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Review Article

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CALCIUM IN PLANT BIOLOGY: NUTRIENT AND SECOND MESSENGER

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Abstract: Calcium (Ca^{2+}) is an essential element required for growth and development of plants both under stressed and non-stressed situations. It not only maintains the integrity of cell wall and membrane, but also serves as a second messenger in many developmental and physiological processes thereby inducing Ca^{2+} influx into cytosol, which decodes into downstream responses like defense against various environmental cues. Therefore, maintenance of intracellular Ca^{2+} homeostasis is essential for Ca^{2+} signalling. In this review, the current knowledge about the Ca^{2+} uptake, transport and signal transduction in different physiological aspects with respect to plant nutrient status will be discussed.

Keywords: Calcium, Kinases, Nutrient signalling, Plant immunity, Second messenger.

INTRODUCTION

Calcium (Ca^{2+}) is necessary for growth and development of plants, which ranges between 0.1 to 5% of dry weight of the shoot (White and Broadley, 2003). It have dual job, first as a structural component of cell wall and membranes and second as second messenger. Therefore to meet the tasks, uptake, supply and storage of Ca^{2+} needs to be tightly regulated. Ca^{2+} availability in sufficient amounts is necessary to fulfil the structural role in plants. Deficiency of Ca^{2+} mainly appears in young developing tissues like leaves and fruits due to decrease in Ca^{2+} remobilization from old to young tissues through phloem, which increases the dependency on supply via the xylem and thus on transpiration. Moreover, the main role of Ca^{2+} is its ability to act as a second messenger from root or pollen tube growth and fertilization to biotic and abiotic stresses (Ortiz-Ramírez *et al.*, 2017; Zhang *et al.*, 2017) in the form of constant, temporary and oscillatory rises in cytosolic $_{(C)}Ca^{2+}$, which serves as a signal and decoded into downstream responses (Thor and Peiter, 2014). In order to act as signal $_{(C)}Ca^{2+}$ level must below about 0.1 μM, which can be achieved by Ca^{2+}-ATPases, H^{+}/Ca^{2+}antiporters and biochemical buffers that transports $_{(C)}Ca^{2+}$ into the intracellular stores or apoplast (Kudla *et al.*, 2018). Thus, to generate the

Ca^{2+}signal, ion move down the concentration gradient into cytosol via protein channels of internal or plasma membrane. In this review, the summarized current knowledge about the role of Ca^{2+} in plants with especial reference to Ca^{2+} signalling will be discussed.

CALCIUM AS STRUCTURAL COMPONENT

Calcium is known to provide rigidity to the cell wall as it is cross-linking negatively charged carboxyl groups of pectin (de-esterified) in middle lamella. Ca^{2+} also stabilizes cell membranes by interacting with phospholipids (Hepler, 2005). Therefore, low Ca^{2+} level weakens cell wall, which is an example in case of root hair or pollen tubes, necessary for tip growth expansion (Bascom *et al*., 2018). In a recent finding, FERONIA (FER) receptor-like kinase associated with root hair development, make softer to cell wall by disturbing the ionic interactions by Na^{+} under salt stress (Duan *et al*., 2010), which was found defected in restoring root growth in fer mutants under similar conditions. These defects were further released by Ca^{2+} and borate application. Feng *et al*., (2018) have reported that FER co-operates with pectin, hence sense the wall damage and triggers Ca^{2+} signal to restore the cell wall integrity.

The exogenous treatment of Ca^{2+} has been found advantageous against biotic and abiotic stresses. Yamazaki *et al*., (2000) have reported that external Ca^{2+} application protected plant against the infection of *Ralstonia solanacearum* and soybean plants from *Phytophthora* (Sugimoto *et al*., 2010). The studies suggests that low Ca^{2+} level causes lower membrane stability and hence increases efflux of sugars like compounds into the apoplast which is responsible for high fungal infection rate (Marschner, 1995). Raz and Fluhr (1992), have reported that excessive Ca^{2+} triggers defense gene expression, which could be due to Ca^{2+} role as second messenger. Moreover, Marschner (1995) have suggested that bacteria and fungi induced cell wall formation enzymes were degraded by Ca^{2+} supplementation, which is the major barrier for invading pathogens after cuticle. These cell wall degrading enzymes triggers Ca^{2+} mediated signalling pathways.

CALCIUM UPTAKE AND DISTRIBUTION IN PLANTS

Calcium uptake from the soil occurs through plasma membrane channels of roots (White *et al*., 2002). On the basis of their electrophysiological properties, Ca^{2+}-permeable channels of root were first classified as hyperpolarization-activated channels (HACCs) and depolarization-activated channels (DACCs) (Miedema *et al*., 2008). Moreover, voltage-independent channels (VICs) have also been defined. On the basis of tissue expression, members of glutamate receptor homologs (GLRs) and cyclic nucleotide-gated (CNGC) family of proteins encode VIC-induced currents while annexins account for HACCs (White *et al*., 2002), although these channels are known for signalling than nutrition. Being an essential nutrient, Ca^{2+} should be easily taken and transported within plant but its role as second messenger affects its path from root to shoot through xylem. Theoretically both apoplastic and symplastic path could be accessible for this transportation; however a submicromolar range of $_{(C)}Ca^{2+}$conc must be maintained to trigger/generate Ca^{2+} signals, as discussed earlier, thus symplastic transport would obstruct the Ca^{2+} signalling. White (2001) suggested apoplastic movement of Ca^{2+} from epidermis to casparian strip (a barrier around endodermal cells) via cortex, which is mainly made up of lignin and suberin and stops water and solutes movement in order to prevent the uptake of toxicants (Schreiber *et al*., 1999). Therefore, in order to reach upto casparian layer, Ca^{2+}will have to enter the cytosol of endodermal cells through channel proteins and be exported into stelar apoplast through Ca^{2+}/H^{+} antiporters or Ca^{2+}- ATPases finally to be into xylem. Besides this pathway (involves both symplast and apoplast), a purely apoplastic pathway have also been suggested by White (2001), where casparian strip are either interrupted or not fully developed like the sites of lateral root emergence or root apex. Once after loading into the xylem, Ca^{2+} is transported to the shoot where it distributed within the leaf cells, as CNGC2 (CYCLIC NUCLEOTIDE-GATED CHANNEL 2) Ca^{2+} channel have been identified in *Arabidopsis* responsible for Ca^{2+} influx into leaf cells (Wang *et al*., 2017).

Calcium as second messenger in signalling networks

Earlier work were focused on the Ca^{2+} role as nutrient and structural component, but from the recent studies it have been clear that the main function of Ca^{2+} is ability to serve as a secondary messenger in a variety of developmental, physiological and defense-related processes. Ca^{2+}signals is a complex process which mainly triggered by the interplay between influx pumps, exporters and channels. As Ca^{2+} signals participates in variety of processes, therefore Dodd *et al*., (2010) suggested that the spatiotemporal pattern of Ca^{2+} rises to determine the corresponding response against different cues called as Ca^{2+}signature, which is determined by different sets of proteins like calcineurin B-like proteins (CBLs), CBL interacting protein kinases (CIPKs), calmodulin (CaM), CaM-like proteins (CMLs) and Ca^{2+}-dependent kinases (CDPKs). The CBLs, CaM, CMLs and CDPKs contain EF-hand Ca^{2+}-binding motifs and CIPKs are activated by interaction with CBLs (Kudla *et al*., 2018). Activation of downstream targets like channels, transporters and transcription factors further transmits the signal to give outputs like gene expression and stomatal closure.

Calcium as nutrient signal in plants

Calcium function as second messenger in nutrient signalling is sometimes found in relation with ammonium, boron, iron, potassium, nitrate and magnesium (Tang and Luan, 2017; Kudla *et al*., 2018). The K^+ deficiency in *Arabidopsis* roots triggers Ca^{2+}signals. In *Arabidopsis*, Ca^{2+} decoding complex comprising of CIPK23 and CBL1/9 regulate transport proteins responsible for the uptake of K^+, HAK5 (high-affinity K^+ transporter 5), and AKT1 (*Arabidopsis* K^+ transporter 1) (Behera *et al*., 2017). CIPK23, which transports iron, also regulates the activity of transceptor IRT1 (iron-regulated transporter 1) along with cadmium, cobalt, manganese, and zinc. According to Dubeaux *et al*., (2018), upon binding of non-iron metals CIPK23 (suggests involvement of Ca^{2+} signalling) phosphorylate IRT1, which consequently leads to its degradation and therefore inhibits unfavorable conc. of other metals in the cytosol. Ho *et al*. (2009) have reported another nutrient transporter NRT1.1 (nitrate transporter 1.1, also CHL1), which is phosphorylated (and regulated by CIPK23) under low-nitrate environments and changes the protein from a low- into a high-affinity transporter and downregulates primary nitrate responses. Later, nitrate-induced, NRT1.1- and phospholipase c-dependent Ca^{2+} signal were reported by Riveras *et al*., (2015).

Calcium as signalling molecule in plant immunity

The immunity signalling starts with ligand recognition by its receptor, which triggers a cascade of reactions like Ca^{2+} influx into cytosol, reactive oxygen species (ROS) production, MAPK signalling, defense gene expression and late responses like stomatal closure and callose deposition. One of the earliest responses of the induced cascades is Ca^{2+}influx into cytosol, which is carried out by two main family channels: CNGCs and GLRs. According to their phenotype, the At CNGC2 locus mutant were named "defense, no death" (dnd1), which showed no HR however still resistant to *Pseudomonas syringae* and a range of virulent pathogens (Yu *et al*., 1998). The autoimmune phenotype of *dnd1* mutants, which is dependent on Ca^{2+} supply in the medium, is dwarf and showed increased level of defense gene expression such as PR1 and salicylic acid (SA) (Clough *et al*., 2000; Wang *et al*., 2017). Chen *et al*., (2003) reported that dwarf character of mutant was dependent on high Ca^{2+} supply like HR suppression; therefore, he suggested that CNGC2- mediated Ca^{2+} unloading into leaf cells is interrupted thereby leading into higher apoplastic Ca^{2+}, which strengthened the cell wall by inhibiting HR. Therefore, hypersensitive response as a part of plant defense appears to be dependent on the nutritional status of plant, i.e. nutritional status of plant especially Ca^{2+} favors its immunity. Recently at aphid feeding sites, GLR3.3 and GLR3.6 along with TPC1 (two-pore channel1) was found to be involved in elevation of $_{(C)}Ca^{2+}$; this elevation in $_{(C)}Ca^{2+}$ was also found dependent on coreceptor BAK1 (Vincent *et al*., 2017).

CONCLUSION

Being an essential element, Ca^{2+} serves as an integral part of cell wall and membranes that upholds the physical barrier against pathogen (exogenous supply of Ca^{2+} improves plant's resistance). Nevertheless, in recent years, Ca^{2+} is emerged as second messenger in different signalling events. Although, a lot of work regarding Ca^{2+} signalling have been done still little is known about Ca^{2+}uptake and distribution mediating proteins, signal transduction and decoding, and how Ca^{2+} contribution in one plant aspect is affecting another and whether the same or different genes are involved in two processes? Therefore, future researches will shed more light on different functions of Ca^{2+} and its interconnection with the others.

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