensor for efficient K⁺ accumulation (Li et al. 2006). The cyclic nucleotide-gated channel (CNGC) and glutamate receptor channel (GLR) are Ca²⁺-permeable channels, localized in the root cells of plants (Michard et al. 2011). This clearly suggests that study of these Ca²⁺ channels during K⁺ deficiency would provide new insight into K⁺ sensing in plants. The activity of pyruvate kinase, a glycolytic enzyme, was regulated by cytosolic K⁺ level (Ramirez-Silva et al. 2001), and K⁺ deficiency condition had significantly reduced its substrate pyruvate content in cytosol (Armengaud et al. 2009). Therefore, pyruvate kinase has been proposed as an intracellular potential sensor to perceive the K⁺ fluctuation inside plants (Schachtman and Shin 2007; Armengaud et al. 2009). Further investigation is needed to understand the sensing role of pyruvate kinase and related enzymes as K⁺ sensors in plants.

3.3 Sensing Gaseous Atmosphere

3.3.1 CO₂ Sensing

Stomatal movement and their development are regulated by CO₂ levels, which directly affect gaseous exchange and stomatal conductance in plants. Low concentration of CO₂ stimulates the opening of stomatal apertures, whereas CO₂ concentration above threshold level promotes the closure of stomatal apertures in plants. The elevated atmospheric CO₂ level enhances the concentration of leaf internal CO₂ (C_i), which represses the stomatal development in plants (Engineer et al. 2016; Santrucek et al. 2014). The guard cells and mesophyll tissues can sense CO₂ level in plants. In most of the plant species, changes in the leaf CO₂ level regulate the aperture of stomatal pores; however, similar phenomena were not observed under increased CO₂ level in a few plant species (Ferris and Taylor 1994). The cellular C_i level depends upon light condition, and a significant increase in leaves C_i level was observed in the night due to respiration, whereas this C_i level rapidly drops in daylight condition (Hanstein et al. 2001). The negative effect of increased CO₂ level is the reduction in total numbers of stomata per unit leaf area and rate of stomatal conductance in plants. The long-term effect of CO₂ is the reduced development of stomata in the leaf epidermis. Decrease in the stomatal conductance protects water loss from leaves (Keenan et al. 2013). Under drought condition, increased CO₂ levels promote heat stress in the leaf due to less evapotranspiration caused by either more closed stomata or less number of stomata present in the leaf (Long and Ort 2010). It has been reported that the higher stomatal conductance can be correlated with better crop performance (Bahar et al. 2009), and therefore reduced stomatal

conductance by elevated CO₂ may be responsible for poor agronomical performance of the crop.

Plant hormone abscisic acid (ABA) is known to regulate stomatal movement and development, and ABA promotes the CO₂ responses in stomata. ABA-insensitive mutants such as *abi1-1* and *abi2-1* showed conditional insensitivity to CO₂ level (Leymarie et al. 1998), whereas partial stomatal response was observed in the case of ABA receptors PYR/RCAR mutants (Merilo et al. 2013). There are three types of plant carbonic anhydrases, alpha, beta and gamma, and among them beta carbonic anhydrases play an important role in CO₂-regulated stomatal movements (Hu et al. 2010). However, the functions of alpha and gamma classes of carbonic anhydrases are needed to be characterized for their CO₂-mediated stomatal regulation in plants. The genetic complementation experiment of carbonic anhydrase double mutants with mammalian carbonic anhydrase restored the wild-type response in *Arabidopsis* (Hu et al. 2010), suggesting the importance of carbonic anhydrase catalytic activity in CO₂ sensing mechanism. Recently, RHC1, a MATE transporter-like protein, has been identified as a bicarbonate sensor (Tian et al. 2015), which may play an important role in CO₂ sensing and signaling. Photosynthesis reduces the C_i level and indirectly controls the CO₂-mediated regulation of stomatal pore in leaves. Though the direct sensing of CO₂ is not known as there are no mutants showing insensitivity to CO₂ level, studies have shown that guard cells (Young et al. 2006) and mesophyll cells (Mott et al. 2008) are involved in direct CO₂ sensing. It is known that C_i affects stomatal conductance than external CO₂ present on the leaf surface. A limited response of CO₂ was observed in the stomata isolated from epidermal tissues whereas increased CO₂ response for mesophyll stomata, suggesting the role of mesophyll tissue CO₂ sensing and signaling (Mott et al. 2008). Further, stomatal response to CO₂ was reversible when mesophyll tissues and leaf epidermis tissues were used together in the experiment (Mott et al. 2008). It was proposed that these responses may involve diffusible small substances like ABA, sugar, or malate (Lawson et al. 2014). Synergistic role of ABA in the CO₂ response is well documented. It has been shown that elevated CO₂ levels inhibit the stomatal development in *Arabidopsis* and this reduced stomatal development was observed in different plant species, suggesting the regulatory role of CO₂ in stomata development. The *hic* mutant, encoding for a putative 3-keto acyl coenzyme A synthase, defective in cell wall wax biosynthesis showed the production of higher number of stomata at elevated CO₂ level (Gray et al. 2000). Further, mutants defective in cell wall wax deposition also showed a defect in stomatal development (Jenks et al. 1995). The signals responsible for stomatal density changes are not known, and it was hypothesized that cuticular waxes may affect the movement of diffusible signals. Carbonic anhydrase mutants also showed increased stomatal development at increased CO₂ levels (Engineer et al. 2014). The *epf2* mutant, encoding for epidermal patterning factor gene EPF2, also showed opposite development of stomata at elevated CO₂ levels (Engineer et al. 2014). EPF2 gene binds to ERECTA receptor kinase to regulate stomatal index, which in turn affects water use efficiency in plants (Masle et al. 2005). It has been shown that the CRSP protease can cleave the EPF2 pro-peptide to produce active EPF2. Mutants of EPF2, CRSP, and carbonic anhydrases (CA1

and CA4) showed similar stomatal development phenotype in response to increased CO₂ level (Engineer et al. 2014). The exact mechanism involving ERECTA, EPF2, CRSP and carbonic anhydrases in stomatal development at elevated CO₂ level is hitherto undiscovered.

3.3.2 Oxygen Sensing

Cellular energy status is regulated through the ATP pool generated by oxidative phosphorylation reaction and molecular di-oxygen (O₂) is required for efficient ATP production in all aerobic organisms. Oxygen acts as an electron acceptor in the electron transport chain reaction that operates inside the mitochondria. When cellular oxygen level drops below the threshold level, the cell senses the altered oxygen level and modulates the expression of genes associated with metabolic and energy consumption processes, which ultimately regulate the growth and development of plants. Plant cells encounter oxygen-limited condition during seed germination and fruit development which could be due to the high rate of metabolic processes and/or slow diffusion of oxygen into highly active meristematic cells (van Dongen and Licausi 2015; Bailey-Serres et al. 2012). Depleted oxygen level inside the cell could be directly sensed by receptor/sensor proteins interacting with the oxygen molecule, which are not yet established in plants. An indirect sensing mechanism may be activated by either fluctuations in energy levels or redox homeostasis involving the formation of nitric oxide (NO), hydrogen peroxide (H₂O₂), and other ROS species in cells (van Dongen and Licausi 2015).

Cells present in the different organs of plants respond differently to the depleted oxygen level. For example, low oxygen level induces high expression of ADH1 in the roots as compared to shoots in *Arabidopsis* (Ismond et al. 2003). It has been observed that roots show tolerance to low oxygen levels by regulating the ethanol fermentation process, whereas such a phenomenon for tolerance has not been detected in the aerial parts of *Arabidopsis* (Ellis et al. 1999). These findings clearly suggest that different oxygen sensing mechanisms are operated in the root and shoot, which required further investigations to delineate the exact mechanism. Another survival strategy for oxygen-depleted condition is the long-distance signaling involving oxygen transport from the areal organ to root (Drew 1997). Oxygen deprivation condition is often encountered during flooding conditions, which create oxygen deprivation condition by reducing the diffusion of oxygen. Submergence of plant creates hypoxia conditions, which promote the transportation of ACC from the root to shoot for the production of ethylene in the presence of oxygen (Shiu et al. 1998). During complete submergence, oxygen deficiency depends on (1) photosynthesis-dependent oxygen replenishment, (2) inward movement of water, and (3) higher metabolic activity for oxygen consumption. Effect of submergence/waterlogging-induced hypoxia is less effective in case of plants like rice, due to the presence of aerenchyma that helps in the gaseous transportation from the submerged region to the aerial region. Lack of aerenchyma in many plants rapidly induces cellular oxygen deficit status during submergence (Voeselek et al. 2006). Mitochondrial

respiration is affected by the reduced level of cellular oxygen, which in turn affects the energy-dependent processes by inhibiting the production of cellular ATP pool (Howell et al. 2007). Cell enhances the oxidative phosphorylation reaction via carbohydrate metabolism to meet the consistently increasing demands for ATP to maintain the proper functioning of associated cellular processes (Banti et al. 2013). In mammals, the transcription factor hypoxia-inducible factor (HIF) 1a/b is directly regulated during oxygen sensing (Kaelin and Ratcliffe 2008). Prolyl hydroxylase-mediated hydroxylation of HIF1a controls its nuclear localization and transcriptional activation function during low oxygen condition (Kaelin and Ratcliffe 2008). Despite the presence of prolyl hydroxylases in plants, such evidence for direct oxygen sensing is lacking due to the absence of HIF1a homologs (Mustroph et al. 2010). Sucrose non-fermenting 1 (SNF1)/AMP-activated protein kinases have been implemented to sense the energy status in animals (Carling et al. 2011). In plants, such kinases, viz., KIN10 and KIN11, have been implemented to cellular energy level in low oxygen condition (Baena-Gonzalez et al. 2007). Sucrose signaling is discussed in detail in Chap. 13.

Another important class of sensing proteins includes the APETALA2 (AP2) domain-containing group VII ERF TFs, which have been shown to regulate low-oxygen responses in plants (van Dongen and Licausi 2015). SUB1A, the group VII ERFs, has been shown to fine-tune gene expressions in hypoxia condition generated during submergence. Further, hypoxia-responsive genes (HER1 and HER2) and knockout mutants (*hre1hre2*) have been characterized for their roles in the seedling survival during oxygen-lacking condition in *Arabidopsis* (Hess et al. 2011). Biochemical, molecular, and genetic characterization of group VII ERF TFs and other related important genes would provide more information about direct and indirect sensing in plants.

3.4 Conclusion

In conclusion, this chapter summarizes the recent findings primarily associated with sensing mechanism and physiological consequences in the regulation of nutrients (NPK), CO₂, and O₂. Studies of the past two decades have provided new insights into signaling mechanisms and adaptive responses, which led to the identification of unique and overlapping signaling responses and associated marker genes in plants (Fig. 3.1). The basic understanding of nitrate sensing pathways has been established, but other nutrient sensors are still not clear. The use of genome-wide association study (GWAS) and other functional genomics techniques will help to characterize these unknown sensors and their NutUE. The ROS, Ca²⁺, metabolic products, and phytohormones constitute the common components in all the studied signaling pathways. Understanding and integration of these overlapping and unique signaling components will help in better understanding of plant responses to changing nutrient levels in the underground environment and oxygen and carbon dioxide in the atmosphere and how plants coordinate and integrate all the information for sustaining energy requirement for their survival.

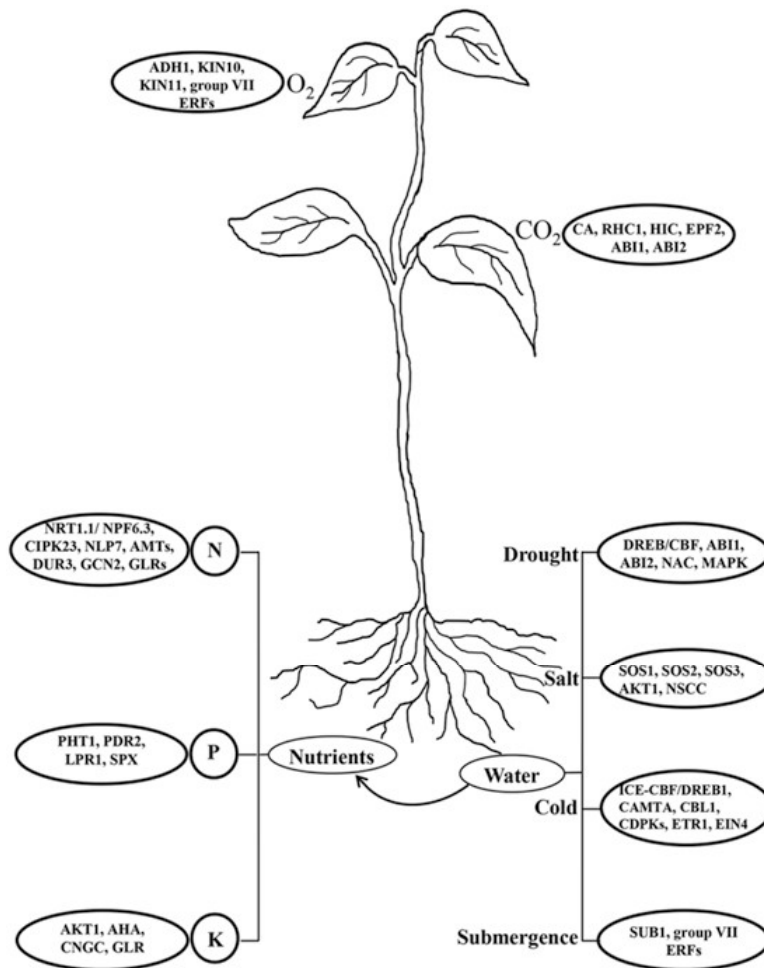


Fig. 3.1 Schematic representation of potential sensing/signaling genes associated with various responses in plants. Environmental factors affecting the corresponding key gene expressions are shown. *ADH1* alcohol dehydrogenase 1, *KIN10* SNF1 kinase homolog 10, *KIN11* SNF1 kinase homolog 11, *group VII ERFs* group VII ethylene response factors, *CA* carbonic anhydrase, *RHC1* resistant to high CO₂ 1, *HIC* high carbon dioxide, *EPF2* epidermal patterning factor gene 2, *ABI1* abscisic acid-insensitive 1, *ABI2* abscisic acid-insensitive 2, *NRT1.1* nitrate transporter 1.1, *CIPK23* CBL-interacting serine/threonine protein kinase 23, *NLP7* NIN-like protein 7, *AMTs* ammonium transporters, *DUR3* degradation of urea 3, *GCN2* general control non-repressible 2, *GLRs* glutamate receptor channels, *PHT1* phosphate transporter 1, *PDR2* phosphate deficiency response 2, *LPR1* low-phosphate root 1, *SPX* SPX domain proteins, *AKT1* *Arabidopsis* K⁺ transporter 1, *AHA* *Arabidopsis* H⁺-ATPase, *CNGC* cyclic nucleotide gated channel, *DREB/CBF* dehydration-responsive element-binding protein/C-repeat binding factor, *NAC* NAM/ATAF/CUC transcription factors, *SOS1* salt overly sensitive 1, *SOS2* salt overly sensitive 2, *SOS3* salt overly sensitive 3, *NSCC* non-selective cation channel, *ICE-CBF/DREB1* inducer of *cbf* expression (ICE)-C-repeat binding factor/DRE binding factor1, *CAMTA* calmodulin-binding transcription activators (CAMTA) factors, *CBL1* calcineurin B-like protein 1, *CDPKs* calcium-dependent protein kinases, *ETR1* ethylene response 1, *EIN4* ethylene-insensitive 4, *SUB1* submergence-tolerant 1

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