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Regulation of calcium and magnesium homeostasis in plants: from transporters to signaling network

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Calcium (Ca^{2+}) and magnesium (Mg^{2+}) are the most abundant divalent cations in plants. As a nutrient and a signaling ion, Ca^{2+} levels in the cell are tightly controlled by an array of channels and carriers that provide mechanistic basis for Ca^{2+} homeostasis and the generation of Ca^{2+} signals. Although a family of CorA-type Mg^{2+} transporters plays a key role in controlling Mg^{2+} homeostasis in plants, more components are yet to be identified. Ca^{2+} and Mg^{2+} appear to have antagonistic interactions in plant cells, and therefore plants depend on a homeostatic balance between Ca^{2+} and Mg^{2+} for optimal growth and development. Maintenance of such a balance in response to changing nutrient status in the soil emerges as a critical feature of plant mineral nutrition. Studies have uncovered signaling mechanisms that perceive nutrient status as a signal and regulate transport activities as adaptive responses. This 'nutrient sensing' network is exemplified by the Ca^{2+}-dependent CBL (calcineurin B-like)-CIPK (CBL-interacting protein kinase) pathway that serves as a major link between environmental nutrient status and transport activities. In this review, we analyze the recent literature on Ca^{2+} and Mg^{2+} transport systems and their regulation and provide our perspectives on future research.

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Introduction

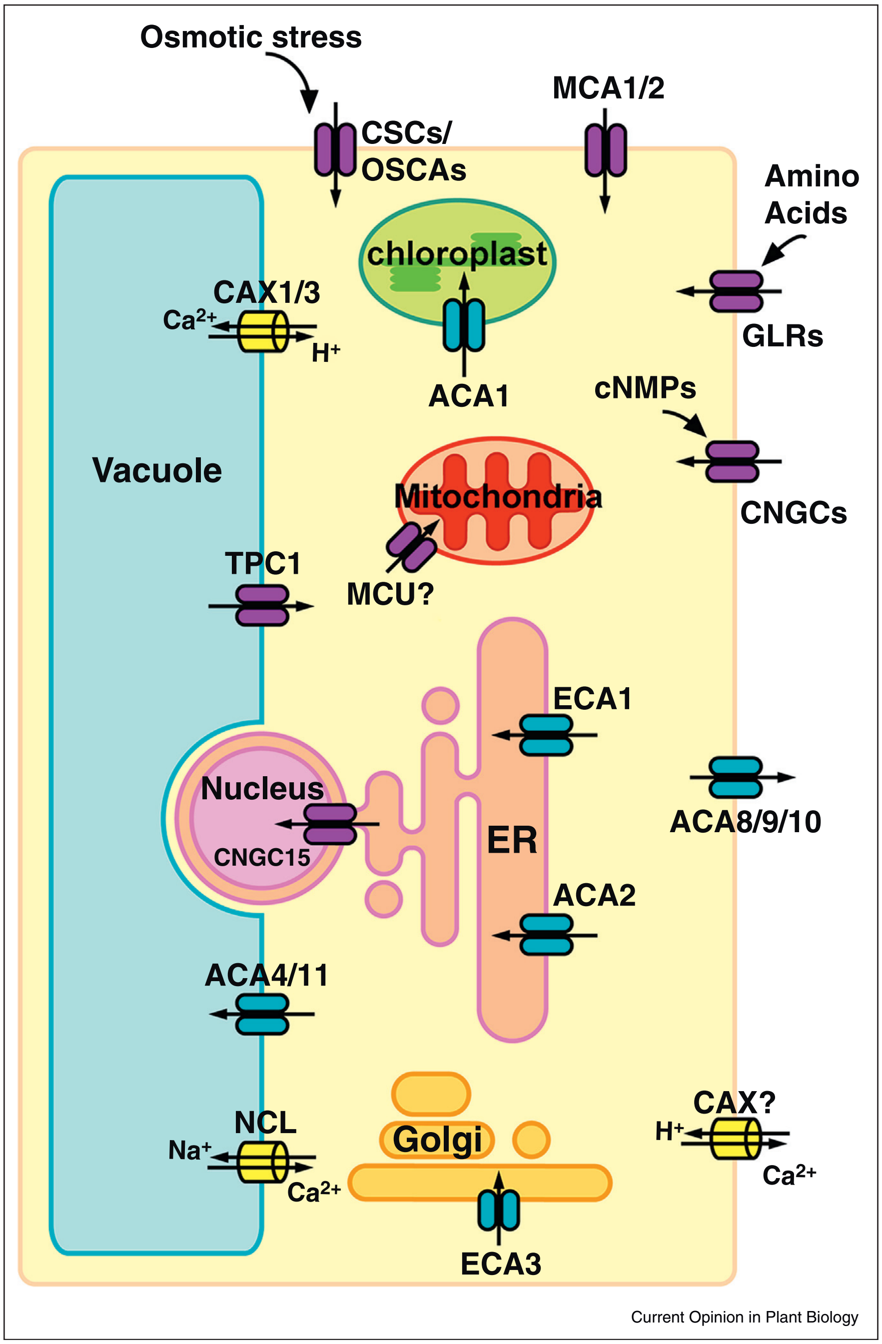
Calcium (Ca) and magnesium (Mg) are abundant metal elements in the earth crust and the ionic forms (Ca^{2+} and Mg^{2+}) in the soil serve as essential plant nutrients. Plants utilize Ca^{2+} to strengthen cell walls, neutralize vacuolar anions, and provide stress protection. In contrast to a high content of total calcium in plant tissues, the basal levels of cytosolic free Ca^{2+} remain extremely low, usually about 100–200 nM [1]. The potent capacities for a rapid increase of cytosolic Ca^{2+} concentration via Ca^{2+} channels have enabled Ca^{2+} to function as a versatile messenger in almost all physiological processes in plants, as well as in other eukaryotes [2]. On the other hand, cellular Mg^{2+} is highly abundant and acts as a cofactor for a wide range of enzymes and serves as the core metal of chlorophyll molecules in green tissues [3]. Both Ca^{2+} and Mg^{2+} are acquired from the soil by plant roots and translocated upward to shoots through xylem. Once deposited, Ca^{2+} is rather immobile whereas Mg^{2+} is more mobile though phloem for recycling in plants. Several families of ion channels and transporters have been identified that contribute to Ca^{2+} and Mg^{2+} transport across plasma membrane and intracellular membranes. Coordination of the activities of these transport systems, at the cell and whole plant levels, governs Ca^{2+} and Mg^{2+} nutrition, and ensures proper control of Ca^{2+} as a second messenger in response to various developmental and environmental cues. Despite their distinct physiological and biochemical roles, homeostasis of Ca^{2+} and Mg^{2+} *in planta* appears to be tightly linked and is likely to be regulated, at least in part, by common signaling networks. In this mini-review, we summarize the recent advances in the mechanisms underlying Ca^{2+} and Mg^{2+} transport and homeostasis in plants.

The ins and outs of Ca^{2+} transport: shaping up the Ca^{2+} signature in plant cells

Calcium is indispensable to plant growth and accounts for 0.1–5% of shoot dry weight. Although calcium is abundant in nature, calcium deficiency can occur in the rapidly growing tissues where high levels of Ca are demanded, causing symptoms such as cell necrosis in young leaves and blossom-end rot in fruits [4]. Calcium deficiency symptoms are usually observed in the young tissues partly because calcium is an immobile nutrient that can hardly be remobilized from old tissues and redistributed via the phloem. In addition to being an essential component of cell wall and other cellular structures, Ca^{2+} plays an arguably more important role as a ubiquitous signaling agent in plant cells [5]. A transient rise in cytosolic free Ca^{2+} concentration can function as an intracellular signal that encodes stimulus-specific information. Formation of stimulus-specific patterns of Ca^{2+} change, namely 'Ca^{2+} signatures' [6], relies on the coordinated actions of distinct Ca^{2+} transporters that mediate Ca^{2+} influx and efflux across cellular membranes (Figure 1).

Influx of Ca^{2+} into the cytoplasm from the apoplast is believed to be mediated by calcium-permeable ion

Figure 1



Ca^{2+} transport systems in a plant cell. See text for detailed information. CNGC, cyclic nucleotide-gated channel; GLR, glutamate receptor; CSC, calcium permeable stress-gated cation channel; OSCA, reduced hyperosmolarity-induced $[Ca^{2+}]_i$ increase channel; MCA, *mid1*-complementing activity; TPC1, two pore channel 1; ACA, autoinhibited Ca^{2+}-ATPase; ECA, ER-type calcium ATPase; CAX, Ca^{2+}/H^+ exchanger; NCL, Na^+/Ca^{2+} exchanger; MCU, mitochondrial calcium uniporter. Plasma membrane Ca^{2+}/H^+ exchange activities are present in plant cells but the coding genes remains to be identified. MCU has been characterized in animal cells and several homologues are present in *Arabidopsis* with predicted mitochondrial localization but unknown functions.