Short title Organellar Ca^{2+} signaling

Corresponding author Alex Costa, alex.costa@unimi.it
Department of Biosciences
University of Milano
Via Celoria 26, I-20133, Milan, Italy
Tel. +39 2503 14831

The signatures of organellar calcium

Francesca Resentini[1], Cristina Ruberti[1], Matteo Grenzi[1], Maria Cristina Bonza[1], Alex Costa[1,2]

[1]Department of Biosciences, University of Milan, via Celoria 26, 20133 Milano, Italy

[2]Institute of Biophysics, National Research Council of Italy (CNR), via Celoria 26, 20133 Milano, Italy

One-sentence summary

The transport of Ca^{2+} across the membranes of subcellular compartments contributes to cytosolic Ca^{2+} homeostasis as well as environmental and developmental responses.

FOOTNOTES

Author Contributions

AC conceived the project and wrote the main body of the article. FR wrote the part on developmental processes. MG prepared Fig 1. and 3. MCB prepared Box. 2. All authors made comments on the manuscript, which were integrated by AC. All authors contributed to the article and approved the submitted version.

Funding Information

This work was supported by Piano di Sviluppo di Ateneo 2019 (University of Milan) (to AC), by Ministero dell’Istruzione, dell’Università e della Ricerca Fondo per Progetti di ricerca di Rilevante Interesse Nazionale 2017 (PRIN 2017ZBBYNC) (to MCB).

Email address of Author for Contact

alex.costa@unimi.it

E-mails of the other authors

FR francesca.resentini@unimi.it, CR cristina.ruberti@unimi.it, MG matteo.grenzi@unimi.it; MCB cristina.bonza@unimi.it.

ORCID identifiers:

Francesca Resentini 0000-0003-0033-6930; Cristina Ruberti 0000-0002-9013-1412; Matteo Grenzi 0000-0003-2295-0018; Maria Cristina Bonza 0000-0001-7096-2967; Alex Costa 0000-0002-2628-1176.

INTRODUCTION

Plants are continuously subjected to environmental changes such as fluctuating light, the day/night cycle, oscillating temperatures, water availability and interaction with other organisms. Often these variations can be adverse, being stressful and thus affecting plant growth, development and, in several cases, causing major yield losses in agriculture. Especially, plants cannot move to a more comfortable environment to survive and they, thus, need to continuously monitor, and possibly anticipate, any upcoming stress (Zhu, 2016).

Plants' early responses to stress often occur in a time frame of seconds or a few minutes in different cell compartments, and in these cases, they mainly rely on quick changes of ions' concentrations (e.g. Ca^{2+}, H^{+}, K^{+}, NO^{3-}, Cl^{-}, etc) which are dependent upon their movements across membranes (Stephan et al., 2016; Behera et al., 2018; Costa et al., 2018; Marti Ruiz et al., 2020; Demes et al., 2020). Among the ions, it is well-accepted that calcium (Ca^{2+}) plays a key role in many signal transduction pathways (Trewavas and Malhó, 1998; Sanders et al., 2002; Dodd et al., 2010; Kudla et al., 2010, 2018; Tian et al., 2020). At rest, in plant cells, the cytosolic free Ca^{2+} concentration ($[Ca^{2+}]_{cyt}$) is in the range of 100-200 nM (Trewavas, 1999; Logan and Knight, 2003; Stael et al., 2012; Jezek and Blatt, 2017), but it can rise up steeply (often to low µM concentrations) in response to the perception of different stimuli (Knight et al., 1997; Ranf et al., 2008). Importantly, the stimulus-induced increase in $[Ca^{2+}]_{cyt}$ is not a "digital signal", but an "analog" one that, depending on the stimulus type and magnitude, assumes a peculiar dynamic often dubbed "cytosolic Ca^{2+} signature" (Sanders et al., 2002; Kudla et al., 2010, 2018; Tian et al., 2020). The model predicts that different signatures activate different Ca^{2+} sensors (e.g. Calmodulin (CaM), Calmodulin-like proteins (CMLs), calcineurin β-like proteins (CBLs)), and Ca^{2+} relays (e.g. Ca^{2+}-dependent protein kinases (CDPKs), or calmodulin-dependent protein kinase (CCaMK)) that trigger precise and tailored responses, altering gene expression and metabolism (**Fig. 1**) (reviewed in Sanders et al., 2002; McCormack et al., 2005; DeFalco et al., 2009; Hamel et al., 2014; Edel et al., 2017; Kudla et al., 2018; Lenzoni et al., 2018; Poovaiah and Du, 2018; Liu et al., 2020; Tang et al., 2020). The understanding of how the Ca^{2+} signature is generated and shaped to assume its "analog nature" is a key aspect to dissect the roots of Ca^{2+} signaling, which is traceable to its movement across membranes. Thus, important questions are: i) how do plant cells generate specific Ca^{2+} signatures? ii) which are the mechanisms for their tight regulation? A simple answer is that generation and shaping of cytosolic Ca^{2+} signatures is dependent on a coordinate and intertwined activity of Ca^{2+} permeable channels, Ca^{2+} transporters, and Ca^{2+} buffers (Sanders et al., 2002; McAinsh and Pittman, 2009; Michard et al., 2011; Costa et al., 2017; Wudick et al., 2018; Behera et al., 2018; Hilleary et al., 2020; Tian et al., 2020). Whereas it is reported that the major source of cytosolic Ca^{2+} is the apoplast and that the movement of Ca^{2+} across the plasma membrane (PM) plays a major role in the generation of cytosolic Ca^{2+} transients (Gao et al., 2004; Stael et al., 2012; Costa et al., 2018; Tian et al., 2019; Lopez-Hernandez, 2020; Tian et al., 2020), increasing evidence demonstrates that subcellular compartments are involved in the shaping of the signatures, working as Ca^{2+} sinks (Qudeimat et al., 2008; Costa et al., 2010; Loro et al., 2012; Nomura et al., 2012; Bonza et al., 2013; Nomura and Shiina, 2014; Wagner et al., 2015; Loro et al., 2016; Lenglet et al., 2017; Behera et al., 2018; Corso et al., 2018, Teardo et al., 2019; Hilleary et al., 2020), as well as Ca^{2+} sources (Wang et al., 2010; Zhu et al., 2010; Tian et al., 2014, Shkolnik et al., 2018). Interestingly, some compartments (i.e. chloroplast and nucleus) can also generate their own organellar Ca^{2+} signature (Xiong et al., 2004; Loro et al., 2016; Sello et al., 2016; 2018; Kelner et al., 2018; Leitão et al., 2019) adding a supplementary level of complexity to Ca^{2+} signaling (**Fig. 1**).

In this update, we will provide readers with evidence that subcellular compartments experience their own Ca^{2+} transients in response to different stimuli, with particular attention to describing those cases where their role in the shaping of cytosolic Ca^{2+} dynamics and in the regulation of downstream responses was experimentally observed. We will give examples to demonstrate that cytosolic and organellar Ca^{2+} are directly intertwined, as well as that dysfunctions in the transport of other ions can lead to altered cytosolic Ca^{2+} signatures and visible phenotypes. For simplicity, we will divide our update into four different fields of cellular signaling: i) plant responses to abiotic stimuli, ii) plant responses to biotic stimuli, iii) stomatal movements, and iv) plant developmental processes. We will not discuss the chloroplast Ca^{2+} signatures observed in responses to light-dark transitions and in response to heat stress (Sai and Johnson, 2002; Loro et al., 2016; Sello et al., 2016; Frank et al., 2019; Lenzoni and Knight, 2019; Martí Ruiz et al., 2020), since those two mechanisms are extensively covered in the update by He et al. (2021) of this Focus Issue.

CONTRIBUTION OF ORGANELLES IN THE SHAPING OF CYTOSOLIC CALCIUM INCREASES IN RESPONSE TO SALT AND OSMOTIC STRESSES

Plants are particularly sensitive to abiotic stress, and their perception elicits i) characteristic $[Ca^{2+}]_{cyt}$ increase, ii) activation of protein kinases and phosphatases, iii) modulation of gene expression and iv) hormone biosynthesis (Gong et al., 1998; van Der Luit et al., 1999; Knight and Knight, 2001; Tracy et al., 2008; Krebs et al., 2012; Choi et al., 2014a; 2014b; Yuan et al., 2014; Wagner et al., 2019; Peleg and Blumwald 2011; Zhu, 2002; 2016). In this section, we will detail recent evidence showing the involvement of different subcellular compartments in the shaping of cytosolic Ca^{2+} signature in response to abiotic stress, focusing on salt and osmotic stress, and reporting, when available, the consequent downstream effects on the plant's physiology.

Salt and osmotic stresses are stimuli that induce in plants a quick $[Ca^{2+}]_{cyt}$ increase with dose-dependent as well as tissue-specific responses (Kiegle et al., 2000). The application of these stresses has been efficiently exploited to design genetic screenings that were instrumental in identifying salt- and osmo- sensors as well as key components involved in the signal transduction (Yuan et al., 2014; Jiang et al., 2019; Chen et al., 2020). Such genetic screenings were based on Arabidopsis (*Arabidopsis thaliana*) seedlings expressing the genetically encoded Ca^{2+} sensor aequorin targeted to the cytosol (**Box 1; Fig. 2**). Moreover, the exposure to salt and osmotic stress of Arabidopsis seedlings expressing genetically encoded Ca^{2+} sensors localised in different subcellular compartments (**Box 1; Fig. 2**) (reviewed in Stael et al., 2012; Costa et al., 2018), highlighted that besides the cytosol, also chloroplasts, non-green plastids, mitochondria, endoplasmic reticulum (ER), Golgi apparatus, and nuclei experience Ca^{2+} transients (Xiong et al., 2004; Loro et al., 2012; Ordenes et al., 2012; Bonza et al., 2013; Sello et al., 2016; Huang et al., 2017; Corso et al., 2018; Kelner et al., 2018; Teardo et al., 2019). In most of the reported cases, the analysed subcellular compartments showed Ca^{2+} transients that followed the $[Ca^{2+}]_{cyt}$ increase, therefore, behaving as sinks and not as sources of Ca^{2+} (reviewed in Stael et al., 2012: Costa et al., 2018). This result allows us to hypothesize a primary role for subcellular compartments in the shaping of the cytosolic Ca^{2+} signature rather than in its generation (McAinsh and Pittman, 2009).

Organellar calcium in salt stress responses

Plants expressing genetically Ca^{2+} sensors targeted to different subcellular compartments (i.e. aequorin, Cameleon, R-GECO1, and G-GECO1.2) (Knight et al., 1991; Miyawaki et al., 1997; Zhao et al., 2011) (**Box 1; Fig. 2**) were instrumental to show that salt stress induces a transient accumulation of Ca^{2+} in the cytosol, ER, chloroplasts/plastids and nucleus (Bonza et al., 2013; Sello et al., 2016; Huang et al., 2017; Corso et al., 2018; Kelner et al., 2018; Teardo et al., 2019). Some pieces of evidence support the role of ER, chloroplasts, and vacuoles in the dampening and/or shaping of the cytosolic Ca^{2+} increase.

The genetic ablation of the ER-localised Arabidopsis Ca^{2+}/cation transporter AtCCX2 (*ccx2*-knockout (KO) mutant) leads to a reduced salt-induced $[Ca^{2+}]_{cyt}$ increase, and less salt-resistant plants compared to wild type. Remarkably, *CCX2* overexpression (*CCX2*-OX) has the opposite effect, with an exacerbation of the $[Ca^{2+}]_{cyt}$ transient maximum and plants more resistant to salt stress compared to wild type (Corso et al., 2018). Thus, a link between the magnitude of the Ca^{2+} signature and plant resistance was proposed. These data highlight the involvement of AtCCX2 and, therefore, of the ER, in the regulation of cytosolic Ca^{2+} in response to salt stress (Corso et al., 2018). The study of AtCCX2 topology in the ER membrane, as well as Ca^{2+} transport analyses in isolated ER fractions from wild type and mutant plants, should allow us to better define the AtCCX2 mode of action and its physiological function.

The role of chloroplasts in the regulation of $[Ca^{2+}]_{cyt}$ increase in response to salt stress (e.g. NaCl) was also demonstrated. This evidence came from a genetic screen of Arabidopsis mutants defective in salt stress-induced $[Ca^{2+}]_{cyt}$ elevation that allowed the identification of the chloroplast-localised glycosyl-transferase QUASIMODO1 (AtQUA1), a protein involved in the stacking of thylakoids grana. Compared to the wild type, the *qua1-4* mutant exhibited a dramatically greater increase in $[Ca^{2+}]_{cyt}$ under NaCl treatment (Zheng et al., 2017), and this effect was linked to the activity of the chloroplast Ca^{2+} sensor Calcium Sensing Receptor (CAS) (Han et al., 2003; Nomura et al., 2008; 2012). There was no measurement of [Ca^{2+}] in the chloroplast stroma or thylakoid lumen of the *qua1-4* mutant, thus, we lack experimental evidence that the alteration of $[Ca^{2+}]_{cyt}$ is directly dependent on a deregulated chloroplast Ca^{2+} handling. Nevertheless, in independent studies, by using Arabidopsis plants expressing the Ca^{2+} sensor aequorin directed to the chloroplasts/plastids stroma (**Box 1, Fig. 2**), it has been shown that these compartments transiently accumulate Ca^{2+} in response to salt stress (Sello et al., 2016, Teardo et al., 2019). At the present time, knowledge about the molecular players (Ca^{2+}-permeable channels or transporters in the outer and/or inner membrane) involved in the chloroplast Ca^{2+} accumulation in response to salt stress is rather limited. The Arabidopsis Glutamate Receptor-Like Channel AtGLR3.4 is permeable to Ca^{2+} (Vincill et al., 2012) (**Box 2; Fig. 3**), and besides being localised in the plasma membrane (PM) (Meyerhoff et al., 2005, Vincill et al., 2012) it was also reported to be present in chloroplasts (Teardo et al., 2011). Two Arabidopsis independent AtGLR3.4 mutant alleles, *atglr3.4-1* and *atglr3.4-2,* showed an impaired NaCl-induced $[Ca^{2+}]_{cyt}$ increase and a more salt-sensitive phenotype during seed germination and post-germination growth compared to wild type plants (Cheng et al., 2018). However, the fact that data regarding the Ca^{2+} dynamics in the chloroplasts/plastids of these mutants are lacking, does not allow clear conclusions to be drawn. In addition, no other evidence has supported the chloroplast localization of GLR3.4, thus this result might require validation.

The role of intracellular compartments in the shaping of $[Ca^{2+}]_{cyt}$ transients in response to salt stress was also found in *Physcomitrium patens* (formerly *Physcomitrella patens*), where the mRNA coding for the tonoplast-localised PIIB-type Ca^{2+}-ATPase (**Box 2; Fig. 3**) PCA1 was shown to be upregulated by NaCl treatment. *PCA1* loss-of-function mutants (*ΔPCA1*) exhibit a sustained elevated $[Ca^{2+}]_{cyt}$ in response to salt, and an enhanced salt susceptibility and higher cell death rates upon treatment. Remarkably, the altered Ca^{2+} response in the *ΔPCA1* lines corresponded with the altered expression level of stress-induced genes, suggesting the disturbance of a stress-associated signaling pathway (Qudeimat et al., 2008). Although direct evidence of an impaired Ca^{2+} accumulation in the vacuole in the *ΔPCA1* was not reported, the well-defined role of PIIB-type Ca^{2+}-ATPases in the transport of Ca^{2+} out of the cytosol (**Box 2**) strongly supports a direct role of PCA1 in the restoration of prestimulus $[Ca^{2+}]_{cyt}$, with the vacuole working as a cytosolic Ca^{2+} capacitor/buffer (Qudeimat et al., 2008). In Arabidopsis, the two tonoplast-localised PIIB-type Ca^{2+}-ATPase isoforms AtACA4 and AtACA11 (**Box 2, Fig. 3**) have a role in the regulation of $[Ca^{2+}]_{cyt}$ in leaf epidermal cells in response to bacterial flagellin (flg22) (see next section) (Hilleary et al., 2020), and in the salicylic acid-dependent programmed cell death pathway (Boursiac et al., 2010), but so far, in plants, no data are available regarding their role in salt stress, even if ACA4 conferred protection against osmotic stress such as high NaCl, KCl, and mannitol when expressed in yeast cells (Geisler et al., 2000). Nevertheless, a key role of the vacuole in the regulation of $[Ca^{2+}]_{cyt}$ in response to this stress was shown in Arabidopsis. Choi and colleagues, by challenging Arabidopsis seedling root tip cells with 100 mM NaCl, demonstrated the existence of a long-distance root-to-shoot cytosolic Ca^{2+} wave responsible for the induction of the expression of stress-regulated genes in the shoot (Choi et al., 2014b). The role of the vacuole in this process was evidenced by the fact that the ablation of the tonoplast-localized two-pore channel AtTPC1 (Peiter et al., 2005) strongly dampened the speed of the Ca^{2+} wave, whereas its overexpression boosted it (Choi et al., 2014b). Importantly, upon salt stress, the *tpc1*-KO mutant did not show the upregulation of stress related marker genes in the shoot such as the Multi-Stress-Responsive Zinc-Finger Protein (*ZAT12)* and the Calmodulin-Related Touch 2 (*TCH2)* (Choi et al., 2014). Despite some controversy about a direct involvement of AtTPC1 in the release of Ca^{2+} from the vacuole (Gradogna et al., 2009; Beyhl et al., 2009; Ranf et al., 2008; Lenglet et al., 2017, Hedrich et al., 2018, Jaślan et al., 2019), these results demonstrate the importance of this compartment in the plant response to salt stress and in the overall strategy that plants adopt to cope with it. Of note, Dindas et al. (2021) have recently proposed, through a modeling approach, that the involvement of AtTPC1 in the long distance signaling is not due to its direct involvement in the release of Ca^{2+} from the vacuole, but rather depends on its capacity to transport K^+ which is regulated by the vacuolar membrane potential. Thus, in accordance with Jezek and Blatt (2017), the cytosolic Ca^{2+} signature could be intimately connected with the flux of ions other than Ca^{2+}.

Defining the importance of the subcellular compartments in the shaping of cytosolic Ca^{2+} signatures in response to salt stress was achieved by an orthogonal approach. Thanks to the expression, in

Arabidopsis plants, of the rat Ca^{2+}-binding protein parvalbumin (PV) fused to either a nuclear export (PV-NES) or a nuclear localization sequence (NLS-PV), the cytosolic or nucleosolic Ca^{2+} were selectively buffered (Huang et al., 2017). When both cytosolic and nuclear Ca^{2+} levels were monitored in root cells by means of the Cameleon Ca^{2+} sensor (YC3.6) (**Box 1, Fig. 2**), both compartments experienced salt- and osmotic-induced [Ca^{2+}] increases. Buffering of nuclear Ca^{2+} prevented the nuclear Ca^{2+} increase but not the cytosolic one, whereas buffering of cytosolic Ca^{2+} did not affect the nuclear Ca^{2+} rise. In both cases, in response to salt stress, the length of the primary root was impaired, and the expression of several abiotic stress-induced genes was deregulated, especially when nuclear Ca^{2+} was buffered (Huang et al., 2017). This latter result strongly supports the idea that the alteration of cellular Ca^{2+} signatures, in particular at the nuclear level, has a direct effect on the regulation of gene transcription and is in accordance with the demonstration that Ca^{2+} can regulate gene expression via CDPK and CaM binding transcription factors (CAMTA) (Reddy et al., 2011; Dubiella et al., 2013; Gao et al., 2013; Whalley and Knight, 2013; Lenzoni and Knight, 2019; Liu et al., 2020).

Organellar calcium in osmotic stress responses

Salt imposes on plant cells both ionic and osmotic stress, but this latter is *per se* detrimental for plant growth (Xiong and Zhu, 2002; Yang and Guo, 2018). Both hyper- and hypo-osmotic stress elicit $[Ca^{2+}]_{cyt}$ increases (Yuan et al., 2014; Basu and Haswell, 2020). Similarly to what occurred with salt stress (see above), the Arabidopsis *ccx2*-KO or *CCX2*-OX plants showed a smaller and a higher $[Ca^{2+}]_{cyt}$ increase respectively compared to the wild type when subjected to both hyper- and hypo-osmotic shocks. Moreover, in response to the same stress, the ER of the *ccx2*-KO accumulated more Ca^{2+} than the wild type. Overall, these data demonstrate that the AtCCX2 transporter is involved in the regulation of Ca^{2+} transport between the ER and cytosol (**Fig. 3**) in response to both hyper- and hypo-osmotic stress (Corso et al., 2018). Interestingly, even if localised to the tonoplast, the *Oryza sativa* (rice) CCX2 (OsCCX2) (**Fig. 3**) that mediates Ca^{2+} /cation transport in yeast, is also upregulated in response to drought stress (Yadav et al., 2015). However, at present, no information about its putative role in the regulation of intracellular Ca^{2+} homeostasis has been reported.

Being triggered by a drop in the soil water potential, hydrotropism can be considered as a response to a sort of osmotic stress (Dietrich, 2018; Fromm, 2019). The involvement of the ER in the regulation of Ca^{2+} signaling was recently highlighted in the hydrotropic response of Arabidopsis roots. The inhibition of AtECA1, a PIIA-type Ca^{2+}-ATPase (**Box 2; Fig. 3**), by the Myc-Interacting Zinc-Finger Protein 1 (AtMIZ1) determined a slow asymmetric rise of $[Ca^{2+}]_{cyt}$ in the elongation zone of root tip cells which was required for the root bending towards areas of higher water potential. The Arabidopsis *eca1*-KO and the pharmacological inhibition of AtECA1 by cyclopiazonic acid in wild type seedlings produced a higher $[Ca^{2+}]_{cyt}$ increase and exacerbated the root bending response, demonstrating the key role of the ER in this signaling pathway (Shkolnik et al., 2018). Remarkably, by using Arabidopsis seedlings expressing an ER-localized Cameleon Ca^{2+} sensor (CRT-D4ER) (Bonza et al., 2013) (**Box 1; Fig. 2**), it was shown that the hydrotropic stimulus triggered a decrease in ER luminal $[Ca^{2+}]$, supporting a role for the ER as a Ca^{2+} source in this process (Shkolnik et al., 2018). This latter result is thus a demonstration of direct involvement of the ER in the generation of a $[Ca^{2+}]_{cyt}$ transient through the inhibition of a Ca^{2+} pump and not through the opening of Ca^{2+}-permeable channels. A better understanding of how PIIA-type Ca^{2+}-ATPases are fine-tuned is a key issue that will deserve attention in the near future.

A recent report demonstrated that the lack of the so called AtcMCU, a member of the mitochondrial calcium uniporter (MCU) family (Baughman et al., 2011; De Stefani et al., 2011; Stael et al., 2012) (**Box 2; Fig. 3**) localised both in mitochondria and chloroplasts (Teardo et al., 2019), reduced the stromal Ca^{2+} accumulation in response to hyper-osmotic stress, with a consequent higher rise of the $[Ca^{2+}]_{cyt}$ peak compared to the wild type (Teardo et al., 2019). The lack of activation of mitogen activated protein kinase 3 and 6 (MAPK3/6) and a deregulated gene expression pattern in the *cmcu*-KO plants, suggested the hypothes that AtcMCU is required for a retrograde chloroplast signaling in response to the osmotic stress (Teardo et al., 2019). On the other hands, the AtcMCU presence in mitochondria (Teardo et al., 2019) would suggest that, in the *cmcu*-KO, the hyper-osmotic induced Ca^{2+} dynamics could be altered also in this compartment, but at the present time, data to support this hypothesis are lacking. Interestingly, AtcMCU did not seem to be involved in the transport of

Ca^{2+} into chloroplasts during salt stress thus suggesting its stress-specific role in the osmotic response (Teardo et al., 2019).

The possibility that plastids/chloroplasts represent a hub for the regulation of cytosolic Ca^{2+} dynamics in response to osmotic stress is sustained by another recent study as well. The lack of two plastidial envelope-localised K^+ exchange antiporter (KEA) transporters, AtKEA1 and AtKEA2 (**Fig. 3**), impaired the rapid hyper-osmotic-induced $[Ca^{2+}]_{cyt}$ increase (Stephan et al., 2016). At present, the mechanism responsible for the alteration of the cytosolic Ca^{2+} signature in the *kea1/kea2* mutant is not understood, and a study of stromal Ca^{2+} dynamics is required.

Based on the cited works, it is evident that ER, vacuole and chloroplasts/plastids are involved in the response to different abiotic stresses by contributing to shaping the cytosolic Ca^{2+} dynamics, and that proper nuclear Ca^{2+} dynamics are important for the regulation of gene transcription. Despite the recent identification of some molecular players involved in the Ca^{2+} accumulation in mitochondria (Wagner et al., 2015; Teardo et al., 2017; Selles et al., 2018), and the proposed role of this organelle in the salt stress response through retrograde signaling (Vanderauwera et al., 2012), there are no direct demonstrations that an impaired Ca^{2+} accumulation in this organelle can affect the cytosolic Ca^{2+} signature in response to abiotic stress.

Even less is known about a possible role of the other compartments, such as the Golgi apparatus, where the Arabidopsis PIIA-type Ca^{2+}-ATPase AtECA3 and the rice PIIB-type Ca^{2+}-ATPase OsACA7 have been localised (**Fig. 3**) (Mills et al., 2008; Singh et al., 2013). Interestingly, yeast cells expressing the OsACA7 are less sensitive to salt tolerance (Singh et al., 2013). However, since a clear role of these two pumps *in planta* has not been reported, further research in this direction is required.

CONTRIBUTION OF ORGANELLES IN THE SHAPING OF CYTOSOLIC CALCIUM INCREASES IN RESPONSES TO BIOTIC STIMULI

One of the earliest events occurring in different plant biotic interactions is a rise in cytosolic and nuclear $[Ca^{2+}]$ (Blume et al., 2000; Oldroyd and Downey, 2006). Plant biotic interactions can be beneficial, as in the case of symbiosis with Rhizobia and Mycorrhiza, or detrimental as in those with a wide range of pathogens (e.g. *Pseudomonas syringae*). In this section, we will briefly touch on the role played by the nuclear Ca^{2+} in symbiotic interactions, and then we will address more extensively recent evidence of how organellar Ca^{2+} homeostasis is involved in the regulation of cytosolic Ca^{2+} signatures in response to pathogen elicitors.

Symbiotic interactions have been mainly studied in Leguminosae in which a clear role of nuclear Ca^{2+} signaling was reported (reviewed in Oldroyd and Downie, 2006; Charpentier, 2018). It is well known that the perception of nodulation (NOD) and mycorrhizal (MYC) factors trigger characteristic nuclear Ca^{2+} oscillations that are then transduced by the nuclear-localized Ca^{2+}- and calmodulin-dependent Ser/Thr protein kinase (CCaMK) (reviewed in Charpentier and Oldroyd, 2013). Since the symbiosis interaction topic and the role played by nuclear Ca^{2+} is so vast, we redirect the readers to a recent review (e.g. Charpentier, 2018). Nonetheless, it is worth noting that one of the major discoveries in the field, made by Charpentier et al. (2016), was the identification of the *Medicago truncatula* cyclic nucleotide gated channel 15 (MtCNGC15) as one of the Ca^{2+}-permeable channels involved in the generation of NOD-induced nuclear Ca^{2+} oscillations (**Box 2; Fig. 3**). Of note, MtCNGC15, being specifically localised in the nuclear envelope (NE), presumably promotes the release of Ca^{2+} from the ER directly into the nucleoplasm (Charpentier et al., 2016) even if a Ca^{2+} depletion from NE was not reported. Previously, it was also demonstrated that the *Medicago* PIIA-type Ca^{2+}-ATPase MtMCA8 is targeted to the inner NE membrane (**Fig. 3**) and is essential for symbiotic Ca^{2+} oscillations, suggesting its role in efficient Ca^{2+} reloading from the nucleoplasm (Capoen et al., 2011). A mathematical modeling approach predicted that besides the need for a Ca^{2+}-permeable channel (i.e. MtCNGC15) and a Ca^{2+}-ATPase (i.e. MtMCA8), the generation of nuclear Ca^{2+} oscillations requires the activity of a Ca^{2+}-activated K^+ channel to counterbalance the movement of positive charges. The Doesn't Make Infections 1 (MtDMI1) channel is permeable to K^+, is localised at the NE and is therefore, presumably the component needed to counterbalance the charge caused by the influx of Ca^{2+} into the nucleoplasm (Granqvist et al., 2012). The same group later demonstrated that Ca^{2+} can diffuse from the nucleus into the cytosol (Kelner et al., 2018), but no physiological function has been ascribed to this $[Ca^{2+}]_{cyt}$ rise.

Pathogen-associated molecular patterns (PAMPs) are recognized by cell surface receptors (pattern-recognition receptors PRR) and activate an array of basal defence responses (PAMP-triggered immunity, PTI) (Zipfel and Oldroyd, 2017; Zhang et al., 2020). In response to PAMPs, the plant immune system relies on two parallel signal transduction pathways based on MAPK and Ca^{2+} signaling leading to transcriptional reprogramming (Boudsocq et al., 2010). In Arabidopsis, the PAMP flagellin (flg22 peptide) induces a quick $[Ca^{2+}]_{cyt}$ increase in leaves and roots (Ranf et al., 2008; Yuan et al., 2017; Emonet et al., 2021; Hilleary et al., 2020). The flg22-induced $[Ca^{2+}]_{cyt}$ rise is suggested to be mediated by different classes of PM-localised Ca^{2+}-permeable channels with evidence supporting a role of both members of GLR and CNGC families (Kwaaitaal et al., 2011; Tian et al., 2019; Bjornson et al., 2021). Nonetheless, in guard cells the flg22-induced $[Ca^{2+}]_{cyt}$ increase is, at least partially, dependent on members of the mechanically activated channel AtOSCA family (AtOSCA1.3 and 1.7) (Thor et al., 2020) suggesting that multiple families of Ca^{2+} channels contribute to the overall pattern-induced Ca^{2+} response in Arabidopsis.

Direct involvement of the subcellular compartments in the generation of the flg22-induced $[Ca^{2+}]_{cyt}$ has been predicted (Ma et al., 2017), but experimental evidence is still lacking. Nevertheless, by using Arabidopsis plants expressing chloroplast-localised aequorin, it was shown that they transiently accumulate Ca^{2+} in the stroma in response to flg22 and that this stromal Ca^{2+} transient temporally follows the $[Ca^{2+}]_{cyt}$ increase (Nomura et al., 2012). Similarly to what was observed in response to salt stress (see the previous section), the lack of the chloroplast Ca^{2+} sensor AtCAS affected flg22-induced chloroplast Ca^{2+} dynamics, and such a CAS-dependent mechanism was involved in transcriptional reprogramming through retrograde signaling (Nomura et al., 2012). Neither clues about the mechanism of Ca^{2+} transport across chloroplasts' membranes, nor consequent impairment of the cytosolic Ca^{2+} signature was reported. The fact that the *cmcu*-KO had an impaired H_2O_2-induced chloroplast Ca^{2+} accumulation (Teardo et al., 2019) makes this channel a putative candidate to mediate the Ca^{2+} influx in response to flg22, but there is no direct evidence for this as yet.

The impairment of Ca^{2+} transport across the tonoplast was also shown to impact the cytosolic Ca^{2+} signature in response to flg22 (Hilleary et al., 2020). The dissection of cytosolic Ca^{2+} dynamics by using the ultrasensitive Ca^{2+} sensor Cameleon YC-Nano 65 (Horikawa et al., 2010; Choi et al., 2014b) in epidermal leaf cells of Arabidopsis plants lacking the two tonoplast-localised PIIB-type Ca^{2+}-ATPase AtACA4 and AtACA11 (**Fig. 3**), revealed that this double KO mutant exhibited higher basal $[Ca^{2+}]_{cyt}$ and a larger flg22-induced Ca^{2+} increase compared to the wild type. This was accompanied by an upregulation of the defense regulator gene *CBP60g* and a higher resistance to *Pst* bacterial challenge at one day post-inoculation (Hilleary et al., 2020). No attempts to measure vacuole Ca^{2+} dynamics were carried out. However, the *aca4/aca11* mutant phenotype was complemented when the PIIB-type PM localised-Ca^{2+}-ATPase AtACA8, was (mis-)targeted to the tonoplast of the mutant. This latter result strongly supports the idea that the observed phenotype of *aca4/aca11* was directly dependent on the impairment of Ca^{2+} import into the vacuole lumen. Very similar observations were made in the Arabidopsis *aca1/aca2/aca7* triple KO mutant lacking three ER-localised PIIB-type Ca^{2+}-ATPases. In comparison to wild type, the triple mutant showed i) a higher $[Ca^{2+}]_{cyt}$ in leaf cells at rest, ii) an increased magnitude and duration of the $[Ca^{2+}]_{cyt}$ transient induced by flg22 treatment, iii) smaller rosettes, and iv) a high frequency of leaf lesions (Ishka et al., 2021). Similarly to the *aca4/aca11* mutant, the lesions phenotype of *aca1/aca2/aca7* was suppressed by the expression of a transgene encoding NahG, an enzyme that degrades salicylic acid (SA) (Ishka et al., 2021). Once again these results demonstrate the importance of the fine tuning of the cytosolic Ca^{2+} homeostasis both at rest and during the recovery of the prestimulus $[Ca^{2+}]_{cyt}$, a process mediated by active Ca^{2+} transporters present in the tonoplast and ER, extruding Ca^{2+} out of the cytosol (Qudeimat et al., 2008; Costa et al., 2017; Hilleary et al., 2020; Ishka et al., 2021) (**Box 2; Fig. 3**).

Besides Arabidopsis, *Nicotiana tabacum* plants have also been used as a model for several studies investigating the role of cytosolic and organellar Ca^{2+} in the response to pathogen elicitors. *N. tabacum* plants are particularly sensitive to cryptogein, a 10-kD protein secreted by the oomycete *Phytophthora cryptogea*, that induces a hypersensitive response (HR) in *Nicotiana tabacum* (var. Xanthi) plants and systemic acquired resistance against various pathogens (Bourque et al., 2002). Experiments using cells of *Nicotiana tabacum* var. Xanthi expressing aequorin localised to the cytosol, chloroplast and mitochondria showed that cryptogein was effective in inducing specific Ca^{2+}

signatures in each compartment with chloroplasts clearly showing a Ca^{2+} increase that peaked after the cytosolic one (Manzoor et al., 2012). Interestingly, a pharmacological approach indicated that inositol trisphosphate (IP3) could play a role in the cryptogein-induced Ca^{2+} signaling, suggesting its possible contribution in promoting a Ca^{2+} release from intracellular Ca^{2+} stores (e.g. vacuole or ER) (Manzoor et al., 2012). Indeed, the silencing of the *N. tabacum* ER-localised PIIB-type Ca^{2+}-ATPase NbCA1 (**Fig. 3**) accelerated the cryptogein-induced cell death in leaf cells (Zhu et al., 2010). Importantly, by using a genetically encoded Ca^{2+} sensor (Case 12) the authors showed that the downregulation of NbCA1 resulted in an altered cryptogein-induced cytosolic Ca^{2+} signature, with an increase of amplitude and duration of Ca^{2+} spikes. These findings suggest that the NbCA1 is involved in the Ca^{2+} efflux pathway that controls cell death during plant innate immune response (Zhu et al., 2010). In addition, other proteinaceous elicitors including flg22 were shown to induce in *N. tabacum* cells, cytosolic and nuclear Ca^{2+} elevations, with this latter apparently dependent on $[Ca^{2+}]_{cyt}$, IP3 and reactive active oxygen species (ROS) (Lecourieux et al., 2005).

The involvement of Ca^{2+} transport across ER in plant-pathogen interactions was also reported by studying Os*XA10*, a *R* gene for resistance to bacterial blight in rice. The OsXA10 protein is localised at the ER membrane where it is assembled as hexamers potentially working as a Ca^{2+} transporter (Tian et al., 2014). It was shown that the expression of OsXA10 in different systems (e.g. rice, *Nicotiana benthamiana*, and mammalian HeLa cells) triggered programmed cell death in a mechanism that is dependent on the release of Ca^{2+} from the ER (Tian et al., 2014). In leaf epidermal cells of *N. benthamiana,* the expression of the OsXA10-mCherry fusion disturbed the Ca^{2+} homeostasis, inducing a Ca^{2+} depletion of the ER accompanied by a $[Ca^{2+}]_{cyt}$ increase. Similar results were also obtained by expressing the OsXA10-RFP fusion in human HeLa cells (Tian et al., 2014). Noticeably, the expression of OsXA10 variants shown to be able to abolish the ER Ca^{2+} depletion also abolished the programmed cell death in *N. benthamiana* and HeLa cells as well as the disease resistance in rice (Tian et al., 2014) strongly supporting, in this specific case, the role of ER as a source of Ca^{2+} in the triggering of a $[Ca^{2+}]_{cyt}$ increase and promoting cell death.

Whereas the OsXA10 protein has an apparent direct role in the plant response to pathogens through the regulation of Ca^{2+} homeostasis in the ER, other indirect evidence highlighted the importance of proper Ca^{2+} homeostasis of this intracellular compartment in response to biotic stress. In Arabidopsis, the ER localised Ca^{2+} binding protein calreticulin 3 (AtCRT3) is essential for the correct maturation of the EF-Tu receptor (EFR) (Saijo et al., 2009) which recognizes the bacterial elicitor elf18 on the cell surface (Zipfel et al., 2006). Although Ca^{2+} measurements in the ER lumen of the At*crt3* mutant are lacking, this result provides indirect evidence about the critical role of ER Ca^{2+} homeostasis in plant immunity.

In conclusion, the involvement of ER, vacuole and chloroplasts in the regulation of cytosolic Ca^{2+} homeostasis/ Ca^{2+} transients induced in response to pathogen elicitors has been clearly demonstrated. In contrast, even if *N. tabacum* plants treated with cryptogein showed an accumulation of Ca^{2+} in the mitochondrial matrix (Manzoor et al., 2012), evidence of a role for mitochondrial Ca^{2+} elevations in this physiological context is still missing. However, the fact that a splicing variant of the Arabidopsis AtGLR3.5 was localized to the inner mitochondrial membrane and that the *glr3.5* mutant showed accelerated leaf senescence (Teardo et al., 2015), allows speculation about a role of mitochondrial Ca^{2+} transport in the plant responses to biotic stress. On the other hand, the *glr3.5* showed a mild phenotype regarding the mitochondrial Ca^{2+} uptake in response to leaf wounding and no mutant showing a strong impairment in the transport of Ca^{2+} has been reported yet. The isolation of such a line would represent a good tool to further investigate any possible role of this compartment in plant-pathogen interactions as well as other responses.

CONTRIBUTION OF ORGANELLES IN THE REGULATION OF CALCIUM HOMEOSTASIS IN STOMATAL MOVEMENTS

Stomata are made of a pair of guard cells present mainly in the leaf epidermis, and through them, plants acquire the CO_2 needed for photosynthesis and release O_2. When stomatal pores are open, plants, besides exchanging gases, lose water via transpiration, and, therefore, to prevent an excessive loss of water with consequent plant wilting, the opening of the pores must be finely controlled (Taiz et al, 2014).

Stomata open in response to light and close in response to drought stress, elevated CO_2, ozone, low humidity, pathogen attack, and other stimuli (reviewed in Kim et al., 2010). The importance of stomata in plant physiology has elected guard cells as a highly developed model system for dissecting signal transduction mechanisms in plants, and for elucidating how individual signaling mechanisms can interact within a network in a single cell (Kim et al., 2010). Indeed, stomatal guard cells represent, together with pollen tubes and root hairs (see below) cell models in which Ca^{2+} signaling has been deeply investigated (reviewed in Kim et al., 2010; Jezek and Blatt, 2017).

The opening and closing of stomata are mechanistically regulated by the coordinated movement across plasma and vacuolar membranes of ions (e.g. K^+, Cl^-) and molecules (e.g. malate, glucose), which by determining the osmotically-driven movement of water, affect cells turgor (Pandey et al., 2007; Wang et al., 2014; Cubero-Font and De Angeli, 2021; Demes et al., 2020; Flütsch et al., 2020a; 2020b). The passage of ions across membranes is dependent upon the activity of different ion channels, the gating of which depends on several actors (e.g. membrane potential, phosphorylation, cytosolic pH, cytosolic Ca^{2+}) (reviewed in Jezek and Blatt, 2017). In response to drought, plants synthesize the hormone abscisic acid (ABA) that induces stomatal closure through both Ca^{2+}-dependent and Ca^{2+}-independent signaling pathways (MacRobbie, 1992; Laanemets et al., 2013; Huang et al., 2019). Guard cells were among the first cell types where *in vivo* analyses of cytosolic Ca^{2+} dynamics were studied by using firstly, Ca^{2+} sensitive dyes and later, genetically encoded Ca^{2+} sensors (McAinsh et al., 1995; Allen et al., 1999; Garcia-Mata et al., 2003). Years of intense studies have shown that ABA, plasma membrane hyperpolarization, ROS, external Ca^{2+}, among other stimuli, activate plasma membrane Ca^{2+} permeable channels leading to cytosolic Ca^{2+} increases (Hamilton et al., 2000; Pei et al., 2000; Murata et al., 2001; Kwak et al., 2003). Interestingly, in guard cells cytosolic Ca^{2+} increases often occur in the form of repetitive Ca^{2+} oscillations whose frequency, duration, amplitude and transient number, which are linked to fluctuations in the membrane voltage and in ions' fluxes, regulate the stomatal aperture (Allen et al., 2001; Minguet-Parramona et al., 2016). Experimental evidence demonstrated that in several cases the generation of cytosolic Ca^{2+} transients and oscillations were dependent upon both an influx of Ca^{2+} from the apoplast (Hamilton et al., 2000; Pei et al., 2000; Murata et al., 2001), and its release from internal stores (Garcia-Mata et al., 2003). Molecules like Nitric Oxide (NO), Cyclic ADP-ribose (cADPR), Inositol trisphosphate

(IP3), and Inositol hexakisphosphate (IP6) were shown to activate endomembrane channels, thus promoting Ca^{2+} release from internal stores (Alexandre et al., 1990; Muir and Sanders, 1996; Wu et al., 1997; Leckie et al., 1998; Grabov and Blatt, 1999; Garcia-Mata et al., 2003; Lemtiri-Chlieh et al., 2003; reviewed in Jezek and Blatt, 2017). Of note, ABA activates the Ca^{2+} permeable channels at the plasma membrane (Hamilton et al., 2000; Pei et al., 2000, Murata et al., 2001; Kwak et al., 2003) and the consequent influx of Ca^{2+} into the cytosol stimulates the Ca^{2+} release from intracellular stores, a process described as Ca^{2+}-induced Ca^{2+} release (CICR) (Grabov and Blatt, 1998, 1999). While computational and modeling approaches have indicated that the release of Ca^{2+} from internal stores may account for more than 95% of the Ca^{2+} entering the cytosol during Ca^{2+} transients increase (Chen et al., 2012; Wang et al., 2014; Minguet-Parramona et al., 2016), the molecular identity of channels or transporters mediating this Ca^{2+} release lags behind.

Since the slow vacuolar ion channel (SV) coded by the At*TPC1* gene (Peiter et al., 2005) is permeable to both K^+ and Ca^{2+} and its activity is modulated by cytosolic Ca^{2+}, AtTPC1 was one of the main candidates predicted to be involved in the CICR process (Hedrich and Neher, 1987; Ward and Schroeder, 1994; Peiter et al., 2005; Gradogna et al., 2009; Dindas et al., 2021). Although data showed that AtTPC1 was required for the inhibition of the light-induced stomatal opening in the presence of external ABA (Peiter et al., 2005), it was later demonstrated that the *tpc1* null mutant closes stomata like the wild type in response to ABA, and Methyl Jasmonate (MeJA), but not in response to external Ca^{2+} (Islam et al., 2010). Interestingly, when cytosolic Ca^{2+} was monitored in Arabidopsis guard cells expressing the Cameleon Ca^{2+} sensor (**Box 1, Fig. 2**), *tpc1* did not show any difference in the Ca^{2+}, ABA, and MeJA induced cytosolic Ca^{2+} oscillations compared to the wild type (Islam et al., 2010). Thus, apparently, in guard cells a direct contribution of AtTPC1 in the CICR process is negligible.

On the other hand, the importance of the transport of ions across the tonoplast for proper regulation of cytosolic Ca^{2+} dynamics has been demonstrated. The Arabidopsis De-Etiolated 3 mutant (*det3)* lacking the subunit C of the vacuolar H^+-ATPase showed, in guard cells, altered cytosolic Ca^{2+} dynamics in response to external Ca^{2+} and ROS (i.e. H_2O_2) compared to wild type (Allen et al., 2000). To be precise, whereas in the wild type external Ca^{2+} and H_2O_2 induced characteristic cytosolic Ca^{2+}

oscillations, the *det3* mutant showed sustained cytosolic Ca^{2+} increases and did not close the stomata (Allen et al., 2000). Conversely, in the same mutant, ABA was effective in inducing stomatal closure, showing a wild type pattern of cytosolic Ca^{2+} oscillations (Allen et al., 2000). Thus, it is plausible that the *det3* mutant, which is defective in H^+ transport across the tonoplast, also presents an impaired Ca^{2+} uptake in the subcellular compartments such as the vacuole and possibly the ER (Schumacher et al., 1999; Allen et al., 2000). The demonstration that several Ca^{2+} transport systems, including CAXs and Ca^{2+}-ATPases (**Box 2**) catalyse a Ca^{2+}/H^+ exchange (Bonza and De Michelis, 2011; Demidchik et al., 2018) supports the prediction that defects in H^+ transport can also affect Ca^{2+} transport and its homeostasis (Hills et al., 2012; Wang et al., 2014; Jezek and Blatt, 2017; Dindas et al., 2021). At present, to the best of our knowledge, no attempts to investigate vacuolar and ER Ca^{2+} dynamics during stomatal movements have been made. As a consequence, the analysis of Ca^{2+} dynamics in these two compartments is an important challenge for future research. Available mutants like the Arabidopsis *aca4/aca11*, and *aca1/aca2/aca7* (Hilleary et al., 2020; Ishka et al., 2021) already represent an important genetic resource to perform analyses in this direction. In support of this, analyses of stomatal conductance carried out in these two mutants showed kinetics that slowed significantly on repeated CO_2 elevations compared to the wild type. These results underpin an important role played by the pools of endomembrane Ca^{2+} in a sort of a "carbon memory" of stomatal responsiveness to light and CO_2 that ultimately affects photosynthesis and water use by the plant (Jezek et al., 2021). Besides ER and vacuole, analyses of nuclear, mitochondrial, peroxisomal, and chloroplasts Ca^{2+} dynamics have been carried out in guard cells, but their contribution in the regulation of stomatal movements is still missing. Stimuli, such as hyper- and hypo-osmotic stress also induce, besides a $[Ca^{2+}]_{cyt}$ increase, nuclear and mitochondrial $[Ca^{2+}]$ rises (Loro et al., 2012) and plasma membrane hyperpolarization triggers cytosolic and peroxisomal Ca^{2+} increases (Costa et al., 2010). Of note, it was demonstrated that the Arabidopsis *cmcu*-KO mutant failed to close the stomata in response to the osmotic stress and lost water faster compared to the wild type under drought stress (Teardo et al., 2019). Unfortunately, analyses of cytosolic and chloroplasts Ca^{2+} dynamics in *cmcu*-KO guard cells are lacking. On the other hand, the dual localisation of cMCU to both chloroplasts and mitochondria would also require the analysis of mitochondrial Ca^{2+} dynamics. As an intriguing component of the chloroplast Ca^{2+} regulatory network, the Ca^{2+} sensing protein CAS localized in chloroplast thylakoid membranes has been associated with guard cell dynamics. In particular, the lack of AtCAS activity in Arabidopsis, prevents the cytosolic Ca^{2+} increase in guard cells and the stomatal closure induced by the administration of external Ca^{2+} (Nomura et al., 2008; Weinl et al., 2008). Nevertheless, the channels and/or Ca^{2+} transporters involved in this mechanism are unknown.

The large size of guard cells' chloroplasts and the fact that their imaging is relatively easy, allowed Ca^{2+} imaging analyses in single organelles (Loro et al., 2016). This analysis showed that the transition from high-to-low-intensity blue light (needed to excite the Cameleon Ca^{2+} sensor) (**Box 1, Fig. 2**), induces a transient Ca^{2+} increase in the stroma. Interestingly, the stromal [Ca^{2+}] rise was characterized by two components: i) a series of Ca^{2+} spiking superimposed to ii) a gradual sustained Ca^{2+} increase (Loro et al., 2016). These Ca^{2+} spikes were dependent on the availability of cytosolic Ca^{2+} and were not synchronized between individual chloroplasts of the same cell. In contrast, the gradual sustained Ca^{2+} increase occurred independently of cytosolic Ca^{2+}, suggesting an intraorganellar Ca^{2+} release (Loro et al., 2016). At present, the molecular identity of the channels and/or transporters involved both in the generation of the sustained and transient stromal Ca^{2+} increases are not known, but the Arabidopsis AtBICATs, and AtcMCU channels are obvious candidates (**Fig. 3**) (Frank et al., 2019, Teardo et al., 2019).

In the future, the combination of modeling, *in vivo* imaging, and genetics will be instrumental to better define the role played by the subcellular compartments in the stomatal movements.

CONTRIBUTION OF ORGANELLAR/CYTOSOLIC CALCIUM HOMEOSTASIS IN PLANT DEVELOPMENTAL PROCESSES

As reported above organellar Ca^{2+} dynamics have been mainly studied in relation to plant responses to both abiotic and biotic stresses. Less is known about their functions during developmental processes, and only a few cases have reported on the roles of different subcellular compartments in the regulation of cytosolic Ca^{2+} dynamics during development. Nevertheless, plants have at least two well-known systems where a precise spatio-temporal regulation of $[Ca^{2+}]_{cyt}$ is required for the execution of the proper growth processes: pollen tubes (PTs) and root hairs (RHs) (Schoenaers et al., 2017). While PTs provide for water-independent propagation of species, RHs confer an increase in root surface area which enhance nutrient and water uptake and better anchor plants to the soil. PTs and RHs are filamentous cells that grow unidirectionally by depositing flexible cell wall material at one side of the cell and exploiting turgor pressure as the driving force for elongation, a process also referred to as tip growth (Schiefelbein et al., 1993; Feijo et al., 2004). Although these tip-growing systems are very similar, they also display differences in their growth-related molecular machineries (Feijo et al., 2004).

Role of organellar calcium in directing pollen tube tip growth

Flowering plant reproduction comprises several sequential steps from pollination to fertilization. PTs growth is essential for reproduction, and they have long been considered outstanding models for cell biology for a variety of reasons. One important feature of PTs is their prominent dependence on ion dynamics to promote and regulate growth (Michard et al., 2017). PTs appropriately adjust turgor pressure by adapting to changes in external osmolarity (Hill et al., 2012). In 1963 it was revealed that Ca^{2+} is essential for *in vitro* PTs cultures (Brewbaker and Kwack, 1963), and the relationship between $[Ca^{2+}]$ and PTs growth has been extensively examined. By using both Ca^{2+} sensitive dyes or genetically encoded Ca^{2+} sensors, it was evident that a tip-focused $[Ca^{2+}]_{cyt}$ gradient occurred in growing PTs showing regular oscillations that correlate with growth (Holdaway-Clarke et al., 1997; Iwano et al., 2009; Michard et al., 2011). It was also shown that the perturbation of the tip $[Ca^{2+}]$ gradient may affect the growth as well as the viability of PTs (Feijo et al., 2001; Zhang et al., 2007; Winship et al., 2017). As in other cell systems, there is clear evidence that the dynamics of Ca^{2+} signals in PTs are largely controlled by Ca^{2+} influx and Ca^{2+} efflux through the plasma membrane (**Box 2**). Just to cite some examples, GLRs (Michard et al., 2011; Wudick et al., 2018), CNGCs (Frietsch et al., 2007; Gao et al., 2016; Pan et al., 2019) and isoforms of PIIB-Ca^{2+}-ATPase (Schiøtt et al., 2004; Ishka et al., 2021) were demonstrated to be required for the proper PT elongation and growth. In a few cases, it was also demonstrated that growth defects were linked to deregulated tip [Ca^{2+}] oscillations (Michard et al., 2011, Chen et al., 2015).

Knowledge about the role of subcellular compartments in the regulation of the tip-Ca^{2+} dynamics is rather limited, but some research has highlighted a potential role of ER and mitochondrial Ca^{2+} in this process (e.g. Holdaway-Clarke et al., 1997; Colaço et al., 2012; Ishka et al., 2021). Of interest, was the demonstration that the treatment of PTs with caffeine reversibly stops their growth and dissipates the tip-Ca^{2+} gradient (Pierson et al., 1996; Diao et al., 2018). In mammalian cells, caffeine is known to promote the release of Ca^{2+} from the ER through the activation of IP3 receptors (IP3Rs) (Taylor and Tovey, 2010; Foskett et al., 2007). Thus, it is reasonable to hypothesize that its effect on pollen could depend on a disturbance of cytosolic Ca^{2+}, dependent on a Ca^{2+} release from the ER. However, no IP3Rs have been identified in superior plants (Edel et al., 2017), and no caffeine-dependent ER-Ca^{2+} release has been reported so far. Nonetheless, the role of Ca^{2+} transport across the ER membrane in the regulation of PTs growth was first highlighted by Iwano and colleagues (Iwano et al., 2009) who analyzed Ca^{2+} dynamics in the cytosol and ER lumen of Arabidopsis pollen tubes by using Cameleon Ca^{2+} sensors localised in the two compartments (YC4.6 and YC3.6 in the ER and in the cytosol, respectively) (Iwano et al., 2009). The administration of cyclopiazonic acid that inhibits the activity of ER-localised PIIA-type Ca^{2+}-ATPases triggered the PTs' growth arrest and an ER luminal [Ca^{2+}] decrease (Iwano et al., 2009). This result allowed the authors to ascribe a role of ER in the fine regulation of the tip-focused $[Ca^{2+}]_{cyt}$ gradient (Iwano et al., 2009). To go deeper inside the ER/cytosolic Ca^{2+} relationships during PTs growth, simultaneous observations of Ca^{2+} dynamics in these two compartments would be required. Whereas there is no genetic evidence that the lack of the ER PIIA-type Ca^{2+}-ATPase AtECA1 activity compromises pollen development and plant fertility, a very recent work showed that the ablation of three ER-localised PIIB-type Ca^{2+}-ATPases, AtACA1, 2, and 7 strongly compromised pollen fertility, with a decrease in pollen transmission efficiency (Ishka et al., 2021). Single knockout mutants did not show any phenotype demonstrating the existence of functional redundancy (Ishka et al., 2021). Neither cytosolic nor ER Ca^{2+} dynamics were however analysed.

As reported in the previous sections, plant mitochondria accumulate Ca^{2+} possibly through the activity of the mitochondrial calcium uniporter complex (MCUC) (Wagner et al., 2015, Teardo et al., 2017), but a demonstration that *in planta* this complex represents the main route for Ca^{2+} import is still missing. Nevertheless, in Arabidopsis, there are six MCU isoforms (Stael et al., 2012) and experimental evidence supports a role for AtMCU1 and AtMCU2 in the regulation of pollen germination. Selles et al. (2018) showed that AtMCU1 and AtMCU2 are expressed in the vegetative cell and in the germinated PTs but were not detectable in the embryo sac. Remarkably, pollen grains germination and PTs elongation were reduced *in vitro* in *mcu2*-KO mutants and this ultimately led to the limited paternal transmission of *mcu2*-KO to the progeny. No reproductive phenotype could be detected in *mcu1*-KO mutants. These results tend to suggest that mitochondrial Ca^{2+} homeostasis is an additional player in pollen germination and PTs growth. However, no measurements of both cytosolic and mitochondrial Ca^{2+} were carried out in the PTs of these mutant lines, thus the conclusion that the observed phenotype is directly linked to a deregulated Ca^{2+} transport could not be drawn yet. Similarly to what was suggested for the ER, simultaneous analysis of Ca^{2+} dynamics during PTs growth in the two compartments would be desirable.

Another link in support of a role played by the Ca^{2+} handling by subcellular compartments in the regulation of PT growth came from the indirect evidence that tonoplast-localized Ca^{2+} sensors are required to control the developmental process. In Arabidopsis, the calcineurin B-like proteins AtCBL2 and AtCBL3 are significantly expressed in pollen and PTs. AtCBL2 and AtCBL3 were described as interacting with the AtCIPK12 at the tonoplast, with evident phenotypic consequences at the level of vacuolar morphology and PTs' polar growth upon mutation or overexpression of *CBL2/3* or *CIPK12* (Steinhorst et al., 2015). Interestingly, Tang et al. (2020) demonstrated that seedlings of the Arabidopsis *cbl2/cbl3* mutant were severely stunted under low K^+ conditions, a phenotype due to an impairment in K^+ remobilization from vacuoles. So, it is tempting to speculate that a similar mechanism could be present in PTs. Since AtCBL2 and AtCBL3 are attached to the tonoplast facing the cytosolic side, it is conceivable that they are sensitive to changes in the cytosolic Ca^{2+} in the tonoplast microdomain (Knight et al., 1996). At present, there is no evidence that the Ca^{2+} regulation of the CBL2/3-CIPK12 complex in the tonoplast is released from the vacuole, but this is a suggested hypothesis that may require further research.

Role of organellar calcium in directing root hair tip growth

RHs are tubular extensions from the surface of root epidermal cells (Schoenaers et al., 2017). This "hairlike" morphology is essential for their role in nutrient and water uptake, plant anchoring in the soil, and microbial interactions (Vèry and Davies, 2000; Charpentier and Oldroyd, 2013). In RHs, the tip [Ca^{2+}] gradient (Wymer et al., 1997, Monshausen et al,. 2007, Monshausen et al., 2008; Candeo et al., 2017) is maintained by an influx of extracellular Ca^{2+} through hyperpolarization activated plasma membrane-localised Ca^{2+} channels (Vèry and Davies 2000), and CNGCs (Brost et al., 2019). Indeed, similarly to PTs, $[Ca^{2+}]_{cyt}$ has emerged as a key component controlling the RHs growth and its perturbation alters the RHs' proper developmental program (Monshausen et al., 2008). It is conceivable that as in PTs, also in RHs the organellar Ca^{2+} transport can impinge on the cytosolic Ca^{2+} dynamics. However, at present, the information available regarding their possible contribution is very scarce. Attempting a comparison with PTs, we might predict that in RHs, the ER and mitochondria Ca^{2+} transport could also affect the developmental process. Only a few pieces of evidence support a possible role of mitochondria in the RHs development. Wang et al. (2010) demonstrated that treatments of Arabidopsis RHs with latrunculin B or jasplakinolide, which depolymerize and polymerize actin filaments respectively, decreased the mitochondrial inner membrane potential, triggered a release of Ca^{2+} from the mitochondria and induced a $[Ca^{2+}]_{cyt}$ increase in the RHs (Wang et al., 2010). Moreover, the authors highlighted the presence of a [Ca^{2+}] gradient in mitochondria from the tip to the base of the RH that was disrupted by the drugs. Even if it is suggestive of a role of mitochondria in the regulation of $[Ca^{2+}]_{cyt}$ in RHs development, genetic evidence in support of this hypothesis is lacking. Teardo et al. (2017) analyzed the roots of seedlings of the *mcu1*-KO and At*MCU1* overexpressing plants without reporting any abnormalities in the RHs development. However, Arabidopsis has six MCU isoforms and at least two of them (At*MCU1* and Atc*MCU*) are expressed in RHs (source: eFP browser) (Winter et al., 2007) and all are expressed in roots (source: Geneinvestigator) (Hruz et al., 2008; Klepikova et al., 2016), therefore the absence of clear RHs phenotypes might be due to functional redundancy. The generation of higher order *mcu* mutants should be pursued to analyse their involvement in mitochondrial Ca^{2+}regulation during RHs development.

Role of calcium in root tip growth

Primary root tip growth is another plant development program that seems to be subject to regulation of $[Ca^{2+}]_{cyt}$ dynamics by subcellular compartments. Leitão et al. (2019) showed that in Arabidopsis, nuclear Ca^{2+} signaling is elemental for proper primary root development, including meristem development and auxin homeostasis. The genetic ablation of the NE localised AtDMI1, a functional analogue of MtDMI1 in root symbioses thus a putative ion channel permeable to K^+ that counterbalances the charge caused by the influx of Ca^{2+} into the nucleus (Granqvist et al., 2012), was able to modulate the nuclear Ca^{2+} signatures, and primary root development (Leitão et al., 2019) (**Fig. 3**). However, the molecular identity of the Ca^{2+} permeable channel responsible for the generation of the nuclear Ca^{2+} transient is still unknown. Based on structural homology analyses, AtDMI1 can be classified as a BK channel (Kim et al., 2019). Interestingly, the LjCASTOR BK channel of *Lotus japonicus*, when expressed in HEK293 cells as a truncated form, lacking the N-terminus and two transmembrane domains, was shown to be both permeable to and regulated by Ca^{2+} (Kim et al., 2019). Based on this piece of evidence we might speculate that AtDMI1 could also be permeable to Ca^{2+} but this needs to be experimentally demonstrated. Nevertheless, it would be of major interest to directly monitor the Ca^{2+} in the NE to have direct proof that this compartment, in continuity with the ER, is responsible for the observed nucleoplasm Ca^{2+} transient.

CONCLUSIONS

Since the publication of the seminal review from McAinsh and Pittman (2009) in which the authors provided and discussed the first available evidence about the role of subcellular compartments in the regulation of the cellular Ca^{2+} homeostasis in plant cells, much progress has been made. In this Update, we have recapitulated the experimental proofs collected in recent years supporting the role of the intracellular compartments in the generation and shaping of $[Ca^{2+}]_{cyt}$ increases observed in response to environmental and developmental stimuli (**Fig. 4**). Forward and reverse genetic approaches coupled to the use of imaging tools have now shed light on key roles played by vacuole, chloroplast/plastid, and ER/NE in the shaping of cytosolic Ca^{2+} dynamics in different physiological/stressful conditions. In some cases, channels and transporters directly involved in the movement of Ca^{2+} across the membranes of these compartments were also identified (**Box 2, Fig. 3**). However, despite this increased knowledge, understanding of the role played by mitochondria in the regulation of cytosolic Ca^{2+} dynamics is still limited. Equally, the organelles' contribution in Ca^{2+}-dependent stomatal movements needs experimental confirmation (see Outstanding questions).

Much work needs to be done. Forward genetic screening based on the use of recently developed organelle localised Ca^{2+} sensors (**Box 1. Fig. 2**), could provide a valuable strategy for the identification of additional players involved in the accumulation and release of Ca^{2+} from internal stores. Moreover, besides using model plants, the identification and the definition of the physiological role of intracellularly localised Ca^{2+} permeable channels and transporters should be extended to important crop species such as rice, for which preliminary results are already available (Singh et al., 2013).

ACKNOWLEDGEMENTS

This Update is dedicated in memory of our friend and colleague Hillel Fromm who passed away on October 12th 2020.

This work was supported by Piano di Sviluppo di Ateneo 2019 (University of Milan) (to AC), by Ministero dell'Istruzione, dell'Università e della Ricerca Fondo per Progetti di ricerca di Rilevante Interesse Nazionale 2017 (PRIN 2017ZBBYNC) (to MCB). We apologize to all authors of papers not mentioned in this manuscript due to space limitations.

FIGURE LEGENDS

Figure 1. Biotic and abiotic stress as well as developmental stimuli can trigger cytosolic and organellar [Ca^{2+}] increases. Cytosolic Ca^{2+} transients are decoded by different Ca^{2+} sensors and

relays such as Calmodulin (CaM), Calmodulin-like proteins (CMLs), calcineurin β-like proteins (CBLs), Ca^{2+}-dependent protein kinases (CDPKs), and calmodulin-dependent protein kinase (CCaMK) that trigger precise and tailored responses altering gene expression and metabolism.

Figure 2. Overview of organelle-targeted genetically encoded Ca^{2+} indicators. ER = endoplasmic reticulum, GA = Golgi Apparatus.

Figure 3. Channels and transporters localised in subcellular compartments reported to have a role in plant developmental processes and stress responses linked to the regulation of Ca^{2+} transport across membranes. The red question marks indicate that further studies are required. Channels are represented in blue, pumps in green and co-transporters in grey. At*: Arabidopsis thaliana;* Lj*: Lotus japonicus;* Mt*: Medicago truncatula;* Nb*: Nicotiana benthamiana;* Pp*: Physcomitrium patens,* Os*: Oryza sativa.*

Fig. 4. Summary of the Ca^{2+} transport mechanisms localised in the subcellular compartments of plant cells involved in the regulation of cytosolic Ca^{2+} dynamics for which a physiological response in different plant tissues/cell types was demonstrated.

REFERENCES

Alexandre J, Lassalles JP, Kado RT (1990) Opening of Ca^{2+} channels in isolated red beet root vacuole membrane by inositol 1,4,5-trisphosphate. Nature **343**: 567-570

Allen GJ, Chu SP, Schumacher K, Shimazaki CT, Vafeados D, Kemper A, Hawke SD, Tallman G, Tsien RY, Harper JF, Chory J, Schroeder JI (2000) Alteration of stimulus-specific guard cell calcium oscillations and stomatal closing in Arabidopsis *det3* mutant. Science **289**: 2338-2342

Allen GJ, Chu SP, Harrington CL, Schumacher K, Hoffmann T, Tang YY, Grill E, Schroeder JI (2001) A defined range of guard cell calcium oscillation parameters encodes stomatal movements. Nature **28**: 1053-1057

Allen GJ, Kwak JM, Chu SP, Llopis J, Tsien RY, Harper JF, Schroeder JI (1999) Cameleon calcium indicator reports cytoplasmic calcium dynamics in Arabidopsis guard cells. Plant J **19**: 735-747

Basu D, Haswell ES (2020) The mechanosensitive ion channel MSL10 potentiates responses to cell swelling in Arabidopsis seedlings. Curr Biol **30**: 2716-2728

Baughman JM, Perocchi F, Girgis HS, Plovanich M, Belcher-Timme CA, Sancak Y, Bao XR, Strittmatter L, Goldberger O, Bogorad RL, Koteliansky V, Mootha VK (2011) Integrative genomics identifies MCU as an essential component of the mitochondrial calcium uniporter. Nature **476**: 341-345

Behera S, Zhaolong X, Luoni L, Bonza MC, Doccula FG, De Michelis MI, Morris RJ, Schwarzländer M, Costa A (2018) Cellular Ca^{2+} signals generate defined pH signatures in plants. Plant Cell **30**: 2704-2719

Beyhl D, Hortensteiner S, Martinoia E, Farmer EE, Fromm J, Marten I, Hedrich R (2009) The *fou2* mutation in the major vacuolar cation channel TPC1 confers tolerance to inhibitory luminal calcium. Plant J **58**: 715-723

Bjornson M, Pimprikar P, Nürnberger , Zipfel C (2021) The transcriptional landscape of Arabidopsis thaliana pattern-triggered immunity. Nat Plants https://doi.org/10.1038/s41477-021-00874-5

Blume B, Nürnberger T, Nass N, Scheel D (2000) Receptor-mediated increase in cytoplasmic free calcium required for activation of pathogen defense in parsley. Plant Cell **12**: 1425-1440

Bonza MC, De Michelis MI (2011) The plant Ca^{2+}-ATPase repertoire: Biochemical features and physiological functions. Plant Biol (Stuttg) **13**: 421-430

Bonza MC, Loro G, Behera S, Wong A, Kudla J, Costa A (2013) Analyses of Ca^{2+} accumulation and dynamics in the endoplasmic reticulum of Arabidopsis root cells using a genetically encoded Cameleon sensor. Plant Physiol **163**: 1230-1241

Boursiac Y, Lee SM, Romanowsky S, Blank R, Sladek C, Chung WS, Harper JF (2010) Disruption of the vacuolar calcium-ATPases in Arabidopsis results in the activation of a salicylic acid-dependent programmed cell death pathway. Plant Physiol **154**: 1158-1171

Boudsocq M, Willmann MR, McCormack M, Lee H, Shan L, He P, Bush J, Cheng SH, Sheen J (2010) Differential innate immune signalling via Ca^{2+} sensor protein kinases. Nature **464**: 418-422

Bourque S, Lemoine R, Sequeira-Legrand A, Fayolle L, Delrot S, Pugin A (2002) The elicitor cryptogein blocks glucose transport in tobacco cells. Plant Physiol **130**: 2177-87

Brewbaker JL, Kwack BH (1963) The essential role of calcium ion in pollen germination and pollen tube growth. American J Bot **50**: 859-865

Brost C, Studtrucker T, Reimann R, Denninger P, Czekalla J, Krebs M, Fabry B, Schumacher K, Grossmann G, Dietrich P (2019) Multiple cyclic nucleotide-gated channels coordinate calcium oscillations and polar growth of root hairs. Plant J **99**: 910-923

Candeo A, Doccula FG, Valentini G, Bassi A, Costa A (2017) Light sheet fluorescence microscopy quantifies calcium oscillations in root hairs of Arabidopsis thaliana. Plant Cell Physiol **58**: 1161-1172

Charpentier M, Oldroyd GE (2013) Nuclear calcium signaling in plants. Plant Physiol **163**: 496-503

Charpentier M, Sun J, Vaz Martins T, Radhakrishnan GV, Findlay K, Soumpourou E, Thouin J, Vèry AA, Sanders D, Morris RJ, Oldroyd GE (2016) Nuclear-localized cyclic nucleotide-gated channels mediate symbiotic calcium oscillations. Science **352**: 1102-1105

Charpentier M (2018) Calcium signals in the plant nucleus: Origin and function. J Exp Bot **69**: 4165-4173

Chen J, Gutjahr C, Bleckmann A, Dresselhaus T (2015) Calcium signaling during reproduction and biotrophic fungal interactions in plants. Mol Plant **8**: 595-611

Chen K, Gao J, Sun S, Zhang Z, Yu B, Li J, Xie C, Li G, Wang P, Song C-P, Bressan RA, Hua

J, Zhu J-K, Zhao Y (2020) BONZAI proteins control global osmotic stress responses in plants. Current Biol **30**: 4815-4825

Cheng Y, Zhang X, Sun T, Tian Q, Zhang WH (2018) Glutamate receptor Homolog 3.4 is involved in regulation of seed germination under salt stress in Arabidopsis. Plant Cell Physiol **59**: 978-988

Capoen W, Sun J, Wysham D, Otegui MS, Venkateshwaran M, Hirsch S, Miwa H, Downie JA, Morris RJ, Ané JM, Oldroyd GE (2011) Nuclear membranes control symbiotic calcium signaling of legumes. Proc Natl Acad Sci USA **108**: 14348-14353

Chen ZH, Hills A, Bätz U, Amtmann A, Lew VL, Blatt MR (2012) Systems dynamic modeling of the stomatal guard cell predicts emergent behaviors in transport, signaling, and volume control. Plant Physiol **159**: 1235-1251

Choi J, Tanaka K, Cao Y, Qi Y, Qiu J, Liang Y, Lee SY, Stacey G (2014a) Identification of a plant receptor for extracellular ATP. Science **343**: 290-294

Choi WG, Toyota M, Kim SH, Hilleary R, Gilroy S (2014b) Salt stress-induced Ca^{2+} waves are associated with rapid, long-distance root-to-shoot signaling in plants. Proc Natl Acad Sci USA **111**: 6497-6502

Colaço R, Moreno N, Feijó JA (2012) "On the fast lane": mitochondria structure, dynamics and function in growing pollen tubes. J of Micros **247**: 106-118

Corso M, Doccula FG, de Melo JRF, Costa A, Verbruggen N (2018) Endoplasmic reticulum-localized CCX2 is required for osmotolerance by regulating ER and cytosolic Ca^{2+} dynamics in Arabidopsis. Proc Natl Acad Sci USA **115**: 3966-3971

Costa A, Drago I, Behera S, Zottini M, Pizzo P, Schroeder JI, Pozzan T, Lo Schiavo F (2010) H_2O_2 in plant peroxisomes: an in vivo analysis uncovers a Ca^{2+}-dependent scavenging system. Plant J **62**: 760-772

Costa A, Luoni L, Marrano CA, Hashimoto K, Köster P, Giacometti S, De Michelis MI, Kudla J, Bonza MC (2017) Ca^{2+}-dependent phosphoregulation of the plasma membrane Ca^{2+}-ATPase ACA8 modulates stimulus-induced calcium signatures. J Exp Bot **68**: 3215-3230

Costa A, Navazio L, Szabo I (2018) The contribution of organelles to plant intracellular Calcium signalling. J Exp Bot **69**: 4175-4193

Cubero-Font P, De Angeli A (2021) Connecting vacuolar and plasma membrane transport networks. New Phytol **229**: 755-762

De Stefani D, Raffaello A, Teardo E, Szabo I, Rizzuto R (2011) A forty-kilodalton protein of the inner membrane is the mitochondrial calcium uniporter. Nature **476**: 336-340

DeFalco TA, Bender KW, Snedden WA (2009) Breaking the code: Ca^{2+} sensors in plant signalling. Biochem J **425**: 27-40

Demes E, Besse L, Cubero-Font P, Satiat-Jeunemaitre B, Thomine S, De Angeli A (2020) Dynamic measurement of cytosolic pH and $[NO_3^-]$ uncovers the role of the vacuolar transporter AtCLCa in cytosolic pH homeostasis. Proc Natl Acad Sci USA **117**: 15343-15353

Demidchik V, Shabala S, Isayenkov S, Cuin TA, Pottosin I (2018) Calcium transport across plant membranes: mechanisms and functions. New Phytol **220**: 49-69

Diao M, Qu X, Huang S (2018) Calcium imaging in Arabidopsis pollen cells using G-CaMP5. J Integr Plant Biol **60**: 897-906

Dietrich D (2018) Hydrotropism: how roots search for water. J Exp Bot **69**: 2759-2771

Dindas J, Dreyer I, Huang S, Hedrich R, Roelfsema MRG (2021) A voltage-dependent Ca^{2+}-homeostat operates in the plant vacuolar membrane. New Phytol doi: 10.1111/nph.17272.

Dodd AN, Kudla J, Sanders D (2010) The language of calcium signaling. Annu Rev Plant Biol **61**: 593-620

Dubiella U, Seybold H, Durian G, Komander E, Lassig R, Witte CP, Schulze WX, Romeis T (2013) Calcium-dependent protein kinase/NADPH oxidase activation circuit is required for rapid defense signal propagation. Proc Natl Acad Sci USA **110**: 8744-8749

Edel KH, Marchadier E, Brownlee C, Kudla J, Hetherington AM (2017) The evolution of Calcium-based signalling in plants. Curr Biol **27**: R667-R679

Emonet A, Zhou F, Vacheron J, Heiman CM, Dénervaud Tendon V, Ma KW, Schulze-Lefert P, Keel C, Geldner N (2021) Spatially restricted immune responses are required for maintaining root meristematic activity upon detection of bacteria. Curr Biol **31**:1012-1028

Feijó JA, Sainhas J, Holdaway-Clarke T, Cordeiro MS, Kunkel JG, Hepler PK (2001) Cellular oscillations and the regulation of growth: the pollen tube paradigm. Bioessays **23**: 86-94

Feijó JA, Costa SS, Prado AM, Becker JD, Certal AC (2004) Signalling by tips. Curr Opin Plant Biol **7**: 589-598.

Flütsch S, Nigro A, Conci F, Fajkus J, Thalmann M, Trtílek M, Panzarová K, Santelia D (2020a) Glucose uptake to guard cells via STP transporters provides carbon sources for stomatal opening and plant growth. EMBO Rep **5**; 21(8):e49719

Flütsch S, Wang Y, Takemiya A, Vialet-Chabrand SRM, Klejchová M, Nigro A, Hills A, Lawson T, Blatt MR, Santelia D (2020b) Guard cell starch degradation yields glucose for rapid stomatal opening in Arabidopsis. Plant Cell **32**: 2325-2344

Foskett JK, White C, Cheung KH, Mak DO (2007) Inositol trisphosphate receptor Ca^{2+} release channels. Physiol Rev **87**: 593-658

Frank J, Happeck R, Meier B, Hoang MTT, Stribny J, Hause G, Ding H, Morsomme P, Baginsky S, Peiter E (2019) Chloroplast-localized BICAT proteins shape stromal calcium signals and are required for efficient photosynthesis. New Phytol **221**: 866-880

Frietsch S, Wang YF, Sladek C, Poulsen LR, Romanowsky SM, Schroeder JI, Harper JF (2007) A cyclic nucleotide-gated channel is essential for polarized tip growth of pollen. Proc Natl Acad Sci USA **104**: 14531-14536

Fromm H (2019) Root plasticity in the pursuit of water. Plants (Basel) **8**: 236

Geisler M, Frangne N, Gomès E, Martinoia E, Palmgren MG (2000) The ACA4 gene of Arabidopsis encodes a vacuolar membrane calcium pump that improves salt tolerance in yeast. Plant Physiol **124**:1814-27

Gao D, Knight MR, Trewavas AJ, Sattelmacher B, Plieth C (2004) Self-reporting Arabidopsis expressing pH and [Ca^{2+}] indicators unveil ion dynamics in the cytoplasm and in the apoplast under abiotic stress. Plant Physiol **134**: 898-908

Gao QF, Gu LL, Wang HQ, Fei CF, Fang X, Hussain J, Sun SJ, Dong JY, Liu H, Wang YF (2016) Cyclic nucleotide-gated channel 18 is an essential Ca^{2+} channel in pollen tube tips for pollen tube guidance to ovules in Arabidopsis. Proc Natl Acad Sci USA **113**: 3096-3101

Gao X, Chen X, Lin W, Chen S, Lu D, Niu Y, Li L, Cheng C, McCormack M, Sheen J, Shan L, He P (2013) Bifurcation of Arabidopsis NLR immune signaling via Ca^{2+}-dependent protein kinases. PLoS Pathog **9**: e1003127

Garcia-Mata C, Gay R, Sokolovski S, Hills A, Lamattina L, Blatt MR (2003) Nitric oxide regulates K^+ and Cl^- channels in guard cells through a subset of abscisic acid-evoked signaling pathways. Proc Natl Acad Sci USA **100**: 11116–11121

Gong M, van der Luit AH, Knight R, Trewavas AJ (1998) Heat-shock-induced changes in intracellular Ca^{2+} level in tobacco seedlings in relation to thermotolerance. Plant Physiol **116**: 429-437

Grabov A, Blatt MR (1998) Membrane voltage initiates Ca^{2+} waves and potentiates Ca^{2+} increases with abscisic acid in stomatal guard cells. Proc Natl Acad Sci USA **95**: 4778-4783

Grabov A, Blatt MR (1999) A steep dependence of inward-rectifying potassium channels on cytosolic free calcium concentration increase evoked by hyperpolarization in guard cells. Plant Physiol **119**: 277-288

Gradogna A, Scholz-Starke J, Gutla PV, Carpaneto A (2009) Fluorescence combined with excised patch: measuring calcium currents in plant cation channels. Plant J **58**: 175-182

Granqvist E, Wysham D, Hazledine S, Kozlowski W, Sun J, Charpentier M, Martins TV, Haleux P, Tsaneva-Atanasova K, Downie JA, Oldroyd GE, Morris RJ (2012) Buffering capacity explains signal variation in symbiotic calcium oscillations. Plant Physiol **160**: 2300-2310

Hamel LP, Sheen J, Séguin A (2014) Ancient signals: comparative genomics of green plant

CDPKs. Trends Plant Sci **19**: 79-89

Hamilton DWA, Hills A, Kohler B, Blatt MR (2000) Ca^{2+} channels at the plasma membrane of stomatal guard cells are activated by hyperpolarization and abscisic acid. Proc Natl Acad Sci USA **97**: 4967-4972

Han S, Tang R, Anderson LK, Woerner TE, Pei ZM (2003) A cell surface receptor mediates extracellular Ca^{2+} sensing in guard cells. Nature **425**: 196-200

He J, Rössner N, Hoang MTT, Alejandro S, Peiter E (2021) Transport, functions, and interaction of calcium and manganese in plant organellar compartments. Plant Physiol doi.org/10.1093/plphys/kiab122

Hedrich R, Mueller TD, Becker D, Marten I (2018) Structure and function of TPC1 Vacuole SV channel gains shape. Mol Plant **11**: 764-775

Hedrich R, Neher E (1987) Cytoplasmic calcium regulates voltage-dependent ion channels in plant vacuoles. Nature **329**: 833-836

Hill AE, Shachar-Hill B, Skepper JN, Powell J, Shachar-Hill Y (2012) An osmotic model of the growing pollen tube. PLoS One **7**: e36585

Hills A, Chen ZH, Amtmann A, Blatt MR, Lew VL (2012) OnGuard, a computational platform for quantitative kinetic modeling of guard cell physiology. Plant Physiol **159**: 1026-1042

Hilleary R, Paez-Valencia J, Vens C, Toyota M, Palmgren M, Gilroy S (2020) Tonoplast-localized Ca^{2+} pumps regulate Ca^{2+} signals during pattern-triggered immunity in *Arabidopsis thaliana*. Proc Natl Acad Sci USA **117**: 18849-18857

Holdaway-Clarke TL, Feijo JA, Hackett GR, Kunkel JG, Hepler PK (1997) Pollen tube growth and the intracellular cytosolic Calcium gradient oscillate in phase while extracellular Calcium influx is delayed. Plant Cell **9**: 1999-2010

Horikawa K, Yamada Y, Matsuda T, Kobayashi K, Hashimoto M, Matsu-ura T, Miyawaki A, Michikawa T, Mikoshiba K, Nagai T (2010) Spontaneous network activity visualized by ultrasensitive Ca^{2+} indicators, yellow Cameleon-Nano. Nat Methods **7**: 729-732

Hruz T, Laule O, Szabo G, Wessendorp F, Bleuler S, Oertle L, Widmayer P, Gruissem W, Zimmermann P (2008) Genevestigator v3: a reference expression database for the meta-analysis of transcriptomes. Adv Bioinformatics 2008:420747

Huang F, Luo J, Ning T, Cao W, Jin X, Zhao H, Wang Y, Han S (2017) Cytosolic and nucleosolic Calcium signaling in response to osmotic and salt stresses are independent of each other in roots of Arabidopsis seedlings. Front Plant Sci **8**: 1648

Huang S, Waadt R, Nuhkat M, Kollist H, Hedrich R, Roelfsema MRG (2019) Calcium signals in guard cells enhance the efficiency by which abscisic acid triggers stomatal closure. New Phytol. **224**: 177-187

Iwano M, Entani T, Shiba H, Kakita M, Nagai T, Mizuno H, Miyawaki A, Shoji T, Kubo K, Isogai A, Takayama S (2009) Fine-tuning of the cytoplasmic Ca^{2+} concentration is essential for pollen tube growth. Plant Physiol **150**: 1322-1334

Ishka MR, Brown E, Rosenberg A, Romanowsky S, Davis J, Choi W-G, Harper JF (2021) Arabidopsis Ca^{2+}-ATPases 1, 2, and 7 in the endoplasmic reticulum contribute to growth and pollen fitness. Plant Physiol doi.org/10.1093/plphys/kiab021

Islam MM, Munemasa S, Hossain MA, Nakamura Y, Mori IC, Murata Y (2010) Roles of AtTPC1, vacuolar two pore channel 1, in Arabidopsis stomatal closure. Plant Cell Physiol **51**: 302-311

Jaślan D, Dreyer I, Lu J, O'Malley R, Dindas J, Marten I, Hedrich R (2019) Voltage-dependent gating of SV channel TPC1 confers vacuole excitability. Nat Commun **10**: 2659

Jezek M, Blatt MR (2017) The membrane transport system of the guard cell and its integration for stomatal dynamics. Plant Physiol **174**: 487-519

Jezek M, Silva-Alvim FAL, Hills A, Donald N, Ishka MR, Shadbolt J, He B, Lawson T, Harper JF, Wang Y, Lew VL, Blatt MR (2021) Guard cell Ca^{2+}-ATPases underpin a 'carbon memory' of photosynthetic assimilation. that impacts on water use efficiency. Nat Plants in press.

Jiang Z, Zhou X, Tao M, Yuan F, Liu L, Wu F, Wu X, Xiang Y, Niu Y, Liu F, Li C, Ye R, Byeon B, Xue Y, Zhao H, Wang HN, Crawford BM, Johnson DM, Hu C, Pei C, Zhou W, Swift GB, Zhang H, Vo-Dinh T, Hu Z, Siedow JN, Pei ZM (2019) Plant cell-surface GIPC sphingolipids sense salt to trigger Ca^{2+} influx. Nature **572**: 341-346

Kelner A, Leitao N, Chabaud M, Charpentier M, de Carvalho-Niebel F (2018) Dual color sensors for simultaneous analysis of Calcium signal dynamics in the nuclear and cytoplasmic compartments of plant cells. Front Plant Sci **9**: 245

Kiegle E, Moore CA, Haseloff J, Tester MA, Knight MR (2000) Cell-type-specific calcium responses to drought, salt and cold in the Arabidopsis root. Plant J **23**: 267-278

Kim S, Zeng W, Bernard S, Liao J, Venkateshwaran M, Ane JM, Jiang Y (2019) Ca^{2+}-regulated Ca^{2+} channels with an RCK gating ring control plant symbiotic associations. Nat Commun **10**: 3703

Kim TH, Böhmer M, Hu H, Nishimura N, Schroeder JI (2010) Guard cell signal transduction network: advances in understanding abscisic acid, CO_2, and Ca^{2+} signaling. Annu Rev Plant Biol. **61**: 561-591

Klepikova AV, Kasianov AS, Gerasimov ES, Logacheva MD, Penin AA (2016) A high resolution map of the Arabidopsis thaliana developmental transcriptome based on RNA-seq profiling. Plant J. Dec **88**: 1058-1070

Knight MR, Campbell AK, Smith SM, Trewavas AJ (1991) Transgenic plant aequorin reports the effects of touch and cold-shock and elicitors on cytoplasmic calcium. Nature **352**: 524-526

Knight H, Trewavas AJ, Knight MR (1996) Cold calcium signaling in Arabidopsis involves two cellular pools and a change in calcium signature after acclimation. Plant Cell **8**: 489-503

Knight H, Trewavas AJ, Knight MR (1997) Calcium signaling in *Arabidopsis thaliana* responding to drought and salinity. Plant J **12:** 1067-1078

Knight H, Knight MR (2001) Abiotic stress signalling pathways: specificity and cross-talk. Trends Plant Sci **6**: 262-267

Kudla J, Batistic O, Hashimoto K (2010) Calcium signals: the lead currency of plant information processing. Plant Cell **22**: 541-563

Kudla J, Becker D, Grill E, Hedrich R, Hippler M, Kummer U, Parniske M, Romeis T,

Schumacher K (2018) Advances and current challenges in calcium signaling. New Phytol **218**: 414-431

Kwaaitaal M, Huisman R, Maintz J, Reinstädler A, Panstruga R (2011) Ionotropic glutamate receptor (iGluR)-like channels mediate MAMP-induced calcium influx in *Arabidopsis thaliana*. Biochem J **440**: 355-365

Kwak JM, Mori IC, Pei ZM, Leonhardt N, Torres MA, Dangl JL, Bloom RE, Bodde S, Jones JDG, Schroeder JI (2003) NADPH oxidase AtrbohD and AtrbohF genes function in ROS-dependent ABA signaling in Arabidopsis. EMBO J **22**: 2623–2633

Krebs M, Held K, Binder A, Hashimoto K, Den Herder G, Parniske M, Kudla J, Schumacher K (2012) FRET-based genetically encoded sensors allow high-resolution live cell imaging of Ca^{2+} dynamics. Plant J **69**: 181-192

Laanemets K, Brandt B, Li J, Merilo E, Wang YF, Keshwani MM, Taylor SS, Kollist H, Schroeder JI (2013) Calcium-dependent and -independent stomatal signaling network and compensatory feedback control of stomatal opening via Ca^{2+} sensitivity priming. Plant Physiol **163**: 504-513

Leckie CP, McAinsh MR, Allen GJ, Sanders D, Hetherington AM (1998) Abscisic acid-induced stomatal closure mediated by cyclic ADP-ribose. Proc Natl Acad Sci USA **95**: 15837-15842

Lecourieux D, Lamotte O, Bourque S, Wendehenne D, Mazars C, Ranjeva R, Pugin A (2005) Proteinaceous and oligosaccharidic elicitors induce different calcium signatures in the nucleus of tobacco cells. Cell Calcium **38**: 527-538

Leitão N, Dangeville P, Carter R, Charpentier M (2019) Nuclear calcium signatures are associated with root development. Nat Commun **10**: 4865

Lemtiri-Chlieh F, MacRobbie EAC, Webb AAR, Manison NF, Brownlee C, Skepper JN, Chen J, Prestwich GD, Brearley CA (2003) Inositol hexakisphosphate mobilizes an endomembrane store of calcium in guard cells. Proc Natl Acad Sci USA **100**: 10091-10095

Lenglet A, Jaslan D, Toyota M, Mueller M, Muller T, Schonknecht G, Marten I, Gilroy S, Hedrich

R, Farmer EE (2017) Control of basal jasmonate signalling and defence through modulation of intracellular cation flux capacity. New Phytol **216**: 1161-1169

Lenzoni G, Liu J, Knight MR (2018) Predicting plant immunity gene expression by identifying the decoding mechanism of calcium signatures. New Phytol **217**: 1598-1609

Lenzoni G, Knight MR (2019) Increases in absolute temperature stimulate free Calcium concentration elevations in the chloroplast. Plant Cell Physiol **60**: 538-548

Liu KH, Diener A, Lin Z, Liu C, Sheen J (2020) Primary nitrate responses mediated by calcium signalling and diverse protein phosphorylation. J Exp Bot **71**: 4428-4441

Logan DC, Knight MR (2003) Mitochondrial and cytosolic calcium dynamics are differentially regulated in plants. Plant Physiol **133**: 21-24

Lopez-Hernandez F, Tryfona T, Rizza A, Yu XL, Harris MOB, Webb AAR, Kotake T, Dupree P (2020) Calcium binding by arabinogalactan polysaccharides is important for normal plant development. Plant Cell **32**: 3346-3369

Loro G, Drago I, Pozzan T, Schiavo FL, Zottini M, Costa A (2012) Targeting of Cameleons to various subcellular compartments reveals a strict cytoplasmic/mitochondrial Ca^{2+} handling relationship in plant cells. Plant J **71**: 1-13

Loro G, Wagner S, Doccula FG, Behera S, Weinl S, Kudla J, Schwarzlander M, Costa A, Zottini M (2016) Chloroplast-specific in vivo Ca^{2+} imaging using Yellow Cameleon fluorescent protein sensors reveals organelle-autonomous Ca^{2+} signatures in the stroma. Plant Physiol **171**: 2317-2330

Luo J, Chen L, Huang F, Gao P, Zhao H, Wang Y, Han S (2020) Intraorganellar calcium imaging in Arabidopsis seedling roots using the GCaMP variants GCaMP6m and R-CEPIA1er. J Plant Physiol **246-247**:153127

Ma Y, Zhao Y, Berkowitz GA (2017) Intracellular Ca^{2+} is important for flagellin-triggered defense in Arabidopsis and involves inositol polyphosphate signaling. J Exp Bot **68**: 3617-3628

Manzoor H, Chiltz A, Madani S, Vatsa P, Schoefs B, Pugin A, Garcia-Brugger A (2012) Calcium signatures and signaling in cytosol and organelles of tobacco cells induced by plant defense elicitors.

Cell Calcium **51**: 434-444

Martí Ruiz MC, Jung HJ, Webb AAR (2020) Circadian gating of dark-induced increases in chloroplast- and cytosolic-free calcium in Arabidopsis. New Phytol **225**: 1993-2005

McAinsh MR, Pittman JK (2009) Shaping the calcium signature. New Phytol **181**: 275-294

McAinsh MR, Webb A, Taylor JE, Hetherington AM (1995) Stimulus-induced oscillations in guard cell cytosolic free Calcium. Plant Cell **7**: 1207-1219

McCormack E, Tsai YC, Braam J (2005) Handling calcium signaling: Arabidopsis CaMs and CMLs. Trends Plant Sci **10**: 383-389

MacRobbie EAC (1992) Calcium and ABA-induced stomatal closure. Phil Trans R Soc Lond B3385-18

Meyerhoff O, Müller K, Roelfsema MR, Latz A, Lacombe B, Hedrich R, Dietrich P, Becker D (2005) AtGLR3.4, a glutamate receptor channel-like gene is sensitive to touch and cold. Planta **222**: 418-427

Michard E, Lima PT, Borges F, Silva AC, Portes MT, Carvalho JE, Gilliham M, Liu L-H, Obermeyer G, Feijó JA (2011) Glutamate receptor-like genes form Ca^{2+} channels in pollen tubes and are regulated by pistil D-serine. Science **332**: 434-437

Michard E, Simon AA, Tavares B, Wudick MM, Feijó JA (2017) Signaling with ions: The keystone for apical cell growth and morphogenesis in pollen tubes. Plant Physiol **173**: 91-111

Mills RF, Doherty ML, López-Marqués RL, Weimar T, Dupree P, Palmgren MG, Pittman JK, Williams LE (2008) ECA3, a Golgi-localized P_{2A}-type ATPase, plays a crucial role in manganese nutrition in Arabidopsis. Plant Physiol **146**: 116-128

Minguet-Parramona C, Wang Y, Hills A, Vialet-Chabrand S, Griffiths H, Rogers S, Lawson T, Lew VL, Blatt MR (2016) An optimal frequency in Ca^{2+} oscillations for stomatal closure is an emergent property of ion transport in guard cells. Plant Physiol **170**: 33-42

Miyawaki A, Llopis J, Heim R, McCaffery JM, Adams JA, Ikura M, Tsien RY (1997) Fluorescent indicators for Ca^{2+} based on green fluorescent proteins and calmodulin. Nature **388**: 882-887

Monshausen GB, Bibikova TN, Messerli MA, Shi C, Gilroy S (2007) Oscillations in extracellular pH and reactive oxygen species modulate tip growth of Arabidopsis root hairs. Proc Natl Acad Sci USA **104**: 20996-21001

Monshausen GB, Messerli MA, Gilroy S (2008) Imaging of the Yellow Cameleon 3.6 indicator reveals that elevations in cytosolic Ca^{2+} follow oscillating increases in growth in root hairs of Arabidopsis. Plant Physiol. **147**: 1690-1698

Muir SR, Sanders D (1996) Pharmacology of Ca^{2+} release from red beet microsomes suggests the presence of ryanodine receptor homologs in higher plants. FEBS Lett **395**: 39-42

Murata Y, Pei ZM, Mori IC, Schroeder J (2001) Abscisic acid activation of plasma membrane Ca^{2+} channels in guard cells requires cytosolic NAD(P)H and is differentially disrupted upstream and downstream of reactive oxygen species production in *abi1-1* and *abi2-1* protein phosphatase 2C mutants. Plant Cell **13**: 2513-2523

Nomura H, Komori T, Kobori M, Nakahira Y, Shiina T (2008) Evidence for chloroplast control of external Ca^{2+}-induced cytosolic Ca^{2+} transients and stomatal closure. Plant J **53**: 988-998

Nomura H, Komori T, Uemura S, Kanda Y, Shimotani K, Nakai K, Furuichi T, Takebayashi K, Sugimoto T, Sano S, Suwastika IN, Fukusaki E, Yoshioka H, Nakahira Y, Shiina T (2012) Chloroplast-mediated activation of plant immune signalling in Arabidopsis. Nat Commun **26**;3:926

Nomura H, Shiina T (2014) Calcium signaling in plant endosymbiotic organelles: mechanism and role in physiology. Mol Plant **7**: 1094-1104

Oldroyd GE, Downie JA (2006) Nuclear calcium changes at the core of symbiosis signalling. Curr Opin Plant Biol **9**: 351-357

Ordenes VR, Moreno I, Maturana D, Norambuena L, Trewavas AJ, Orellana A (2012) In vivo analysis of the calcium signature in the plant Golgi apparatus reveals unique dynamics. Cell Calcium **52**: 397-404

Pan Y, Chai X, Gao Q, Zhou L, Zhang S, Li L, Luan S (2019) Dynamic interactions of plant CNGC subunits and calmodulins drive oscillatory Ca^{2+} channel activities. Dev Cell **48**: 710-725

Pandey S, Zhang W, Assmann SM (2007) Roles of ion channels and transporters in guard cell signal transduction. FEBS Lett **581**: 2325-2336

Pei ZM, Murata Y, Benning G, Thomine S, Klüsener B, Allen GJ, Grill E, Schroeder JI (2000) Calcium channels activated by hydrogen peroxide mediate abscisic acid signalling in guard cells. Nature **406**: 731–734

Peiter E, Maathuis FJ, Mills LN, Knight H, Pelloux J, Hetherington AM, Sanders D (2005) The vacuolar Ca^{2+}-activated channel TPC1 regulates germination and stomatal movement. Nature **434**: 404-408

Peleg Z. Blumwald E (2011) Hormone balance and abiotic stress tolerance in crop plants. Curr Opin Plant Biol **14**: 290-295

Pierson ES, Miller DD, Callaham DA, van Aken J, Hackett G, Hepler PK (1996) Tip-localized calcium entry fluctuates during pollen tube growth. Dev Biol **174**: 160-173

Poovaiah BW, Du L (2018) Calcium signaling: decoding mechanism of calcium signatures. New Phytol **217**: 1394-1396

Qudeimat E, Faltusz AM, Wheeler G, Lang D, Holtorf H, Brownlee C, Reski R, Frank W (2008) A PIIB-type Ca^{2+}-ATPase is essential for stress adaptation in *Physcomitrella patens*. Proc Natl Acad Sci USA **105**:19555-19560

Ranf S, Wunnenberg P, Lee J, Becker D, Dunkel M, Hedrich R, Scheel D, Dietrich P (2008) Loss of the vacuolar cation channel, AtTPC1, does not impair Ca^{2+} signals induced by abiotic and biotic stresses. Plant J **53**: 287-299

Reddy AS, Ali GS, Celesnik H, Day IS (2011) Coping with stresses: roles of calcium- and calcium/calmodulin-regulated gene expression. Plant Cell **23**: 2010-2032

Sai J, Johnson CH (2002) Dark-stimulated calcium ion fluxes in the chloroplast stroma and cytosol. Plant Cell **14**:1279-1291

Saijo Y, Tintor N, Lu X, Rauf P, Pajerowska-Mukhtar K, Häweker H, Dong X, Robatzek S, Schulze-Lefert P (2009) Receptor quality control in the endoplasmic reticulum for plant innate immunity. EMBO J **28**: 3439-3449

Sanders D, Pelloux J, Brownlee C, Harper JF (2002) Calcium at the crossroads of signaling. Plant Cell **14**: S401–S417

Schiefelbein J, Galway M, Masucci J, Ford S (1993) Pollen tube and root-hair tip growth is disrupted in a mutant of *Arabidopsis thaliana*. Plant Physiol **103**: 979-985

Schiøtt M, Romanowsky SM, Baekgaard L, Jakobsen MK, Palmgren MG, Harper JF (2004) A plant plasma membrane Ca^{2+} pump is required for normal pollen tube growth and fertilization. Proc Natl Acad Sci USA **101**: 9502-9507

Schoenaers S, Balcerowicz D, Vissenberg K (2017) Molecular mechanisms regulating root hair tip growth: A comparison with pollen tubes. In: Obermeyer G., Feijó J. (eds) Pollen Tip Growth. Springer, Cham doi.org/10.1007/978-3-319-56645-0_9

Schumacher K, Vafeados D, McCarthy M, Sze H, Wilkins T, Chory J (1999) The Arabidopsis *det3* mutant reveals a central role for the vacuolar H^{+}-ATPase in plant growth and development. Genes Dev **15**: 3259-3270

Selles B, Michaud C, Xiong TC, Leblanc O, Ingouff M (2018) Arabidopsis pollen tube germination and growth depend on the mitochondrial calcium uniporter complex. New Phytol **219**: 58-65

Sello S, Perotto J, Carraretto L, Szabo I, Vothknecht UC, Navazio L (2016) Dissecting stimulus-specific Ca^{2+} signals in amyloplasts and chloroplasts of *Arabidopsis thaliana* cell suspension cultures. J Exp Bot **67**: 3965-3974

Sello S, Moscatiello R, Mehlmer N, Leonardelli M, Carraretto L, Cortese E, Zanella FG, Baldan B, Szabo I, Vothknecht UC, Navazio L (2018) Chloroplast Ca^{2+} fluxes into and across thylakoids revealed by thylakoid-targeted aequorin probes. Plant Physiol **177**: 38-51

Shkolnik D, Nuriel R, Bonza MC, Costa A, Fromm H (2018) MIZ1 regulates ECA1 to generate a slow, long-distance phloem-transmitted Ca^{2+} signal essential for root water tracking in Arabidopsis.

Proc Natl Acad Sci USA **115**: 8031-8036

Singh A, Kanwar P, Yadav AK, Mishra M, Jha SK, Baranwal V, Pandey A, Kapoor S, Tyagi AK, Pandey GK (2014) Genome-wide expressional and functional analysis of calcium transport elements during abiotic stress and development in rice. FEBS J **281**: 894-915

Stael S, Wurzinger B, Mair A, Mehlmer N, Vothknecht UC, Teige M (2012) Plant organellar calcium signalling: an emerging field. J Exp Bot **63**: 1525-1542

Steinhorst L, Mähs A, Ischebeck T, Zhang C, Zhang X, Arendt S, Schültke S, Heilmann I, Kudla J (2015) Vacuolar CBL-CIPK12 Ca^{2+}-sensor-kinase complexes are required for polarized pollen tube growth. Curr Biol **25**: 1475-1482

Stephan AB, Kunz HH, Yang E, Schroeder JI (2016) Rapid hyperosmotic-induced Ca^{2+} responses in Arabidopsis thaliana exhibit sensory potentiation and involvement of plastidial KEA transporters. Proc Natl Acad Sci USA **113**: E5242-5249

Taiz L, Zeiger E, Møller IM, Murphy A (2014) Plant Physiology and Development. Sixth Edition. ISBN: 9781605352558

Tang RJ, Zhao FG, Yang Y, Wang C, Li K, Kleist TJ, Lemaux PG, Luan S (2020) A calcium signalling network activates vacuolar K^+ remobilization to enable plant adaptation to low-K environments. Nat Plants **6**: 384-393

Taylor CW, Tovey SC (2010) IP(3) receptors: toward understanding their activation. Cold Spring Harb Perspect Biol **2**: a004010

Teardo E, Formentin E, Segalla A, Giacometti GM, Marin O, Zanetti M, Lo Schiavo F, Zoratti M, Szabo I (2011) Dual localization of plant glutamate receptor AtGLR3.4 to plastids and plasma membrane. Biochim Biophys Acta **1807**: 359-367

Teardo E, Carraretto L, De Bortoli S, Costa A, Behera S, Wagner R, Lo Schiavo F, Formentin E, Szabo I (2015) Alternative splicing-mediated targeting of the Arabidopsis GLUTAMATE RECEPTOR3.5 to mitochondria affects organelle morphology. Plant Physiol **167**: 216-227

Teardo E, Carraretto L, Wagner S, Formentin E, Behera S, De Bortoli S, Larosa V, Fuchs P, Lo

Schiavo F, Raffaello A, Rizzuto R, Costa A, Schwarzlander M, Szabo I (2017) Physiological characterization of a plant mitochondrial Calcium uniporter in vitro and in vivo. Plant Physiol **173**: 1355-1370

Teardo E, Carraretto L, Moscatiello R, Cortese E, Vicario M, Festa M, Maso L, De Bortoli S, Calì T, Vothknecht UC, Formentin E, Cendron L, Navazio L, Szabo I (2019) A chloroplast-localized mitochondrial calcium uniporter transduces osmotic stress in Arabidopsis. Nat Plants **5**: 581-588

Thor K, Jiang S, Michard E, George J, Scherzer S, Huang S, Dindas J, Derbyshire P, Leitão N, DeFalco TA, Köster P, Hunter K, Kimura S, Gronnier J, Stransfeld L, Kadota Y, Bücherl CA, Charpentier M, Wrzaczek M, MacLean D, Oldroyd GED, Menke FLH, Roelfsema MRG, Hedrich R, Feijó J, Zipfel C (2020) The calcium-permeable channel OSCA1.3 regulates plant stomatal immunity. Nature **585**: 569-573

Tian D, Wang J, Zeng X, Gu K, Qiu C, Yang X, Zhou Z, Goh M, Luo Y, Murata-Hori M, White FF, Yin Z (2014) The rice TAL effector-dependent resistance protein XA10 triggers cell death and calcium depletion in the endoplasmic reticulum. Plant Cell **26**: 497-515

Tian W, Hou C, Ren Z, Wang C, Zhao F, Dahlbeck D, Hu S, Zhang L, Niu Q, Li L, Staskawicz BJ, Luan S (2019) A calmodulin-gated calcium channel links pathogen patterns to plant immunity. Nature **572**:131-135

Tian W, Wang C, Gao Q, Li L, Luan S (2020) Calcium spikes, waves and oscillations in plant development and biotic interactions. Nat Plants **6**: 750-759

Tracy FE, Gilliham M, Dodd AN, Webb AA, Tester M (2008) NaCl-induced changes in cytosolic free Ca^{2+} in Arabidopsis thaliana are heterogeneous and modified by external ionic composition. Plant Cell Environ **31**: 1063-1073.

Trewavas AJ (1999) Le calcium, c'est la vie: Calcium makes waves. Plant Physiol **120**: 1-6

Trewavas AJ, Malhó R (1998) Ca^{2+} signalling in plant cells: the big network! Curr Opin Plant Biol **1**: 428-433

Véry AA, Davies JM (2000) Hyperpolarization-activated calcium channels at the tip of Arabidopsis root hairs. Proc Natl Acad Sci USA **97**: 9801-9806

van Der Luit AH, Olivari C, Haley A, Knight MR, Trewavas AJ (1999) Distinct calcium signaling pathways regulate calmodulin gene expression in tobacco. Plant Physiol **121**: 705-714

Vanderauwera S, Vandenbroucke K, Inzé A, van de Cotte B, Mühlenbock P, De Rycke R, Naouar N, Van Gaever T, Van Montagu MC, Van Breusegem F (2012) AtWRKY15 perturbation abolishes the mitochondrial stress response that steers osmotic stress tolerance in Arabidopsis. Proc Natl Acad Sci USA **109**: 20113-20118

Vincill ED, Bieck AM, Spalding EP (2012) Ca^{2+} conduction by an amino acid-gated ion channel related to glutamate receptors. Plant Physiol **59**: 40-46

Wagner S, Behera S, De Bortoli S, Logan DC, Fuchs P, Carraretto L, Teardo E, Cendron L, Nietzel T, Fussl M, Doccula FG, Navazio L, Fricker MD, Van Aken O, Finkemeier I, Meyer AJ, Szabo I, Costa A, Schwarzlander M (2015) The EF-Hand Ca^{2+} binding protein MICU choreographs mitochondrial Ca^{2+} dynamics in Arabidopsis. Plant Cell **27**: 3190-3212

Wagner S, Steinbeck J, Fuchs P, Lichtenauer S, Elsässer M, Schippers JHM, Nietzel T, Ruberti C, Van Aken O, Meyer AJ, Van Dongen JT, Schmidt RR, Schwarzländer M (2019) Multiparametric real-time sensing of cytosolic physiology links hypoxia responses to mitochondrial electron transport. New Phytol **224**: 1668-1684

Wang Y, Zhu Y, Ling Y, Zhang H, Liu P, Baluska F, Samaj J, Lin J, Wang Q (2010) Disruption of actin filaments induces mitochondrial Ca^{2+} release to the cytoplasm and $[Ca^{2+}]_c$ changes in Arabidopsis root hairs. BMC Plant Biol **10**: 53

Wang Y, Hills A, Blatt MR (2014) Systems analysis of guard cell membrane transport for enhanced stomatal dynamics and water use efficiency. Plant Physiol **164**: 1593-1599

Ward JM, Schroeder JI (1994) Calcium-activated K^+ channels and calcium-induced calcium release by slow vacuolar ion channels in guard cell vacuoles implicated in the control of stomatal closure. Plant Cell **6:** 669-683

Weinl S, Held K, Schlücking K, Steinhorst L, Kuhlgert S, Hippler M, Kudla J (2008) A plastid protein crucial for Ca^{2+}-regulated stomatal responses. New Phytol **179**: 675–686

Whalley HJ, Knight MR (2013) Calcium signatures are decoded by plants to give specific gene responses. New Phytol **197**: 690-693

Wymer CL, Bibikova TN, Gilroy S (1997) Cytoplasmic free calcium distributions during the development of root hairs of Arabidopsis thaliana. Plant J **12**: 427-439

Winship LJ, Rounds C, Hepler PK (2017) Perturbation analysis of Calcium, alkalinity and secretion during growth of lily pollen tubes. Plants (Basel); **6**(1): 3

Winter D, Vinegar B, Nahal H, Ammar R, Wilson GV, Provart NJ (2007) An "Electronic Fluorescent Pictograph" browser for exploring and analyzing large-scale biological data sets. PLoS One **2**: e718

Wu Y, Kuzma J, Maréchal E, Graeff R, Lee HC, Foster R, Chua NH (1997) Abscisic acid signaling through cyclic ADP-ribose in plants. Science **278**: 2126-2130

Wudick MM, Michard E, Oliveira Nunes C, Feijó JA (2018) Comparing plant and animal glutamate receptors: Common traits but different fates? J Exp Bot **69**: 4151-4163

Xiong L, Zhu JK (2002) Molecular and genetic aspects of plant responses to osmotic stress. Plant Cell Environ **25**: 131-139

Xiong TC, Jauneau A, Ranjeva R, Mazars C (2004) Isolated plant nuclei as mechanical and thermal sensors involved in calcium signalling. Plant J **40**: 12-21

Yadav AK, Shankar A, Jha SK, Kanwar P, Pandey A, Pandey GK (2015) A rice tonoplastic calcium exchanger, OsCCX2 mediates Ca^{2+}/cation transport in yeast. Sci Rep **26**;5:17117

Yang Y, Guo Y (2018) Elucidating the molecular mechanisms mediating plant salt-stress responses. New Phytol **217**: 523-539

Yuan F, Yang H, Xue Y, Kong D, Ye R, Li C, Zhang J, Theprungsirikul L, Shrift T, Krichilsky B, Johnson DM, Swift GB, He Y, Siedow JN, Pei ZM (2014) OSCA1 mediates osmotic-stress-evoked

Ca^{2+} increases vital for osmosensing in Arabidopsis. Nature **514**: 367-371

Yuan P, Jauregui E, Du L, Tanaka K, Poovaiah BW (2017) Calcium signatures and signaling events orchestrate plant–microbe interactions. Curr Opin Plant Biol **38**: 173–183

Zipfel C, Kunze G, Chinchilla D, Caniard A, Jones JD, Boller T, Felix G (2006) Perception of the bacterial PAMP EF-Tu by the receptor EFR restricts Agrobacterium-mediated transformation. Cell **125**: 749-760

Zipfel C, Oldroyd GE (2017) Plant signalling in symbiosis and immunity. Nature **543:** 328–336

Zhang J, Liu J, Chena Z, Lina J (2007) *In vitro* germination and growth of lily pollen tubes is affected by calcium inhibitor with reference to calcium distribution. Flora **202**: 581-588

Zhang J, Coaker G, Zhou JM, Dong X (2020) Plant immune mechanisms: From reductionistic to holistic points of view. Mol Plant **13**: 1358-1378

Zhao Y, Araki S, Wu J, Teramoto T, Chang YF, Nakano M, Abdelfattah AS, Fujiwara M, Ishihara T, Nagai T, Campbell RE (2011) An expanded palette of genetically encoded Ca^{2+} indicators. Science **333**: 1888-1891

Zheng Y, Liao C, Zhao S, Wang C, Guo Y (2017) The glycosyltransferase QUA1 regulates chloroplast-associated Calcium signaling during salt and drought stress in Arabidopsis. Plant Cell Physiol **58**: 329-341

Zhu JK (2002) Salt and drought stress signal transduction in plants. Annu Rev Plant Biol **53**: 247-273

Zhu JK (2016) Abiotic stress signaling and responses in plants. Cell **167**: 313-324

Zhu X, Caplan J, Mamillapalli P, Czymmek K, Dinesh-Kumar SP (2010) Function of endoplasmic reticulum calcium ATPase in innate immunity-mediated programmed cell death. EMBO J **29**: 1007-1018

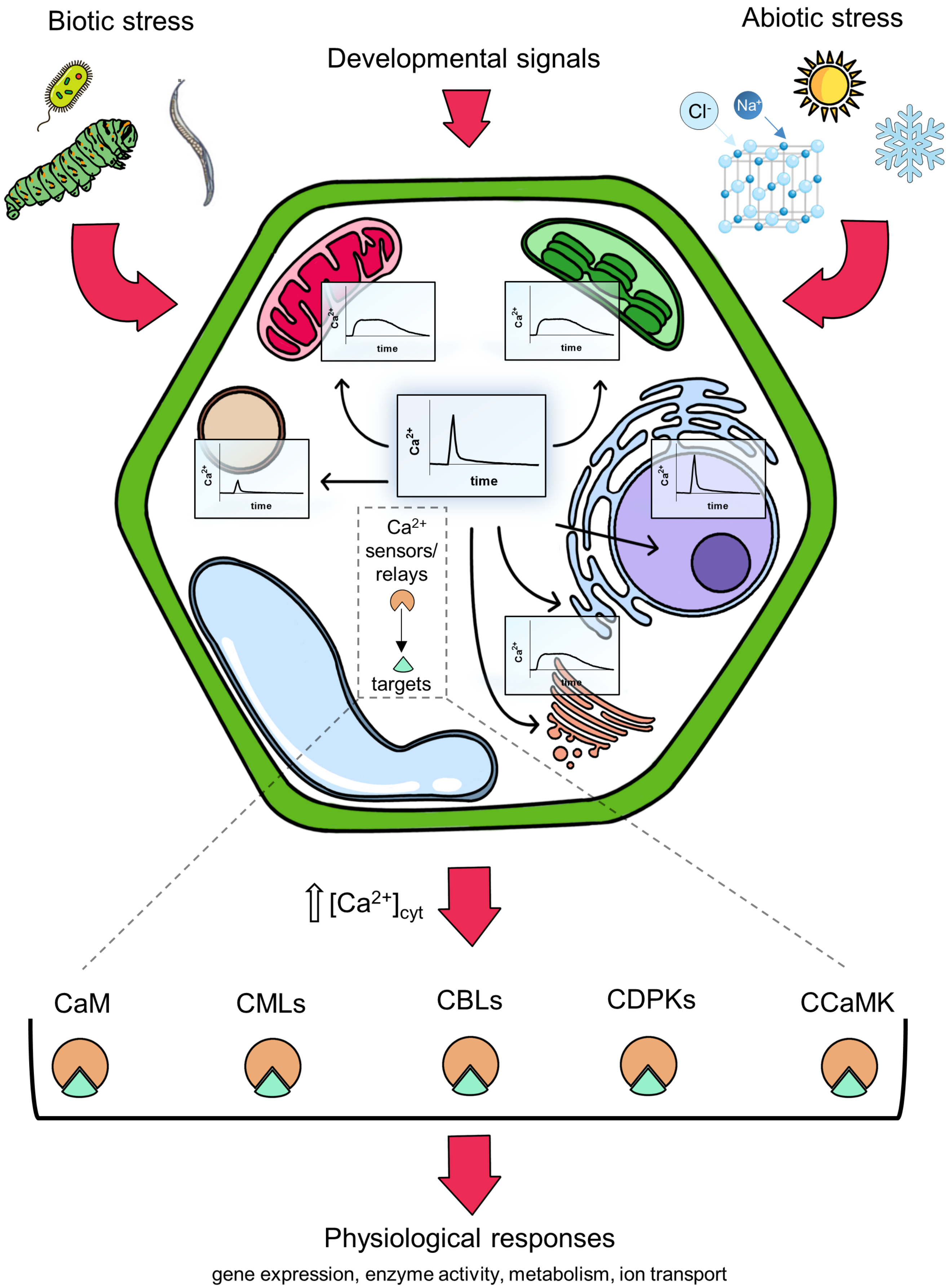


Figure 1. Biotic and abiotic stress as well as developmental stimuli can trigger cytosolic and organellar $[Ca^{2+}]$ increases. Cytosolic Ca^{2+} transients are decoded by different Ca^{2+} sensors and relays such as Calmodulin (CaM), Calmodulin-like proteins (CMLs), calcineurin β-like proteins (CBLs), Ca^{2+}-dependent protein kinases (CDPKs), and calmodulin-dependent protein kinase (CCaMK) that trigger precise and tailored responses altering gene expression and metabolism.

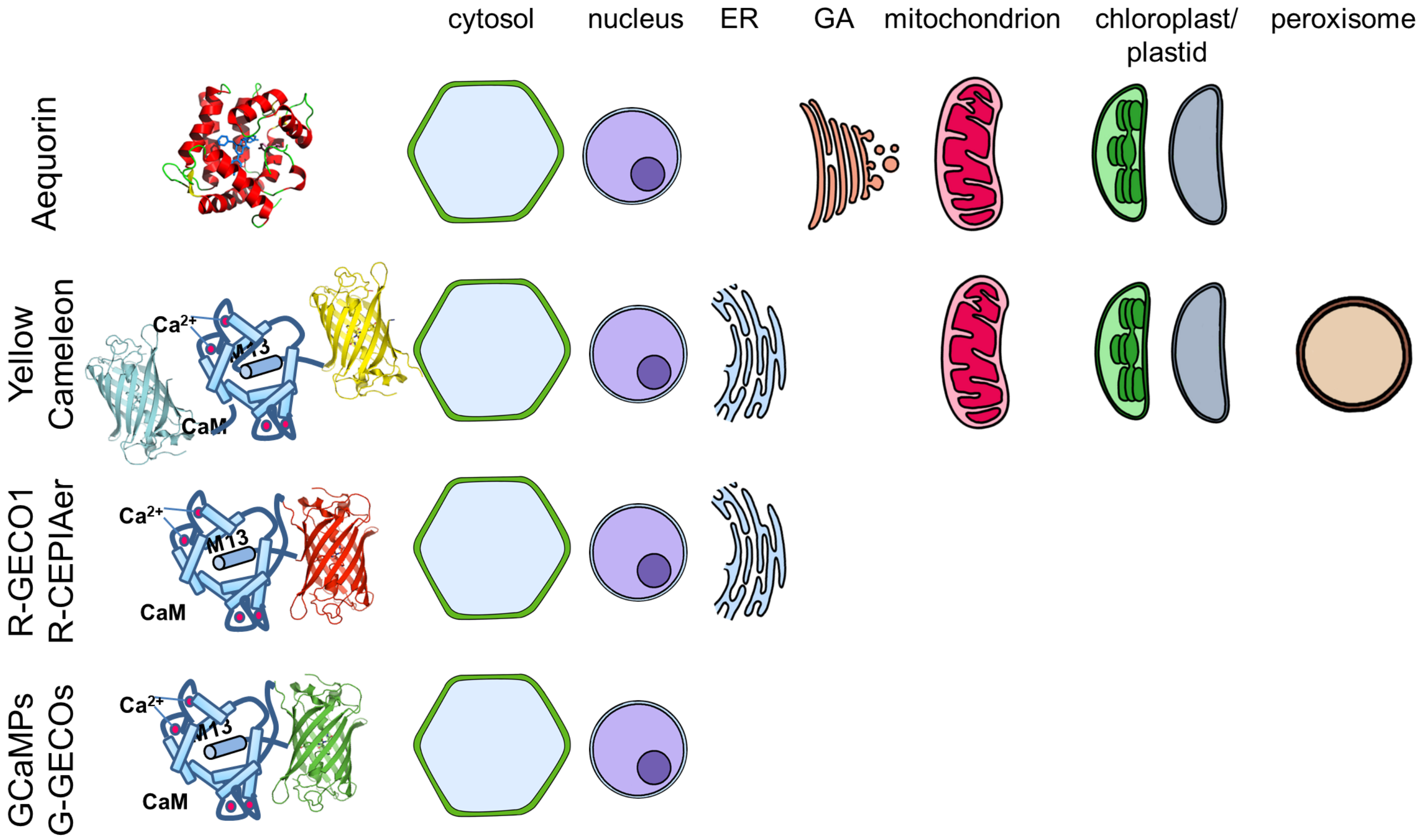


Figure 2. Overview of organelle-targeted genetically encoded Ca^{2+} indicators. ER = endoplasmic reticulum, GA = Golgi Apparatus.

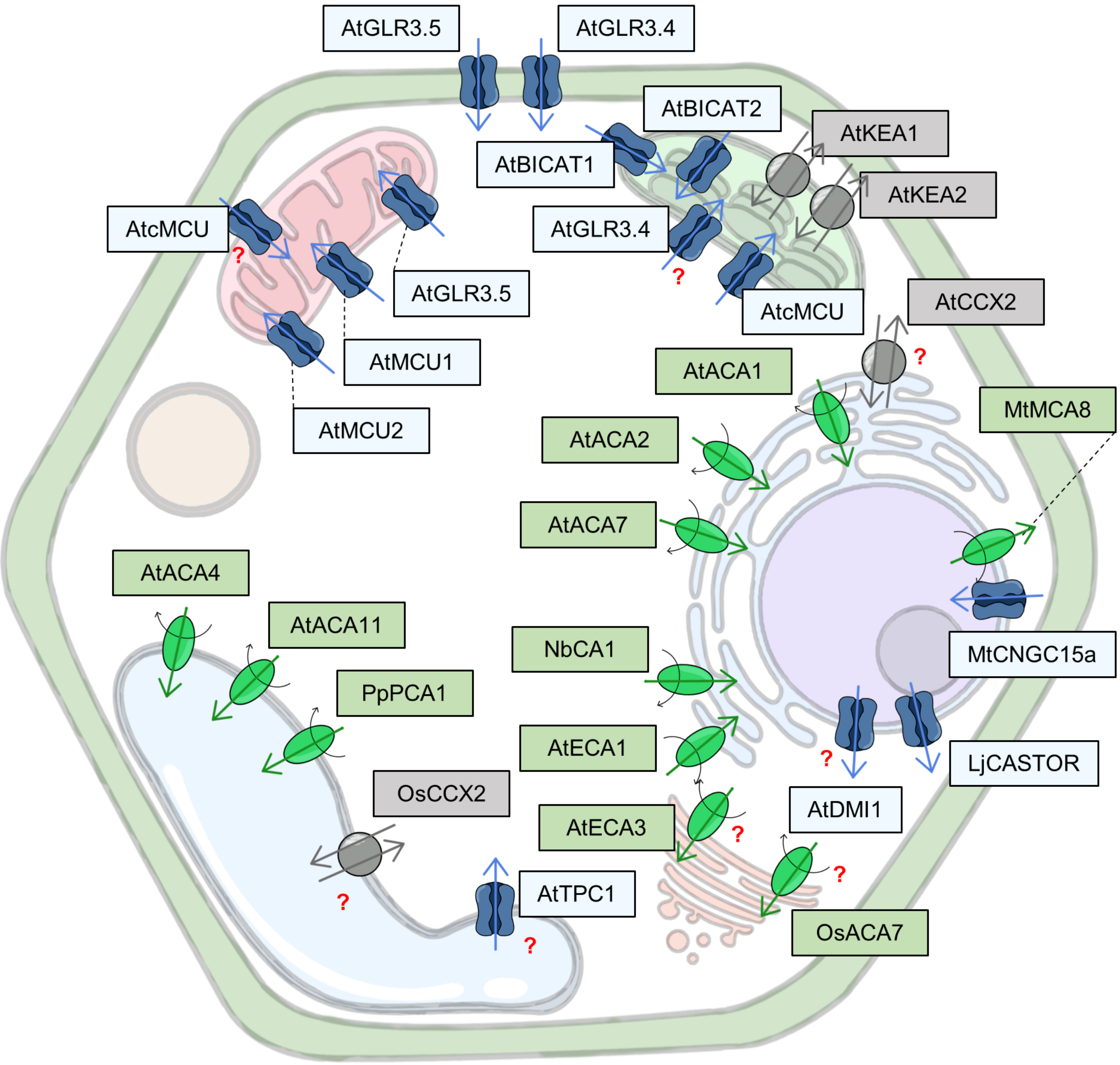


Figure 3. Channels and transporters in subcellular compartments showing a role in plant developmental processes and stress responses linked to the regulation of Ca^{2+} transport across membranes. The red question marks indicate that further studies are required. Channels are represented in blue, pumps in green and co-transporters in grey. At: *Arabidopsis thaliana;* Lj: *Lotus japonicus;* Mt: *Medicago truncatula;* Nb*: Nicotiana benthamiana;* Pp*: Physcomitrium patens;* Os*: Oryza sativa.*

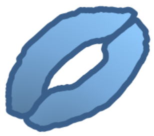
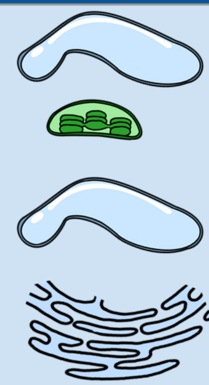
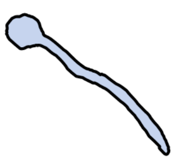
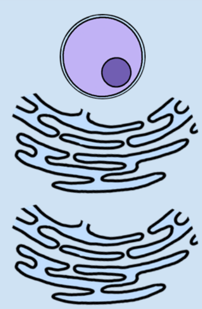
Tissue or cell types	Type of stimulus	Protein name	Compartment involved	References
	Drought stress, CO_2	AtTPC1 AtcMCU AtACA4 AtACA11 AtACA1 AtACA2 AtACA7		Peitier et al., 2005 Islam et al., 2010 Teardo et al., 2019 Jezek et al., 2021 Jezek et al., 2021
	Plant-pathogen interaction; wounding, high light	AtACA4 AtACA11 NbCA1 AtACA1 AtACA2 AtACA7 AtTPC1		Hilleary et al., 2020 Zhu et al., 2010 Ishka et al., 2021 Kiep et al., 2015; Vincent et al., 2017
	Pollen germination and development	AtECAs AtACA1 AtACA2 AtACA7		Iwano et al., 2009 Ishka et al., 2021
	Root hairs growth	???		Wang et al., 2010
	Salt and osmotic stress, hydrotropism; root meristem development	AtDMI1 AtECA1 AtCCX2		Leitao et al. 2019 Shkolnik et al. 2018 Corso et al. 2018

Figure 4. Summary of the Ca^{2+} transport mechanisms localised in the subcellular compartments of plant cells involved in the regulation of cytosolic Ca^{2+} dynamics for which a physiological response in different plant tissues/cell types was demonstrated.

ADVANCES

- Genetically encoded sensors allow the *in vivo* analysis of Ca^{2+} dynamics in different subcellular compartments.
- Clear *in vivo* evidence demonstrates that subcellular compartments accumulate and release Ca^{2+} ions.
- The alteration of Ca^{2+} transport in the subcellular compartments alters cytosolic Ca^{2+} signatures with downstream effects on gene regulation and sensitivity to stress.
- Direct and indirect evidence supports the role of the endoplasmic reticulum as both a sink and source of Ca^{2+}.
- Indirect evidence supports the role of the vacuole as both a sink and source of Ca^{2+}.

OUTSTANDING QUESTIONS

- How are the Ca^{2+} transport systems of different subcellular compartments regulated?
- Does mitochondrial Ca^{2+} transport impinge on cytosolic dynamics in the responses to stress or in developmental processes?
- What is the role of AtcMCU in mitochondria?
- What is the role of Golgi apparatus in Ca^{2+} signaling?
- What is the role of AtECA3 and OsACA7 in the Golgi apparatus?
- Which are the organellar Ca^{2+} transport systems involved in the regulation of stomatal movements?
- Can the design of new genetic screenings help to identify additional Ca^{2+} transporters of subcellular compartments?

BOX 1. Genetically encoded Ca^{2+} indicators

Genetically Encoded Calcium Indicators (GECI) allow a non-invasive monitoring of free Ca^{2+} concentrations ($[Ca^{2+}]$) in different subcellular compartments. In plants, the two mainly used GECIs have been aequorin and Cameleon.

Aequorin enables monitoring of Ca^{2+} dynamics by photon emission measurements in transformed plants after reconstitution of the aequorin holoenzyme with the exogenously applied prosthetic group coelenterazine (Knight et al., 1991). Due to its low quantum yield, aequorin suffers from poor spatial resolution. Aequorin has been targeted to the cytosol, nucleus, endoplasmic reticulum (ER), the Golgi apparatus, mitochondria, chloroplasts, and apoplast (reviewed in Costa et al., 2018). To improve the spatial resolution the use of fluorescent Ca^{2+} sensors was exploited. The ratiometric Ca^{2+} reporter Cameleon was the first fluorescent GECI expressed in plant cells (Allen et al., 1999). Cameleon exploits the Förster Resonance Energy Transfer (FRET) property occurring between one fluorescent protein that acts as a donor (e.g. CFP) that, when excited, transfers absorbed energy to a second fluorescent protein, the acceptor (e.g. YFP or cpVenus). The efficiency of FRET depends on the donor-acceptor distance which is dependent upon the CaM-M13 Ca^{2+}-dependent interaction. The CaM-M13 sensor is sandwiched between the two fluorophores (Miyawaki et al., 1997). With Cameleon, the readout is the ratio between acceptor and donor fluorescence emissions which reduces artefacts due to the expression level of the sensor or focus changes. Cameleon has been targeted to the cytosol, nucleus, ER, mitochondria, chloroplasts, and peroxisomes (Costa et al., 2018).

Intensiometric GFP-based Ca^{2+} sensors have also been developed and successfully used in plants. We can cite GCaMP3, GCaMP6, and the green and red variants of GECO1 or CEPIA (Zhao et al., 2011; Costa et al., 2018; Kelner et al., 2018; Luo et al., 2020). All these GECIs rely on a change in the sensor quantum yield, measured as a change of the intensity of the emitted fluorescence which depends upon the amount of Ca^{2+} bound to the sensory domain. A change of $[Ca^{2+}]$ affects the CaM conformation which is transmitted to a circularly permuted variant of green (e.g. cpGFP) or red (e.g. cpmApple) fluorescent proteins. Intensiometric biosensors exhibit a higher signal change compared to a FRET-based sensor, but a change of their expression level could be misinterpreted as a change in free Ca^{2+} concentration (Costa et al., 2018). GCaMPs, R-GECO1 and R-CEPIA have been targeted to the cytosol, nucleus, and ER (Kelner et al., 2018; Luo et al., 2020).

BOX 2. Ca^{2+} transport systems in plants

Even though plants do not possess canonical Ca^{2+} channels, they are equipped with Ca^{2+}-permeable channels that establish a hydrophilic path for Ca^{2+} diffusion down its electrochemical gradient. Different Ca^{2+}-permeable channel families are localized at the plasma membrane (PM), facilitating Ca^{2+} influx from the apoplast, but can be also resident at the inner membranes, such as those surrounding the endoplasmic reticulum (ER), Golgi apparatus, mitochondria, chloroplasts, vacuole and possibly peroxisomes.

Ca^{2+}-extruding systems actively remove Ca^{2+} from the cytosol either by transporting it out of the cell across the PM or into internal organelles. These transporters include Ca^{2+} pumps and Ca^{2+}/cation antiporters (CaCAs).

Ca^{2+}-ATPases are the major active transport system that ensures the compartmentalization of Ca^{2+}. They are members of the P-type ATPases superfamily that use the energy of ATP hydrolysis to pump Ca^{2+} from the cytoplasm to the apoplast or into intracellular compartments. Plant cells possess two types of Ca^{2+}-pumping ATPase, belonging to subgroups PIIA-type (ER-type Ca^{2+}-ATPase) and PIIB-type (Auto-Inhibited Ca^{2+}-ATPase) that have been found at the tonoplast, PM, ER, Golgi, nucleus and perhaps also at the plastid envelope. While the autoinhibitory regulative mechanism of PIIB-type members has been extensively studied and characterized, very little is known about the regulation of those belonging to PIIA-type subfamily in plants.

The CaCA superfamily comprises cation/Ca^{2+} exchangers (CCX) and Ca^{2+}/proton exchangers (CAX) that derive the energy needed to mediate active Ca^{2+} transport from the electrochemical gradient of protons across membranes facing the cytosol.

While Ca^{2+} pumps are high affinity and low capacity systems, exchangers are characterized by low-affinity but high-capacity Ca^{2+} sequestration. The coordinated action of both extrusion mechanisms covers a wide range of physiological cytosolic Ca^{2+} concentrations.

A detailed analysis of different Ca^{2+} transport mechanisms across plant membranes has been extensively reviewed in Demidchik et al. (2018).

Parsed Citations

Alexandre J, Lassalles JP, Kado RT (1990) Opening of Ca2+ channels in isolated red beet root vacuole membrane by inositol 1,4,5-trisphosphate. Nature 343: 567-570
Google Scholar: Author Only Title Only Author and Title

Allen GJ, Chu SP, Schumacher K, Shimazaki CT, Vafeados D, Kemper A, Hawke SD, Tallman G, Tsien RY, Harper JF, Chory J, Schroeder JI (2000) Alteration of stimulus-specific guard cell calcium oscillations and stomatal closing in Arabidopsis det3 mutant. Science 289: 2338-2342
Google Scholar: Author Only Title Only Author and Title

Allen GJ, Chu SP, Harrington CL, Schumacher K, Hoffmann T, Tang YY, Grill E, Schroeder JI (2001) A defined range of guard cell calcium oscillation parameters encodes stomatal movements. Nature 28: 1053-1057
Google Scholar: Author Only Title Only Author and Title

Allen GJ, Kwak JM, Chu SP, Llopis J, Tsien RY, Harper JF, Schroeder JI (1999) Cameleon calcium indicator reports cytoplasmic calcium dynamics in Arabidopsis guard cells. Plant J 19: 735-747
Google Scholar: Author Only Title Only Author and Title

Basu D, Haswell ES (2020) The mechanosensitive ion channel MSL10 potentiates responses to cell swelling in Arabidopsis seedlings. Curr Biol 30: 2716-2728
Google Scholar: Author Only Title Only Author and Title

Baughman JM, Perocchi F, Girgis HS, Plovanich M, Belcher-Timme CA, Sancak Y, Bao XR, Strittmatter L, Goldberger O, Bogorad RL, Koteliansky V, Mootha VK (2011) Integrative genomics identifies MCU as an essential component of the mitochondrial calcium uniporter. Nature 476: 341-345
Google Scholar: Author Only Title Only Author and Title

Behera S, Zhaolong X, Luoni L, Bonza MC, Doccula FG, De Michelis MI, Morris RJ, Schwarzländer M, Costa A (2018) Cellular Ca2+ signals generate defined pH signatures in plants. Plant Cell 30: 2704-2719
Google Scholar: Author Only Title Only Author and Title

Beyhl D, Hortensteiner S, Martinoia E, Farmer EE, Fromm J, Marten I, Hedrich R (2009) The fou2 mutation in the major vacuolar cation channel TPC1 confers tolerance to inhibitory luminal calcium. Plant J 58: 715-723
Google Scholar: Author Only Title Only Author and Title

Bjornson M, Pimprikar P, Nürnberger , Zipfel C (2021) The transcriptional landscape of Arabidopsis thaliana pattern-triggered immunity. Nat Plants https://doi.org/10.1038/s41477-021-00874-5
Google Scholar: Author Only Title Only Author and Title

Blume B, Nürnberger T, Nass N, Scheel D (2000) Receptor-mediated increase in cytoplasmic free calcium required for activation of pathogen defense in parsley. Plant Cell 12: 1425-1440
Google Scholar: Author Only Title Only Author and Title

Bonza MC, De Michelis MI (2011) The plant Ca2+-ATPase repertoire: Biochemical features and physiological functions. Plant Biol (Stuttg) 13: 421-430
Google Scholar: Author Only Title Only Author and Title

Bonza MC, Loro G, Behera S, Wong A, Kudla J, Costa A (2013) Analyses of Ca2+ accumulation and dynamics in the endoplasmic reticulum of Arabidopsis root cells using a genetically encoded Cameleon sensor. Plant Physiol 163: 1230-1241
Google Scholar: Author Only Title Only Author and Title

Boursiac Y, Lee SM, Romanowsky S, Blank R, Sladek C, Chung WS, Harper JF (2010) Disruption of the vacuolar calcium-ATPases in Arabidopsis results in the activation of a salicylic acid-dependent programmed cell death pathway. Plant Physiol 154: 1158-1171
Google Scholar: Author Only Title Only Author and Title

Boudsocq M, Willmann MR, McCormack M, Lee H, Shan L, He P, Bush J, Cheng SH, Sheen J (2010) Differential innate immune signalling via Ca2+ sensor protein kinases. Nature 464: 418-422
Google Scholar: Author Only Title Only Author and Title

Bourque S, Lemoine R, Sequeira-Legrand A, Fayolle L, Delrot S, Pugin A (2002) The elicitor cryptogein blocks glucose transport in tobacco cells. Plant Physiol 130: 2177-87
Google Scholar: Author Only Title Only Author and Title

Brewbaker JL, Kwack BH (1963) The essential role of calcium ion in pollen germination and pollen tube growth. American J Bot 50: 859-865
Google Scholar: Author Only Title Only Author and Title

Brost C, Studtrucker T, Reimann R, Denninger P, Czekalla J, Krebs M, Fabry B, Schumacher K, Grossmann G, Dietrich P (2019) Multiple cyclic nucleotide-gated channels coordinate calcium oscillations and polar growth of root hairs. Plant J 99: 910-923
Google Scholar: Author Only Title Only Author and Title

Candeo A, Doccula FG, Valentini G, Bassi A, Costa A (2017) Light sheet fluorescence microscopy quantifies calcium oscillations in root

hairs of Arabidopsis thaliana. Plant Cell Physiol 58: 1161-1172
Google Scholar: Author Only Title Only Author and Title

Charpentier M, Oldroyd GE (2013) Nuclear calcium signaling in plants. Plant Physiol 163: 496-503
Google Scholar: Author Only Title Only Author and Title

Charpentier M, Sun J, Vaz Martins T, Radhakrishnan GV, Findlay K, Soumpourou E, Thouin J, Very AA, Sanders D, Morris RJ, Oldroyd GE (2016) Nuclear-localized cyclic nucleotide-gated channels mediate symbiotic calcium oscillations. Science 352: 1102-1105
Google Scholar: Author Only Title Only Author and Title

Charpentier M (2018) Calcium signals in the plant nucleus: Origin and function. J Exp Bot 69: 4165-4173
Google Scholar: Author Only Title Only Author and Title

Chen J, Gutjahr C, Bleckmann A, Dresselhaus T (2015) Calcium signaling during reproduction and biotrophic fungal interactions in plants. Mol Plant 8: 595-611
Google Scholar: Author Only Title Only Author and Title

Chen K, Gao J, Sun S, Zhang Z, Yu B, Li J, Xie C, Li G, Wang P, Song C-P, Bressan RA, Hua J, Zhu J-K, Zhao Y (2020) BONZAI proteins control global osmotic stress responses in plants. Current Biol 30: 4815-4825
Google Scholar: Author Only Title Only Author and Title

Cheng Y, Zhang X, Sun T, Tian Q, Zhang WH (2018) Glutamate receptor Homolog 3.4 is involved in regulation of seed germination under salt stress in Arabidopsis. Plant Cell Physiol 59: 978-988
Google Scholar: Author Only Title Only Author and Title

Capoen W, Sun J, Wysham D, Otegui MS, Venkateshwaran M, Hirsch S, Miwa H, Downie JA, Morris RJ, Ané JM, Oldroyd GE (2011) Nuclear membranes control symbiotic calcium signaling of legumes. Proc Natl Acad Sci USA 108: 14348-14353
Google Scholar: Author Only Title Only Author and Title

Chen ZH, Hills A, Bätz U, Amtmann A, Lew VL, Blatt MR (2012) Systems dynamic modeling of the stomatal guard cell predicts emergent behaviors in transport, signaling, and volume control. Plant Physiol 159: 1235-1251
Google Scholar: Author Only Title Only Author and Title

Choi J, Tanaka K, Cao Y, Qi Y, Qiu J, Liang Y, Lee SY, Stacey G (2014a) Identification of a plant receptor for extracellular ATP. Science 343: 290-294
Google Scholar: Author Only Title Only Author and Title

Choi WG, Toyota M, Kim SH, Hilleary R, Gilroy S (2014b) Salt stress-induced Ca2+ waves are associated with rapid, long-distance root-to-shoot signaling in plants. Proc Natl Acad Sci USA 111: 6497-6502
Google Scholar: Author Only Title Only Author and Title

Colaço R, Moreno N, Feijó JA (2012) "On the fast lane": mitochondria structure, dynamics and function in growing pollen tubes. J of Micros 247: 106-118
Google Scholar: Author Only Title Only Author and Title

Corso M, Doccula FG, de Melo JRF, Costa A, Verbruggen N (2018) Endoplasmic reticulum-localized CCX2 is required for osmotolerance by regulating ER and cytosolic Ca2+ dynamics in Arabidopsis. Proc Natl Acad Sci USA 115: 3966-3971
Google Scholar: Author Only Title Only Author and Title

Costa A, Drago I, Behera S, Zottini M, Pizzo P, Schroeder JI, Pozzan T, Lo Schiavo F (2010) H2O2 in plant peroxisomes: an in vivo analysis uncovers a Ca2+-dependent scavenging system. Plant J 62: 760-772
Google Scholar: Author Only Title Only Author and Title

Costa A, Luoni L, Marrano CA, Hashimoto K, Köster P, Giacometti S, De Michelis MI, Kudla J, Bonza MC (2017) Ca2+-dependent phosphoregulation of the plasma membrane Ca2+-ATPase ACA8 modulates stimulus-induced calcium signatures. J Exp Bot 68: 3215-3230
Google Scholar: Author Only Title Only Author and Title

Costa A, Navazio L, Szabo I (2018) The contribution of organelles to plant intracellular Calcium signalling. J Exp Bot 69: 4175-4193
Google Scholar: Author Only Title Only Author and Title

Cubero-Font P, De Angeli A (2021) Connecting vacuolar and plasma membrane transport networks. New Phytol 229: 755-762
Google Scholar: Author Only Title Only Author and Title

De Stefani D, Raffaello A, Teardo E, Szabo I, Rizzuto R (2011) A forty-kilodalton protein of the inner membrane is the mitochondrial calcium uniporter. Nature 476: 336-340
Google Scholar: Author Only Title Only Author and Title

DeFalco TA, Bender KW, Snedden WA (2009) Breaking the code: Ca2+ sensors in plant signalling. Biochem J 425: 27-40
Google Scholar: Author Only Title Only Author and Title

Demes E, Besse L, Cubero-Font P, Satiat-Jeunemaitre B, Thomine S, De Angeli A (2020) Dynamic measurement of cytosolic pH and [NO3-] uncovers the role of the vacuolar transporter AtCLCa in cytosolic pH homeostasis. Proc Natl Acad Sci USA 117: 15343-15353
Google Scholar: Author Only Title Only Author and Title

Demidchik V, Shabala S, Isayenkov S, Cuin TA, Pottosin I (2018) Calcium transport across plant membranes: mechanisms and functions. New Phytol 220: 49-69
Google Scholar: Author Only Title Only Author and Title

Diao M, Qu X, Huang S (2018) Calcium imaging in Arabidopsis pollen cells using G-CaMP5. J Integr Plant Biol 60: 897-906
Google Scholar: Author Only Title Only Author and Title

Dietrich D (2018) Hydrotropism: how roots search for water. J Exp Bot 69: 2759-2771
Google Scholar: Author Only Title Only Author and Title

Dindas J, Dreyer I, Huang S, Hedrich R, Roelfsema MRG (2021) A voltage-dependent Ca2+-homeostat operates in the plant vacuolar membrane. New Phytol doi: 10.1111/nph.17272.
Google Scholar: Author Only Title Only Author and Title

Dodd AN, Kudla J, Sanders D (2010) The language of calcium signaling. Annu Rev Plant Biol 61: 593-620
Google Scholar: Author Only Title Only Author and Title

Dubiella U, Seybold H, Durian G, Komander E, Lassig R, Witte CP, Schulze WX, Romeis T (2013) Calcium-dependent protein kinase/NADPH oxidase activation circuit is required for rapid defense signal propagation. Proc Natl Acad Sci USA 110: 8744-8749
Google Scholar: Author Only Title Only Author and Title

Edel KH, Marchadier E, Brownlee C, Kudla J, Hetherington AM (2017) The evolution of Calcium-based signalling in plants. Curr Biol 27: R667-R679
Google Scholar: Author Only Title Only Author and Title

Emonet A, Zhou F, Vacheron J, Heiman CM, Dénervaud Tendon V, Ma KW, Schulze-Lefert P, Keel C, Geldner N (2021) Spatially restricted immune responses are required for maintaining root meristematic activity upon detection of bacteria. Curr Biol 31:1012-1028
Google Scholar: Author Only Title Only Author and Title

Feijó JA, Sainhas J, Holdaway-Clarke T, Cordeiro MS, Kunkel JG, Hepler PK (2001) Cellular oscillations and the regulation of growth: the pollen tube paradigm. Bioessays 23: 86-94
Google Scholar: Author Only Title Only Author and Title

Feijó JA, Costa SS, Prado AM, Becker JD, Certal AC (2004) Signalling by tips. Curr Opin Plant Biol 7: 589-598.
Google Scholar: Author Only Title Only Author and Title

Flütsch S, Nigro A, Conci F, Fajkus J, Thalmann M, Trtílek M, Panzarová K, Santelia D (2020a) Glucose uptake to guard cells via STP transporters provides carbon sources for stomatal opening and plant growth. EMBO Rep 5; 21(8):e49719
Google Scholar: Author Only Title Only Author and Title

Flütsch S, Wang Y, Takemiya A, Vialet-Chabrand SRM, Klejchová M, Nigro A, Hills A, Lawson T, Blatt MR, Santelia D (2020b) Guard cell starch degradation yields glucose for rapid stomatal opening in Arabidopsis. Plant Cell 32: 2325-2344
Google Scholar: Author Only Title Only Author and Title

Foskett JK, White C, Cheung KH, Mak DO (2007) Inositol trisphosphate receptor Ca2+ release channels. Physiol Rev 87: 593-658
Google Scholar: Author Only Title Only Author and Title

Frank J, Happeck R, Meier B, Hoang MTT, Stribny J, Hause G, Ding H, Morsomme P, Baginsky S, Peiter E (2019) Chloroplast-localized BICAT proteins shape stromal calcium signals and are required for efficient photosynthesis. New Phytol 221: 866-880
Google Scholar: Author Only Title Only Author and Title

Frietsch S, Wang YF, Sladek C, Poulsen LR, Romanowsky SM, Schroeder JI, Harper JF (2007) A cyclic nucleotide-gated channel is essential for polarized tip growth of pollen. Proc Natl Acad Sci USA 104: 14531-14536
Google Scholar: Author Only Title Only Author and Title

Fromm H (2019) Root plasticity in the pursuit of water. Plants (Basel) 8: 236
Google Scholar: Author Only Title Only Author and Title

Geisler M, Frangne N, Gomès E, Martinoia E, Palmgren MG (2000) The ACA4 gene of Arabidopsis encodes a vacuolar membrane calcium pump that improves salt tolerance in yeast. Plant Physiol 124:1814-27
Google Scholar: Author Only Title Only Author and Title

Gao D, Knight MR, Trewavas AJ, Sattelmacher B, Plieth C (2004) Self-reporting Arabidopsis expressing pH and [Ca2+] indicators unveil ion dynamics in the cytoplasm and in the apoplast under abiotic stress. Plant Physiol 134: 898-908
Google Scholar: Author Only Title Only Author and Title

Gao QF, Gu LL, Wang HQ, Fei CF, Fang X, Hussain J, Sun SJ, Dong JY, Liu H, Wang YF (2016) Cyclic nucleotide-gated channel 18 is an essential Ca2+ channel in pollen tube tips for pollen tube guidance to ovules in Arabidopsis. Proc Natl Acad Sci USA 113: 3096-3101
Google Scholar: Author Only Title Only Author and Title

Gao X, Chen X, Lin W, Chen S, Lu D, Niu Y, Li L, Cheng C, McCormack M, Sheen J, Shan L, He P (2013) Bifurcation of Arabidopsis NLR immune signaling via Ca^{2+}-dependent protein kinases. PLoS Pathog 9: e1003127
Google Scholar: Author Only Title Only Author and Title

Garcia-Mata C, Gay R, Sokolovski S, Hills A, Lamattina L, Blatt MR (2003) Nitric oxide regulates K+ and Cl− channels in guard cells through a subset of abscisic acid-evoked signaling pathways. Proc Natl Acad Sci USA 100: 11116–11121
Google Scholar: Author Only Title Only Author and Title

Gong M, van der Luit AH, Knight R, Trewavas AJ (1998) Heat-shock-induced changes in intracellular Ca2+ level in tobacco seedlings in relation to thermotolerance. Plant Physiol 116: 429-437
Google Scholar: Author Only Title Only Author and Title

Grabov A, Blatt MR (1998) Membrane voltage initiates Ca2+ waves and potentiates Ca2+ increases with abscisic acid in stomatal guard cells. Proc Natl Acad Sci USA 95: 4778-4783
Google Scholar: Author Only Title Only Author and Title

Grabov A, Blatt MR (1999) A steep dependence of inward-rectifying potassium channels on cytosolic free calcium concentration increase evoked by hyperpolarization in guard cells. Plant Physiol 119: 277-288
Google Scholar: Author Only Title Only Author and Title

Gradogna A, Scholz-Starke J, Gutla PV, Carpaneto A (2009) Fluorescence combined with excised patch: measuring calcium currents in plant cation channels. Plant J 58: 175-182
Google Scholar: Author Only Title Only Author and Title

Granqvist E, Wysham D, Hazledine S, Kozlowski W, Sun J, Charpentier M, Martins TV, Haleux P, Tsaneva-Atanasova K, Downie JA, Oldroyd GE, Morris RJ (2012) Buffering capacity explains signal variation in symbiotic calcium oscillations. Plant Physiol 160: 2300-2310
Google Scholar: Author Only Title Only Author and Title

Hamel LP, Sheen J, Séguin A (2014) Ancient signals: comparative genomics of green plant CDPKs. Trends Plant Sci 19: 79-89
Google Scholar: Author Only Title Only Author and Title

Hamilton DWA, Hills A, Kohler B, Blatt MR (2000) Ca2+ channels at the plasma membrane of stomatal guard cells are activated by hyperpolarization and abscisic acid. Proc Natl Acad Sci USA 97: 4967-4972
Google Scholar: Author Only Title Only Author and Title

Han S, Tang R, Anderson LK, Woerner TE, Pei ZM (2003) A cell surface receptor mediates extracellular Ca2+ sensing in guard cells. Nature 425: 196-200
Google Scholar: Author Only Title Only Author and Title

He J, Rössner N, Hoang MTT, Alejandro S, Peiter E (2021) Transport, functions, and interaction of calcium and manganese in plant organellar compartments. Plant Physiol doi.org/10.1093/plphys/kiab122
Google Scholar: Author Only Title Only Author and Title

Hedrich R, Mueller TD, Becker D, Marten I (2018) Structure and function of TPC1 Vacuole SV channel gains shape. Mol Plant 11: 764-775
Google Scholar: Author Only Title Only Author and Title

Hedrich R, Neher E (1987) Cytoplasmic calcium regulates voltage-dependent ion channels in plant vacuoles. Nature 329: 833-836
Google Scholar: Author Only Title Only Author and Title

Hill AE, Shachar-Hill B, Skepper JN, Powell J, Shachar-Hill Y (2012) An osmotic model of the growing pollen tube. PLoS One 7: e36585
Google Scholar: Author Only Title Only Author and Title

Hills A, Chen ZH, Amtmann A, Blatt MR, Lew VL (2012) OnGuard, a computational platform for quantitative kinetic modeling of guard cell physiology. Plant Physiol 159: 1026-1042
Google Scholar: Author Only Title Only Author and Title

Hilleary R, Paez-Valencia J, Vens C, Toyota M, Palmgren M, Gilroy S (2020) Tonoplast-localized Ca2+ pumps regulate Ca2+ signals during pattern-triggered immunity in Arabidopsis thaliana. Proc Natl Acad Sci USA 117: 18849-18857
Google Scholar: Author Only Title Only Author and Title

Holdaway-Clarke TL, Feijo JA, Hackett GR, Kunkel JG, Hepler PK (1997) Pollen tube growth and the intracellular cytosolic Calcium gradient oscillate in phase while extracellular Calcium influx is delayed. Plant Cell 9: 1999-2010
Google Scholar: Author Only Title Only Author and Title

Horikawa K, Yamada Y, Matsuda T, Kobayashi K, Hashimoto M, Matsu-ura T, Miyawaki A, Michikawa T, Mikoshiba K, Nagai T (2010) Spontaneous network activity visualized by ultrasensitive Ca2+ indicators, yellow Cameleon-Nano. Nat Methods 7: 729-732
Google Scholar: Author Only Title Only Author and Title

Hruz T, Laule O, Szabo G, Wessendorp F, Bleuler S, Oertle L, Widmayer P, Gruissem W, Zimmermann P (2008) Genevestigator v3: a reference expression database for the meta-analysis of transcriptomes. Adv Bioinformatics 2008:420747
Google Scholar: Author Only Title Only Author and Title

Huang F, Luo J, Ning T, Cao W, Jin X, Zhao H, Wang Y, Han S (2017) Cytosolic and nucleosolic Calcium signaling in response to osmotic and salt stresses are independent of each other in roots of Arabidopsis seedlings. Front Plant Sci 8: 1648
Google Scholar: Author Only Title Only Author and Title

Huang S, Waadt R, Nuhkat M, Kollist H, Hedrich R, Roelfsema MRG (2019) Calcium signals in guard cells enhance the efficiency by which abscisic acid triggers stomatal closure. New Phytol. 224: 177-187
Google Scholar: Author Only Title Only Author and Title

Iwano M, Entani T, Shiba H, Kakita M, Nagai T, Mizuno H, Miyawaki A, Shoji T, Kubo K, Isogai A, Takayama S (2009) Fine-tuning of the cytoplasmic Ca2+ concentration is essential for pollen tube growth. Plant Physiol 150: 1322-1334
Google Scholar: Author Only Title Only Author and Title

Ishka MR, Brown E, Rosenberg A, Romanowsky S, Davis J, Choi W-G, Harper JF (2021) Arabidopsis Ca2+-ATPases 1, 2, and 7 in the endoplasmic reticulum contribute to growth and pollen fitness. Plant Physiol doi.org/10.1093/plphys/kiab021
Google Scholar: Author Only Title Only Author and Title

Islam MM, Munemasa S, Hossain MA, Nakamura Y, Mori IC, Murata Y (2010) Roles of AtTPC1, vacuolar two pore channel 1, in Arabidopsis stomatal closure. Plant Cell Physiol 51: 302-311
Google Scholar: Author Only Title Only Author and Title

Jaślan D, Dreyer I, Lu J, O'Malley R, Dindas J, Marten I, Hedrich R (2019) Voltage-dependent gating of SV channel TPC1 confers vacuole excitability. Nat Commun 10: 2659
Google Scholar: Author Only Title Only Author and Title

Jezek M, Blatt MR (2017) The membrane transport system of the guard cell and its integration for stomatal dynamics. Plant Physiol 174: 487-519
Google Scholar: Author Only Title Only Author and Title

Jezek M, Silva-Alvim FAL, Hills A, Donald N, Ishka MR, Shadbolt J, He B, Lawson T, Harper JF, Wang Y, Lew VL, Blatt MR (2021) Guard cell Ca2+-ATPases underpin a 'carbon memory' of photosynthetic assimilation. that impacts on water use efficiency. Nat Plants in press.
Google Scholar: Author Only Title Only Author and Title

Jiang Z, Zhou X, Tao M, Yuan F, Liu L, Wu F, Wu X, Xiang Y, Niu Y, Liu F, Li C, Ye R, Byeon B, Xue Y, Zhao H, Wang HN, Crawford BM, Johnson DM, Hu C, Pei C, Zhou W, Swift GB, Zhang H, Vo-Dinh T, Hu Z, Siedow JN, Pei ZM (2019) Plant cell-surface GIPC sphingolipids sense salt to trigger Ca2+ influx. Nature 572: 341-346
Google Scholar: Author Only Title Only Author and Title

Kelner A, Leitao N, Chabaud M, Charpentier M, de Carvalho-Niebel F (2018) Dual color sensors for simultaneous analysis of Calcium signal dynamics in the nuclear and cytoplasmic compartments of plant cells. Front Plant Sci 9: 245
Google Scholar: Author Only Title Only Author and Title

Kiegle E, Moore CA, Haseloff J, Tester MA, Knight MR (2000) Cell-type-specific calcium responses to drought, salt and cold in the Arabidopsis root. Plant J 23: 267-278
Google Scholar: Author Only Title Only Author and Title

Kim S, Zeng W, Bernard S, Liao J, Venkateshwaran M, Ane JM, Jiang Y (2019) Ca2+-regulated Ca2+ channels with an RCK gating ring control plant symbiotic associations. Nat Commun 10: 3703
Google Scholar: Author Only Title Only Author and Title

Kim TH, Böhmer M, Hu H, Nishimura N, Schroeder JI (2010) Guard cell signal transduction network: advances in understanding abscisic acid, CO2, and Ca2+ signaling. Annu Rev Plant Biol. 61: 561-591
Google Scholar: Author Only Title Only Author and Title

Klepikova AV, Kasianov AS, Gerasimov ES, Logacheva MD, Penin AA (2016) A high resolution map of the Arabidopsis thaliana developmental transcriptome based on RNA-seq profiling. Plant J. Dec 88: 1058-1070
Google Scholar: Author Only Title Only Author and Title

Knight MR, Campbell AK, Smith SM, Trewavas AJ (1991) Transgenic plant aequorin reports the effects of touch and cold-shock and elicitors on cytoplasmic calcium. Nature 352: 524-526
Google Scholar: Author Only Title Only Author and Title

Knight H, Trewavas AJ, Knight MR (1996) Cold calcium signaling in Arabidopsis involves two cellular pools and a change in calcium signature after acclimation. Plant Cell 8: 489-503
Google Scholar: Author Only Title Only Author and Title

Knight H, Trewavas AJ, Knight MR (1997) Calcium signaling in Arabidopsis thaliana responding to drought and salinity. Plant J 12: 1067-1078
Google Scholar: Author Only Title Only Author and Title

Knight H, Knight MR (2001) Abiotic stress signalling pathways: specificity and cross-talk. Trends Plant Sci 6: 262-267
Google Scholar: Author Only Title Only Author and Title

Kudla J, Batistic O, Hashimoto K (2010) Calcium signals: the lead currency of plant information processing. Plant Cell 22: 541-563
Google Scholar: Author Only Title Only Author and Title

Kudla J, Becker D, Grill E, Hedrich R, Hippler M, Kummer U, Parniske M, Romeis T, Schumacher K (2018) Advances and current challenges in calcium signaling. New Phytol 218: 414-431

Google Scholar: Author Only Title Only Author and Title

Kwaaitaal M, Huisman R, Maintz J, Reinstädler A, Panstruga R (2011) Ionotropic glutamate receptor (iGluR)-like channels mediate MAMP-induced calcium influx in Arabidopsis thaliana. Biochem J 440: 355-365
Google Scholar: Author Only Title Only Author and Title

Kwak JM, Mori IC, Pei ZM, Leonhardt N, Torres MA, Dangl JL, Bloom RE, Bodde S, Jones JDG, Schroeder JI (2003) NADPH oxidase AtrbohD and AtrbohF genes function in ROS-dependent ABA signaling in Arabidopsis. EMBO J 22: 2623–2633
Google Scholar: Author Only Title Only Author and Title

Krebs M, Held K, Binder A, Hashimoto K, Den Herder G, Parniske M, Kudla J, Schumacher K (2012) FRET-based genetically encoded sensors allow high-resolution live cell imaging of Ca^{2+} dynamics. Plant J 69: 181-192
Google Scholar: Author Only Title Only Author and Title

Laanemets K, Brandt B, Li J, Merilo E, Wang YF, Keshwani MM, Taylor SS, Kollist H, Schroeder JI (2013) Calcium-dependent and -independent stomatal signaling network and compensatory feedback control of stomatal opening via Ca2+ sensitivity priming. Plant Physiol 163: 504-513
Google Scholar: Author Only Title Only Author and Title

Leckie CP, McAinsh MR, Allen GJ, Sanders D, Hetherington AM (1998) Abscisic acid-induced stomatal closure mediated by cyclic ADP-ribose. Proc Natl Acad Sci USA 95: 15837-15842
Google Scholar: Author Only Title Only Author and Title

Lecourieux D, Lamotte O, Bourque S, Wendehenne D, Mazars C, Ranjeva R, Pugin A (2005) Proteinaceous and oligosaccharidic elicitors induce different calcium signatures in the nucleus of tobacco cells. Cell Calcium 38: 527-538
Google Scholar: Author Only Title Only Author and Title

Leitão N, Dangeville P, Carter R, Charpentier M (2019) Nuclear calcium signatures are associated with root development. Nat Commun 10: 4865
Google Scholar: Author Only Title Only Author and Title

Lemtiri-Chlieh F, MacRobbie EAC, Webb AAR, Manison NF, Brownlee C, Skepper JN, Chen J, Prestwich GD, Brearley CA (2003) Inositol hexakisphosphate mobilizes an endomembrane store of calcium in guard cells. Proc Natl Acad Sci USA 100: 10091-10095
Google Scholar: Author Only Title Only Author and Title

Lenglet A, Jaslan D, Toyota M, Mueller M, Muller T, Schonknecht G, Marten I, Gilroy S, Hedrich R, Farmer EE (2017) Control of basal jasmonate signalling and defence through modulation of intracellular cation flux capacity. New Phytol 216: 1161-1169
Google Scholar: Author Only Title Only Author and Title

Lenzoni G, Liu J, Knight MR (2018) Predicting plant immunity gene expression by identifying the decoding mechanism of calcium signatures. New Phytol 217: 1598-1609
Google Scholar: Author Only Title Only Author and Title

Lenzoni G, Knight MR (2019) Increases in absolute temperature stimulate free Calcium concentration elevations in the chloroplast. Plant Cell Physiol 60: 538-548
Google Scholar: Author Only Title Only Author and Title

Liu KH, Diener A, Lin Z, Liu C, Sheen J (2020) Primary nitrate responses mediated by calcium signalling and diverse protein phosphorylation. J Exp Bot 71: 4428-4441
Google Scholar: Author Only Title Only Author and Title

Logan DC, Knight MR (2003) Mitochondrial and cytosolic calcium dynamics are differentially regulated in plants. Plant Physiol 133: 21-24
Google Scholar: Author Only Title Only Author and Title

Lopez-Hernandez F, Tryfona T, Rizza A, Yu XL, Harris MOB, Webb AAR, Kotake T, Dupree P (2020) Calcium binding by arabinogalactan polysaccharides is important for normal plant development. Plant Cell 32: 3346-3369
Google Scholar: Author Only Title Only Author and Title

Loro G, Drago I, Pozzan T, Schiavo FL, Zottini M, Costa A (2012) Targeting of Cameleons to various subcellular compartments reveals a strict cytoplasmic/mitochondrial Ca2+ handling relationship in plant cells. Plant J 71: 1-13
Google Scholar: Author Only Title Only Author and Title

Loro G, Wagner S, Doccula FG, Behera S, Weinl S, Kudla J, Schwarzlander M, Costa A, Zottini M (2016) Chloroplast-specific in vivo Ca2+ imaging using Yellow Cameleon fluorescent protein sensors reveals organelle-autonomous Ca2+ signatures in the stroma. Plant Physiol 171: 2317-2330
Google Scholar: Author Only Title Only Author and Title

Luo J, Chen L, Huang F, Gao P, Zhao H, Wang Y, Han S (2020) Intraorganellar calcium imaging in Arabidopsis seedling roots using the GCaMP variants GCaMP6m and R-CEPIA1er. J Plant Physiol 246-247:153127
Google Scholar: Author Only Title Only Author and Title

Ma Y, Zhao Y, Berkowitz GA (2017) Intracellular Ca2+ is important for flagellin-triggered defense in Arabidopsis and involves inositol

polyphosphate signaling. J Exp Bot 68: 3617-3628
Google Scholar: Author Only Title Only Author and Title

Manzoor H, Chiltz A, Madani S, Vatsa P, Schoefs B, Pugin A, Garcia-Brugger A (2012) Calcium signatures and signaling in cytosol and organelles of tobacco cells induced by plant defense elicitors. Cell Calcium 51: 434-444
Google Scholar: Author Only Title Only Author and Title

Martí Ruiz MC, Jung HJ, Webb AAR (2020) Circadian gating of dark-induced increases in chloroplast- and cytosolic-free calcium in Arabidopsis. New Phytol 225: 1993-2005
Google Scholar: Author Only Title Only Author and Title

McAinsh MR, Pittman JK (2009) Shaping the calcium signature. New Phytol 181: 275-294
Google Scholar: Author Only Title Only Author and Title

McAinsh MR, Webb A, Taylor JE, Hetherington AM (1995) Stimulus-induced oscillations in guard cell cytosolic free Calcium. Plant Cell 7: 1207-1219
Google Scholar: Author Only Title Only Author and Title

McCormack E, Tsai YC, Braam J (2005) Handling calcium signaling: Arabidopsis CaMs and CMLs. Trends Plant Sci 10: 383-389
Google Scholar: Author Only Title Only Author and Title

MacRobbie EAC (1992) Calcium and ABA-induced stomatal closure. Phil Trans R Soc Lond B3385-18
Google Scholar: Author Only Title Only Author and Title

Meyerhoff O, Müller K, Roelfsema MR, Latz A, Lacombe B, Hedrich R, Dietrich P, Becker D (2005) AtGLR3.4, a glutamate receptor channel-like gene is sensitive to touch and cold. Planta 222: 418-427
Google Scholar: Author Only Title Only Author and Title

Michard E, Lima PT, Borges F, Silva AC, Portes MT, Carvalho JE, Gilliham M, Liu L-H, Obermeyer G, Feijó JA (2011) Glutamate receptor-like genes form Ca2+ channels in pollen tubes and are regulated by pistil D-serine. Science 332: 434-437
Google Scholar: Author Only Title Only Author and Title

Michard E, Simon AA, Tavares B, Wudick MM, Feijó JA (2017) Signaling with ions: The keystone for apical cell growth and morphogenesis in pollen tubes. Plant Physiol 173: 91-111
Google Scholar: Author Only Title Only Author and Title

Mills RF, Doherty ML, López-Marqués RL, Weimar T, Dupree P, Palmgren MG, Pittman JK, Williams LE (2008) ECA3, a Golgi-localized P2A-type ATPase, plays a crucial role in manganese nutrition in Arabidopsis. Plant Physiol 146: 116-128
Google Scholar: Author Only Title Only Author and Title

Minguet-Parramona C, Wang Y, Hills A, Vialet-Chabrand S, Griffiths H, Rogers S, Lawson T, Lew VL, Blatt MR (2016) An optimal frequency in Ca2+ oscillations for stomatal closure is an emergent property of ion transport in guard cells. Plant Physiol 170: 33-42
Google Scholar: Author Only Title Only Author and Title

Miyawaki A, Llopis J, Heim R, McCaffery JM, Adams JA, Ikura M, Tsien RY (1997) Fluorescent indicators for Ca2+ based on green fluorescent proteins and calmodulin. Nature 388: 882-887
Google Scholar: Author Only Title Only Author and Title

Monshausen GB, Bibikova TN, Messerli MA, Shi C, Gilroy S (2007) Oscillations in extracellular pH and reactive oxygen species modulate tip growth of Arabidopsis root hairs. Proc Natl Acad Sci USA 104: 20996-21001
Google Scholar: Author Only Title Only Author and Title

Monshausen GB, Messerli MA, Gilroy S (2008) Imaging of the Yellow Cameleon 3.6 indicator reveals that elevations in cytosolic Ca2+ follow oscillating increases in growth in root hairs of Arabidopsis. Plant Physiol. 147: 1690-1698
Google Scholar: Author Only Title Only Author and Title

Muir SR, Sanders D (1996) Pharmacology of Ca2+ release from red beet microsomes suggests the presence of ryanodine receptor homologs in higher plants. FEBS Lett 395: 39-42
Google Scholar: Author Only Title Only Author and Title

Murata Y, Pei ZM, Mori IC, Schroeder J (2001) Abscisic acid activation of plasma membrane Ca2+ channels in guard cells requires cytosolic NAD(P)H and is differentially disrupted upstream and downstream of reactive oxygen species production in abi1-1 and abi2-1 protein phosphatase 2C mutants. Plant Cell 13: 2513-2523
Google Scholar: Author Only Title Only Author and Title

Nomura H, Komori T, Kobori M, Nakahira Y, Shiina T (2008) Evidence for chloroplast control of external Ca2+-induced cytosolic Ca2+ transients and stomatal closure. Plant J 53: 988-998
Google Scholar: Author Only Title Only Author and Title

Nomura H, Komori T, Uemura S, Kanda Y, Shimotani K, Nakai K, Furuichi T, Takebayashi K, Sugimoto T, Sano S, Suwastika IN, Fukusaki E, Yoshioka H, Nakahira Y, Shiina T (2012) Chloroplast-mediated activation of plant immune signalling in Arabidopsis. Nat Commun 26;3:926
Google Scholar: Author Only Title Only Author and Title

Nomura H, Shiina T (2014) Calcium signaling in plant endosymbiotic organelles: mechanism and role in physiology. Mol Plant 7: 1094-1104
Google Scholar: Author Only Title Only Author and Title

Oldroyd GE, Downie JA (2006) Nuclear calcium changes at the core of symbiosis signalling. Curr Opin Plant Biol 9: 351-357
Google Scholar: Author Only Title Only Author and Title

Ordenes VR, Moreno I, Maturana D, Norambuena L, Trewavas AJ, Orellana A (2012) In vivo analysis of the calcium signature in the plant Golgi apparatus reveals unique dynamics. Cell Calcium 52: 397-404
Google Scholar: Author Only Title Only Author and Title

Pan Y, Chai X, Gao Q, Zhou L, Zhang S, Li L, Luan S (2019) Dynamic interactions of plant CNGC subunits and calmodulins drive oscillatory Ca2+ channel activities. Dev Cell 48: 710-725
Google Scholar: Author Only Title Only Author and Title

Pandey S, Zhang W, Assmann SM (2007) Roles of ion channels and transporters in guard cell signal transduction. FEBS Lett 581: 2325-2336
Google Scholar: Author Only Title Only Author and Title

Pei ZM, Murata Y, Benning G, Thomine S, Klüsener B, Allen GJ, Grill E, Schroeder JI (2000) Calcium channels activated by hydrogen peroxide mediate abscisic acid signalling in guard cells. Nature 406: 731–734
Google Scholar: Author Only Title Only Author and Title

Peiter E, Maathuis FJ, Mills LN, Knight H, Pelloux J, Hetherington AM, Sanders D (2005) The vacuolar Ca2+-activated channel TPC1 regulates germination and stomatal movement. Nature 434: 404-408
Google Scholar: Author Only Title Only Author and Title

Peleg Z. Blumwald E (2011) Hormone balance and abiotic stress tolerance in crop plants. Curr Opin Plant Biol 14: 290-295
Google Scholar: Author Only Title Only Author and Title

Pierson ES, Miller DD, Callaham DA, van Aken J, Hackett G, Hepler PK (1996) Tip-localized calcium entry fluctuates during pollen tube growth. Dev Biol 174: 160-173
Google Scholar: Author Only Title Only Author and Title

Poovaiah BW, Du L (2018) Calcium signaling: decoding mechanism of calcium signatures. New Phytol 217: 1394-1396
Google Scholar: Author Only Title Only Author and Title

Qudeimat E, Faltusz AM, Wheeler G, Lang D, Holtorf H, Brownlee C, Reski R, Frank W (2008) A PIIB-type Ca2+-ATPase is essential for stress adaptation in Physcomitrella patens. Proc Natl Acad Sci USA 105:19555-19560
Google Scholar: Author Only Title Only Author and Title

Ranf S, Wunnenberg P, Lee J, Becker D, Dunkel M, Hedrich R, Scheel D, Dietrich P (2008) Loss of the vacuolar cation channel, AtTPC1, does not impair Ca2+ signals induced by abiotic and biotic stresses. Plant J 53: 287-299
Google Scholar: Author Only Title Only Author and Title

Reddy AS, Ali GS, Celesnik H, Day IS (2011) Coping with stresses: roles of calcium- and calcium/calmodulin-regulated gene expression. Plant Cell 23: 2010-2032
Google Scholar: Author Only Title Only Author and Title

Sai J, Johnson CH (2002) Dark-stimulated calcium ion fluxes in the chloroplast stroma and cytosol. Plant Cell 14:1279-1291
Google Scholar: Author Only Title Only Author and Title

Saijo Y, Tintor N, Lu X, Rauf P, Pajerowska-Mukhtar K, Häweker H, Dong X, Robatzek S, Schulze-Lefert P (2009) Receptor quality control in the endoplasmic reticulum for plant innate immunity. EMBO J 28: 3439-3449
Google Scholar: Author Only Title Only Author and Title

Sanders D, Pelloux J, Brownlee C, Harper JF (2002) Calcium at the crossroads of signaling. Plant Cell 14: S401–S417
Google Scholar: Author Only Title Only Author and Title

Schiefelbein J, Galway M, Masucci J, Ford S (1993) Pollen tube and root-hair tip growth is disrupted in a mutant of Arabidopsis thaliana. Plant Physiol 103: 979-985
Google Scholar: Author Only Title Only Author and Title

Schiøtt M, Romanowsky SM, Baekgaard L, Jakobsen MK, Palmgren MG, Harper JF (2004) A plant plasma membrane Ca2+ pump is required for normal pollen tube growth and fertilization. Proc Natl Acad Sci USA 101: 9502-9507
Google Scholar: Author Only Title Only Author and Title

Schoenaers S, Balcerowicz D, Vissenberg K (2017) Molecular mechanisms regulating root hair tip growth: A comparison with pollen tubes. In: Obermeyer G., Feijó J. (eds) Pollen Tip Growth. Springer, Cham doi.org/10.1007/978-3-319-56645-0_9
Google Scholar: Author Only Title Only Author and Title

Schumacher K, Vafeados D, McCarthy M, Sze H, Wilkins T, Chory J (1999) The Arabidopsis det3 mutant reveals a central role for the vacuolar H+-ATPase in plant growth and development. Genes Dev 15: 3259-3270
Google Scholar: Author Only Title Only Author and Title

Selles B, Michaud C, Xiong TC, Leblanc O, Ingouff M (2018) Arabidopsis pollen tube germination and growth depend on the mitochondrial calcium uniporter complex. New Phytol 219: 58-65
Google Scholar: Author Only Title Only Author and Title

Sello S, Perotto J, Carraretto L, Szabo I, Vothknecht UC, Navazio L (2016) Dissecting stimulus-specific Ca2+ signals in amyloplasts and chloroplasts of Arabidopsis thaliana cell suspension cultures. J Exp Bot 67: 3965-3974
Google Scholar: Author Only Title Only Author and Title

Sello S, Moscatiello R, Mehlmer N, Leonardelli M, Carraretto L, Cortese E, Zanella FG, Baldan B, Szabo I, Vothknecht UC, Navazio L (2018) Chloroplast Ca2+ fluxes into and across thylakoids revealed by thylakoid-targeted aequorin probes. Plant Physiol 177: 38-51
Google Scholar: Author Only Title Only Author and Title

Shkolnik D, Nuriel R, Bonza MC, Costa A, Fromm H (2018) MIZ1 regulates ECA1 to generate a slow, long-distance phloem-transmitted Ca2+ signal essential for root water tracking in Arabidopsis. Proc Natl Acad Sci USA 115: 8031-8036
Google Scholar: Author Only Title Only Author and Title

Singh A, Kanwar P, Yadav AK, Mishra M, Jha SK, Baranwal V, Pandey A, Kapoor S, Tyagi AK, Pandey GK (2014) Genome-wide expressional and functional analysis of calcium transport elements during abiotic stress and development in rice. FEBS J 281: 894-915
Google Scholar: Author Only Title Only Author and Title

Stael S, Wurzinger B, Mair A, Mehlmer N, Vothknecht UC, Teige M (2012) Plant organellar calcium signalling: an emerging field. J Exp Bot 63: 1525-1542
Google Scholar: Author Only Title Only Author and Title

Steinhorst L, Mähs A, Ischebeck T, Zhang C, Zhang X, Arendt S, Schültke S, Heilmann I, Kudla J (2015) Vacuolar CBL-CIPK12 Ca2+-sensor-kinase complexes are required for polarized pollen tube growth. Curr Biol 25: 1475-1482
Google Scholar: Author Only Title Only Author and Title

Stephan AB, Kunz HH, Yang E, Schroeder JI (2016) Rapid hyperosmotic-induced Ca2+ responses in Arabidopsis thaliana exhibit sensory potentiation and involvement of plastidial KEA transporters. Proc Natl Acad Sci USA 113: E5242-5249
Google Scholar: Author Only Title Only Author and Title

Taiz L, Zeiger E, Møller IM, Murphy A (2014) Plant Physiology and Development. Sixth Edition. ISBN: 9781605352558
Google Scholar: Author Only Title Only Author and Title

Tang RJ, Zhao FG, Yang Y, Wang C, Li K, Kleist TJ, Lemaux PG, Luan S (2020) A calcium signalling network activates vacuolar K+ remobilization to enable plant adaptation to low-K environments. Nat Plants 6: 384-393
Google Scholar: Author Only Title Only Author and Title

Taylor CW, Tovey SC (2010) IP(3) receptors: toward understanding their activation. Cold Spring Harb Perspect Biol 2: a004010
Google Scholar: Author Only Title Only Author and Title

Teardo E, Formentin E, Segalla A, Giacometti GM, Marin O, Zanetti M, Lo Schiavo F, Zoratti M, Szabo I (2011) Dual localization of plant glutamate receptor AtGLR3.4 to plastids and plasma membrane. Biochim Biophys Acta 1807: 359-367
Google Scholar: Author Only Title Only Author and Title

Teardo E, Carraretto L, De Bortoli S, Costa A, Behera S, Wagner R, Lo Schiavo F, Formentin E, Szabo I (2015) Alternative splicing-mediated targeting of the Arabidopsis GLUTAMATE RECEPTOR3.5 to mitochondria affects organelle morphology. Plant Physiol 167: 216-227
Google Scholar: Author Only Title Only Author and Title

Teardo E, Carraretto L, Wagner S, Formentin E, Behera S, De Bortoli S, Larosa V, Fuchs P, Lo Schiavo F, Raffaello A, Rizzuto R, Costa A, Schwarzlander M, Szabo I (2017) Physiological characterization of a plant mitochondrial Calcium uniporter in vitro and in vivo. Plant Physiol 173: 1355-1370
Google Scholar: Author Only Title Only Author and Title

Teardo E, Carraretto L, Moscatiello R, Cortese E, Vicario M, Festa M, Maso L, De Bortoli S, Calì T, Vothknecht UC, Formentin E, Cendron L, Navazio L, Szabo I (2019) A chloroplast-localized mitochondrial calcium uniporter transduces osmotic stress in Arabidopsis. Nat Plants 5: 581-588
Google Scholar: Author Only Title Only Author and Title

Thor K, Jiang S, Michard E, George J, Scherzer S, Huang S, Dindas J, Derbyshire P, Leitão N, DeFalco TA, Köster P, Hunter K, Kimura S, Gronnier J, Stransfeld L, Kadota Y, Bücherl CA, Charpentier M, Wrzaczek M, MacLean D, Oldroyd GED, Menke FLH, Roelfsema MRG, Hedrich R, Feijó J, Zipfel C (2020) The calcium-permeable channel OSCA1.3 regulates plant stomatal immunity. Nature 585: 569-573
Google Scholar: Author Only Title Only Author and Title

Tian D, Wang J, Zeng X, Gu K, Qiu C, Yang X, Zhou Z, Goh M, Luo Y, Murata-Hori M, White FF, Yin Z (2014) The rice TAL effector-dependent resistance protein XA10 triggers cell death and calcium depletion in the endoplasmic reticulum. Plant Cell 26: 497-515
Google Scholar: Author Only Title Only Author and Title

Tian W, Hou C, Ren Z, Wang C, Zhao F, Dahlbeck D, Hu S, Zhang L, Niu Q, Li L, Staskawicz BJ, Luan S (2019) A calmodulin-gated calcium channel links pathogen patterns to plant immunity. Nature 572:131-135

Google Scholar: Author Only Title Only Author and Title

Tian W, Wang C, Gao Q, Li L, Luan S (2020) Calcium spikes, waves and oscillations in plant development and biotic interactions. Nat Plants 6: 750-759
Google Scholar: Author Only Title Only Author and Title

Tracy FE, Gilliham M, Dodd AN, Webb AA, Tester M (2008) NaCl-induced changes in cytosolic free Ca2+ in Arabidopsis thaliana are heterogeneous and modified by external ionic composition. Plant Cell Environ 31: 1063-1073.
Google Scholar: Author Only Title Only Author and Title

Trewavas AJ (1999) Le calcium, c'est la vie: Calcium makes waves. Plant Physiol 120: 1-6
Google Scholar: Author Only Title Only Author and Title

Trewavas AJ, Malhó R (1998) Ca2+ signalling in plant cells: the big network! Curr Opin Plant Biol 1: 428-433
Google Scholar: Author Only Title Only Author and Title

Véry AA, Davies JM (2000) Hyperpolarization-activated calcium channels at the tip of Arabidopsis root hairs. Proc Natl Acad Sci USA 97: 9801-9806
Google Scholar: Author Only Title Only Author and Title

van Der Luit AH, Olivari C, Haley A, Knight MR, Trewavas AJ (1999) Distinct calcium signaling pathways regulate calmodulin gene expression in tobacco. Plant Physiol 121: 705-714
Google Scholar: Author Only Title Only Author and Title

Vanderauwera S, Vandenbroucke K, Inzé A, van de Cotte B, Mühlenbock P, De Rycke R, Naouar N, Van Gaever T, Van Montagu MC, Van Breusegem F (2012) AtWRKY15 perturbation abolishes the mitochondrial stress response that steers osmotic stress tolerance in Arabidopsis. Proc Natl Acad Sci USA 109: 20113-20118
Google Scholar: Author Only Title Only Author and Title

Vincill ED, Bieck AM, Spalding EP (2012) Ca2+ conduction by an amino acid-gated ion channel related to glutamate receptors. Plant Physiol 59: 40-46
Google Scholar: Author Only Title Only Author and Title

Wagner S, Behera S, De Bortoli S, Logan DC, Fuchs P, Carraretto L, Teardo E, Cendron L, Nietzel T, Fussl M, Doccula FG, Navazio L, Fricker MD, Van Aken O, Finkemeier I, Meyer AJ, Szabo I, Costa A, Schwarzlander M (2015) The EF-Hand Ca2+ binding protein MICU choreographs mitochondrial Ca2+ dynamics in Arabidopsis. Plant Cell 27: 3190-3212
Google Scholar: Author Only Title Only Author and Title

Wagner S, Steinbeck J, Fuchs P, Lichtenauer S, Elsässer M, Schippers JHM, Nietzel T, Ruberti C, Van Aken O, Meyer AJ, Van Dongen JT, Schmidt RR, Schwarzländer M (2019) Multiparametric real-time sensing of cytosolic physiology links hypoxia responses to mitochondrial electron transport. New Phytol 224: 1668-1684
Google Scholar: Author Only Title Only Author and Title

Wang Y, Zhu Y, Ling Y, Zhang H, Liu P, Baluska F, Samaj J, Lin J, Wang Q (2010) Disruption of actin filaments induces mitochondrial Ca2+ release to the cytoplasm and [Ca2+]c changes in Arabidopsis root hairs. BMC Plant Biol 10: 53
Google Scholar: Author Only Title Only Author and Title

Wang Y, Hills A, Blatt MR (2014) Systems analysis of guard cell membrane transport for enhanced stomatal dynamics and water use efficiency. Plant Physiol 164: 1593-1599
Google Scholar: Author Only Title Only Author and Title

Ward JM, Schroeder JI (1994) Calcium-activated K+ channels and calcium-induced calcium release by slow vacuolar ion channels in guard cell vacuoles implicated in the control of stomatal closure. Plant Cell 6: 669-683
Google Scholar: Author Only Title Only Author and Title

Weinl S, Held K, Schlücking K, Steinhorst L, Kuhlgert S, Hippler M, Kudla J (2008) A plastid protein crucial for Ca2+-regulated stomatal responses. New Phytol 179: 675–686
Google Scholar: Author Only Title Only Author and Title

Whalley HJ, Knight MR (2013) Calcium signatures are decoded by plants to give specific gene responses. New Phytol 197: 690-693
Google Scholar: Author Only Title Only Author and Title

Wymer CL, Bibikova TN, Gilroy S (1997) Cytoplasmic free calcium distributions during the development of root hairs of Arabidopsis thaliana. Plant J 12: 427-439
Google Scholar: Author Only Title Only Author and Title

Winship LJ, Rounds C, Hepler PK (2017) Perturbation analysis of Calcium, alkalinity and secretion during growth of lily pollen tubes. Plants (Basel); 6(1): 3
Google Scholar: Author Only Title Only Author and Title

Winter D, Vinegar B, Nahal H, Ammar R, Wilson GV, Provart NJ (2007) An "Electronic Fluorescent Pictograph" browser for exploring and analyzing large-scale biological data sets. PLoS One 2: e718
Google Scholar: Author Only Title Only Author and Title

Wu Y, Kuzma J, Maréchal E, Graeff R, Lee HC, Foster R, Chua NH (1997) Abscisic acid signaling through cyclic ADP-ribose in plants. Science 278: 2126-2130
Google Scholar: Author Only Title Only Author and Title

Wudick MM, Michard E, Oliveira Nunes C, Feijó JA (2018) Comparing plant and animal glutamate receptors: Common traits but different fates? J Exp Bot 69: 4151-4163
Google Scholar: Author Only Title Only Author and Title

Xiong L, Zhu JK (2002) Molecular and genetic aspects of plant responses to osmotic stress. Plant Cell Environ 25: 131-139
Google Scholar: Author Only Title Only Author and Title

Xiong TC, Jauneau A, Ranjeva R, Mazars C (2004) Isolated plant nuclei as mechanical and thermal sensors involved in calcium signalling. Plant J 40: 12-21
Google Scholar: Author Only Title Only Author and Title

Yadav AK, Shankar A, Jha SK, Kanwar P, Pandey A, Pandey GK (2015) A rice tonoplastic calcium exchanger, OsCCX2 mediates Ca2+/cation transport in yeast. Sci Rep 26;5:17117
Google Scholar: Author Only Title Only Author and Title

Yang Y, Guo Y (2018) Elucidating the molecular mechanisms mediating plant salt-stress responses. New Phytol 217: 523-539
Google Scholar: Author Only Title Only Author and Title

Yuan F, Yang H, Xue Y, Kong D, Ye R, Li C, Zhang J, Theprungsirikul L, Shrift T, Krichilsky B, Johnson DM, Swift GB, He Y, Siedow JN, Pei ZM (2014) OSCA1 mediates osmotic-stress-evoked Ca2+ increases vital for osmosensing in Arabidopsis. Nature 514: 367-371
Google Scholar: Author Only Title Only Author and Title

Yuan P, Jauregui E, Du L, Tanaka K, Poovaiah BW (2017) Calcium signatures and signaling events orchestrate plant–microbe interactions. Curr Opin Plant Biol 38: 173–183
Google Scholar: Author Only Title Only Author and Title

Zipfel C, Kunze G, Chinchilla D, Caniard A, Jones JD, Boller T, Felix G (2006) Perception of the bacterial PAMP EF-Tu by the receptor EFR restricts Agrobacterium-mediated transformation. Cell 125: 749-760
Google Scholar: Author Only Title Only Author and Title

Zipfel C, Oldroyd GE (2017) Plant signalling in symbiosis and immunity. Nature 543: 328–336
Google Scholar: Author Only Title Only Author and Title

Zhang J, Liu J, Chena Z, Lina J (2007) In vitro germination and growth of lily pollen tubes is affected by calcium inhibitor with reference to calcium distribution. Flora 202: 581-588
Google Scholar: Author Only Title Only Author and Title

Zhang J, Coaker G, Zhou JM, Dong X (2020) Plant immune mechanisms: From reductionistic to holistic points of view. Mol Plant 13: 1358-1378
Google Scholar: Author Only Title Only Author and Title

Zhao Y, Araki S, Wu J, Teramoto T, Chang YF, Nakano M, Abdelfattah AS, Fujiwara M, Ishihara T, Nagai T, Campbell RE (2011) An expanded palette of genetically encoded Ca^{2+} indicators. Science 333: 1888-1891
Google Scholar: Author Only Title Only Author and Title

Zheng Y, Liao C, Zhao S, Wang C, Guo Y (2017) The glycosyltransferase QUA1 regulates chloroplast-associated Calcium signaling during salt and drought stress in Arabidopsis. Plant Cell Physiol 58: 329-341
Google Scholar: Author Only Title Only Author and Title

Zhu JK (2002) Salt and drought stress signal transduction in plants. Annu Rev Plant Biol 53: 247-273
Google Scholar: Author Only Title Only Author and Title

Zhu JK (2016) Abiotic stress signaling and responses in plants. Cell 167: 313-324
Google Scholar: Author Only Title Only Author and Title

Zhu X, Caplan J, Mamillapalli P, Czymmek K, Dinesh-Kumar SP (2010) Function of endoplasmic reticulum calcium ATPase in innate immunity-mediated programmed cell death. EMBO J 29: 1007-1018
Google Scholar: Author Only Title Only Author and Title