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Unveiling the intricate mechanisms of plant defense

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Plants may lack mobility, but they are not defenseless against the constant threats posed by pathogens and pests. Pattern Recognition Receptors (PRRs), which are located on the plasma membrane, enable plants to effectively recognize intruders. These receptors function by sensing elicitors or fragments of the cell wall that arise from damage. Recent studies underscore the significance of maintaining cell wall integrity in the coordination of defense mechanisms following the detection of parasitism. Pathogen invasion often triggers alterations in cell wall structure, which leads to the release of molecules like β -glucans and oligogalacturonides. These small molecules are then recognized by PRRs, which stimulate downstream signaling pathways that involve both receptor-like kinases and calcium-dependent signaling. Here, we present the latest insights into plant signaling that play a vital role in immunity: the maintenance of cell wall integrity; the intricate interplay between receptor-like kinases; and the involvement of calcium ions. The goal of the review is to provide readers with a deeper understanding of the intricate mechanisms underlying plant defense strategies.

KEYWORDS

cell wall, calcium, damage, immune responses, pathogens

Introduction

The sessile nature of the plant kingdom has driven the evolution of intricate signaling mechanisms that can effectively detect, as well as combat, the biotic stresses imposed by pathogens and pests (Glazebrook, 2005). The plant cell wall serves as the primary barrier against these stressors, and is crucial not only for protection, but also for sensing external attack (Cosgrove, 2005). In the quest to identify potential threats, plants have developed a sophisticated surveillance system that relies on the recognition of distinct molecules known as microbe-associated molecular patterns (MAMPs), pathogen-associated molecular patterns (PAMPs), damage-associated molecular patterns (DAMPs), and even herbivore-associated molecular patterns (HAMPs) (Chisholm et al., 2006). These molecular patterns are detected by specialized pattern recognition receptors (PRRs) (Jones and Dangl, 2006) as well as surface receptors, e.g., receptor-like kinases (RLKs) and wall-associated kinases (WAKs) (Decreux and Messiaen, 2005; Decreux et al., 2006). Recent advances have provided insight into how plants maintain cell wall integrity (Bacete and Hamann,

2020). In addition to orchestrating the immune response, the cell wall has the vital function of detecting both mechanical and pathogen-induced stress (Cosgrove, 2005). Specific RLKs play pivotal roles in detecting cell wall damages and can engage plant defense complexes to subsequently initiate pattern-triggered immunity (PTI). Alongside protons (H^+), calcium (Ca^{2+}) has recently emerged as a pivotal bivalent cation that is essential for plant nutrition, cellular structure, and stress responses (Thor, 2019). In plants, the maintenance of the cell wall integrity along with the perception of cell wall damages, are intricately linked to Ca^{2+} ions, which can participate in the cross-linking of negative charges at the cell wall interface; as such, the cell wall is effectively a Ca^{2+} reservoir in plants (Hepler and Winship, 2010). In plants, the primary role of Ca^{2+} is to transmit electrical signals to neighboring cells and other plant organs so that specific messages can be relayed once distinct cues are detected (Bush, 1995; Choi et al., 2017). Interestingly, recent research has revealed that calcium ions act as crucial secondary messengers during cell wall damages perception, cell wall integrity regulation, and the plant immune response.

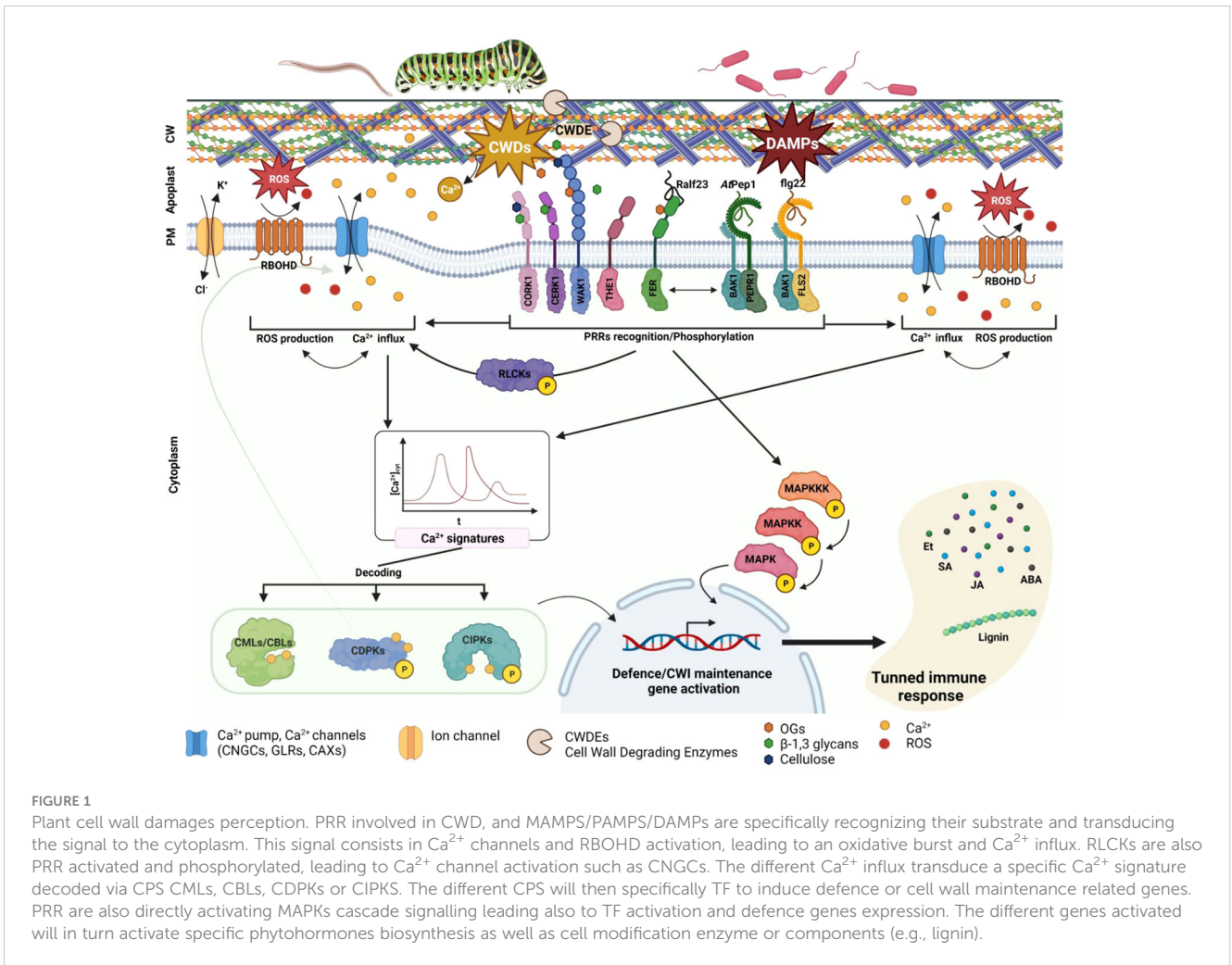
In this review, we initially describe the realm of cell wall-related plant immunity with a specific focus on the role of RLKs in both plant defense mechanisms and cell wall integrity regulation. Next, we explore the emerging evidence that Ca^{2+} acts as a pivotal secondary messenger in both cell wall integrity regulation and plant immunity.

Plant cell wall perception and signaling in immune responses

The plant cell wall (CW) serves as the primary barrier for deterring pathogens; as such, there has been strong evolutionary pressure for the development of cell wall perception, remodeling, and reinforcement mechanisms in plant defense strategies (Cosgrove, 2005; Glazebrook, 2005). The primary cell wall is predominantly composed of oligosaccharides (e.g., cellulose, hemicellulose, and pectin), while the secondary cell wall has a similar composition but lower lignin content (Bidlack, 1992; Cosgrove and Jarvis, 2012). Additionally, the plant cell wall contains a substantial proportion of proteins, which account for approximately one-tenth of the total biomass (Keller, 1993; Cassab, 1998). These proteins play a pivotal role in modifying the CW, facilitating perception, and enabling signal transduction. Recent empirical findings highlight how the maintenance of CW integrity is critical to detecting parasitism and monitoring plant defense responses (Vaahtera et al., 2019; Wan et al., 2021). Intrusion by pathogens or parasites is frequently correlated with changes in CW structure (Gigli-Bisceglia et al., 2020). For instance, pathogens secrete cell-wall degrading enzymes (CWDEs), such as cellulases, glucanases, and xylanases (van den Brink and de Vries, 2011), and the action of these enzymes releases various elicitors into the apoplast. These elicitors include β -1,2-glucans, degradation product of cellulose, β -1,3-glucans, degradation product of callose, and α -1,4-oligogalacturonides (OGs), which is the degradation product of pectins. As a result of cell wall degradation, Ca^{2+} cations, which were originally present in the pectin and hemicellulose components of the cell wall, are released into the apoplast (Jarvis, 1982; Engelsdorf et al.,

2016). This triggers an influx of Ca^{2+} into the cytoplasm (Clapham, 2007). The degradation products of CWDE activity fall under a class of molecules known as DAMPs, which are recognized by pattern PRRs (Bacete and Hamann, 2020; Souza et al., 2017). Following the perception of cell wall damage, PRRs transmit downstream signals via receptor-like kinases (RLKs) or calcium (Ca^{2+})-dependent signaling to ultimately initiate MAPK signaling cascades, which stimulates the production of phytohormones such as jasmonate (JA), salicylic acid (SA), ethylene (ET), and abscisic acid (ABA) (Figure 1, Zhou and Zhang, 2020). The rapid influx of Ca^{2+} into the cytoplasm activates enzymes that are responsible for the biosynthesis of phytohormones, as well as stimulates the transcription factors that regulate genes linked with phytohormone production (Zhou and Zhang, 2020). Changes in apoplastic Ca^{2+} levels also mediate cell wall loosening and adjustments via the action of PECTIN METHYL-TRANSFERASES (PMEs), which require Ca^{2+} for activation and the cross-linking of pectin (Wu et al., 2018; Gale et al., 2019). Moreover, shifts in distinct phytohormone pools will activate the expression of specific genes, leading to modifications in MAPKs signaling and subsequent changes in cell wall structure and the defense response (Engelsdorf and Hamann, 2014; Miedes et al., 2014; Zipfel, 2014; Bacete et al., 2017; Wolf, 2017).

The membrane-localized PRRs are a central part of how plants detect damage from external pathogens via the perception of PAMPs/DAMPs/MAMPs. Among these, the most extensively studied is the LRR-RKs receptor FLAGELLIN-SENSING2 (FLS2), which operates in conjunction with the co-receptor BRASSINOSTEROID INSENSITIVE 1-ASSOCIATED KINASE 1 (BAK1 or SERK3) from the SOMATIC EMBRYOGENESIS RECEPTOR KINASES (SERK) family (Table 1, Gómez-Gómez and Boller, 2000; Chinchilla et al., 2007; Heese et al., 2007). In terms of the mechanism, FLS2 binds the PAMP-peptide flg22, which promotes FLS2/BAK1/BIK1 complex formation and the subsequent phosphorylation of BOTRYTIS INDUCED KINASE 1 (BIK1) cytoplasmic domains by BRI1-ASSOCIATED RECEPTOR KINASE 1 (BAK1) (Lu et al., 2010). These phosphorylation events are sensed by RECEPTOR-LIKE CYTOPLASMIC KINASES (RLCKs) to initiate phosphorylation cascades that culminate in the activation of target proteins; this is an example of PAMP-triggered immunity (PTI) (Liang and Zhou, 2018; DeFalco and Zipfel, 2021). Another significant LRR-RK receptor, PEPR1, has recently emerged as a key player in the perception of CW damages (Yamaguchi et al., 2010). Like FLS2, PEPR1 is a ligand-specific receptor that recognizes the endogenous peptide signal DAMP-associated PEPTIDE 1 (AtPep1). This AtPep1 peptide forms following the C-terminal cleavage of AtProPep1, a product of the *PROPEP1* gene. *PROPEP1* expression is strongly induced during cell wall degradation, wound responses, and the recognition of elicitors such as jasmonic acid (JA) and ethylene (Et) (Huffaker et al., 2006). PEPR1 also operates by activating the immune response, which exemplifies the convergence of bacterial elicitor sensing and the perception of degradation products from cell wall damage. The modes of action of both FLS2 and PEPR1, which are members of the LRR-RKs family, highlight the intricate interplay between MAMP/PAMP recognition and the perception of cell wall degradation products (Figure 1; Table 1).



The intricate role of receptor kinases in calcium signaling and cell wall perception

WALL-ASSOCIATED KINASES (WAKs) are a type of pattern recognition receptors (PRRs) that are responsible for detecting oligogalacturonides (OGs), the degradation products of pectin (Brutus et al., 2010). The WAK-like (WAKL) family, which comprises 26 members in *Arabidopsis thaliana*, plays a crucial role in this process (Verica and He, 2002). More specifically, WAK1 and WAK2 are receptors that can bind OGs, yet require Ca^{2+} for binding to the OG backbone (Vallarino and Osorio, 2012; Benedetti et al., 2015). While WAK1 is not directly involved in early PTI, it eventually forms a complex with FLS2 (Danna et al., 2012). WAKL5 and WAKL7 are induced in response to mechanical damage (Verica et al., 2003). Following the perception of OGs, WAK1 and WAK2 activate downstream signaling pathways via stimulating a Ca^{2+} influx, reactive oxygen species (ROS) production, CDPK activation, and MAPK3,6 phosphorylation, all of which can subsequently activate the transcription of genes linked with the defense response (Brutus et al., 2010; Galletti et al., 2011; Kohorn and Kohorn, 2012; Gravino et al., 2015). The redundancy

among the WAKL genes complicates the comprehensive characterization of specific functions; as such, further investigation is required because distinct WAKL members appear to be differentially involved in the specific defense responses against pests across various crop species (Li et al., 2009; Hurni et al., 2015; Zuo et al., 2015; Tripathi et al., 2021; Barghahn et al., 2021). Another PRR receptor that is activated upon OG binding is the PROLINE-RICH EXTENSIN-LIKE RECEPTOR KINASE 4 (PERK4). Unlike members of the WAK family, PERK4 binds pectin and is involved in cell-wall loosening. Remarkably, PERK4 can inhibit root growth by stimulating ABA signaling and, intriguingly, disrupts Ca^{2+} homeostasis to induce CW loosening under mechanical stress (Bai et al., 2009). LYSIN MOTIF-RECEPTOR KINASE 5 (LYK5) and CHITIN ELICITOR RECEPTOR KINASE 1 (CERK1/LYK1) represent well-documented PRRs that are essential for the recognition of chitin, which is a fungal elicitor (Petutschnig et al., 2010; Liu et al., 2012; Cao et al., 2014). CERK1, in particular, has a critical role in glycan-based MAMP perception and was recently identified as vital for 1,3- β -D-glucan-triggered immunity in *Plectosphaerella cucumerina* (Mélida et al., 2018). CERK1 initiates ROS production via the Rho GTPase pathway, which triggers an oxidative burst that prompts a Ca^{2+} influx. Upon sensing this transient increase in Ca^{2+} levels, CDPK activates downstream

TABLE 1 Membrane localized Pattern-Recognition-Receptors (PRRs) and their specific DAMPS identified in *Arabidopsis thaliana*.

	Receptor	Elicitor/DAMP	Domain	Signalling trademarks	References
Peptides	PEPR1,2	Pep1	LRR	Ca ²⁺ , ROS, MAPK3,MAPK6, ET, NO Ca ²⁺ , ROS, MAPK3, MAPK6, MKKK7,	Krol et al. (2010)
	FLS2	Flg22	LRR	MEKK1-MKK4,5	Chinchilla et al. (2007); Roux et al. (2011)
	FER	Ralf1 ,23/OGs	Malectin-LRR	Ca ²⁺ , ROS, GTPases	Haruta et al. (2014); Gonneau et al., 2018
	THE1	Ralf34	Malectin-LRR	Ca ²⁺ , ROS, ABA, JA, SA	Van Der Does et al. (2017); Gonneau et al., 2018
Oligosaccharides	PERK4	Pectin	Proline-rich	Ca ²⁺	Bai et al. (2009)
	WAK1	OGs DP10-16	EGF-like repeat	Ca ²⁺ , ROS, MAPK3 , MAPK6, ANPs	Brutus et al. (2010)
	CERK1	β-1,3 glycans	Lysin motif	Ca ²⁺ , MAPK3, MAPK6	Kaku et al. (2006); Miya et al. (2007); Shimizu et al. (2010);
	CORK1	β-1,4 glycans, cellobiose	Malectin	Ca ²⁺	Tseng et al. (2022)
	IGP2,3,4	β-1,3/ 1,4 glycans dioligosaccharides, cellobiose	Malectin	Ca ²⁺	Rebaque et al. (2021); Barghahn et al. (2021); Matin-Dacal et al. (2022)
	CAP1	nd	Malectin-LRR	Ca ²⁺ , ROS	Snedden and Fomm, (2001); Bai et al., (2014);
	HERK1,2	nd	Malectin-LRR	Ca ²⁺ , ROS	Galindo-Trigo et al., (2020); ; Gigli-Bisceglia et al., (2022)
	CVY1	nd	Malectin-LRR	Ca ²⁺ , ROS	Gachomo et al., 2014 · Engelsdorf et al., 2018

OGs, o/igoga/acturonides; Nd, Not determined; LRR, Leucine-Rich Repeat; ROS, Reactive Oxygen Species; MAPK, Mitogen-Activated Protein Kinase.

signaling cascades that trigger specific immune responses (Cao et al., 2014; Keinath et al., 2015; Espinoza et al., 2017; Yuan et al., 2017).

Recently, MALECTIN-LIKE RECEPTOR KINASES (MLRKs) or *Catharanthus roseus* RECEPTOR-LIKE KINASE 1-LIKE PROTEINS (*CrRLK1*Ls) have received increased research attention. At present, 17 members of this family have been identified, with 10 well-characterized in *Arabidopsis thaliana* (Lindner et al., 2012; Li et al., 2016; Nissen et al., 2016; Franck et al., 2018). Prior research has shown that *CrRLK1*Ls are involved in various cellular processes, including cell growth, morphogenesis, reproduction, hormone signaling, immunity, and stress responses (Duan et al., 2010; Schoenaers et al., 2017; Feng et al., 2018; Solis-Miranda et al., 2021).

The THESEUS1 (*THE1*) and FERONIA/SIRENE (*FER/SIR*) receptors, both of which are MLRKs, were recently found to perceive cell wall damage as well as play key roles in innate plant immunity (Franck et al., 2018; Bacete and Hamann, 2020; Gonneau et al., 2018). In this signaling cascade, *THE1* operates upstream of MID1-COMPLEMENTING ACTIVITY 1 (*MCA1*), with the activation of signaling ultimately inducing jasmonic acid (JA), salicylic acid (SA), and lignin production (Figure 1, Denness et al., 2011); this chain of signaling hints at collaborative interactions between maintenance of CW integrity and immune responses during the reaction to biotic stressors (Furuichi et al., 2012; Engelsdorf et al., 2018; Basu and Haswell, 2020; Hématy et al., 2007). Research has also revealed that *THE1* interacts with

GUANINE EXCHANGE FACTOR4 (*GEF4*) to elicit downstream responses, yet further exploration is needed to completely unravel the signaling pathway (Qu et al., 2017). *FER*, a member of the *CrRLK1*Ls family, is also involved in CW integrity maintenance and has a direct impact on innate immunity. More specifically, *FER* can bind rapid alkalization 23 (*RALF23*; peptide secreted in response to a rapid alkalization of the extracellular compartment; Blackburn et al., 2020) peptide OGs and trigger cell specific Ca²⁺ fluxes, especially in response to salt stress; thus, this receptor contributes to CW integrity stability (Feng et al., 2018). Recent research has revealed that *FER* activity positively influences PTI by enhancing interactions between *FLS2*, *BAK1*, and *EFR* (Stegmann et al., 2017; Smakowska-Luzan et al., 2018).

The recently identified CELLO-OLIGOMER RECEPTOR 1 (*CORK1*)/IMPAIRED IN GLYCAN PERCEPTION 1 (*IGP1*), which is an LRR/MALECTIN-RECEPTOR-LIKE KINASE (LRR-MAL-RLK), is involved in activating PTI upon the recognition of cello-oligomers, such as cello-triose, which are another degradation products of cellulose (Tseng et al., 2022; Martín-Dacal et al., 2022). In addition, *IGP4* has been shown to be involved in plant immunity not only through the perception of cell wall damage, but also via the stimulation of Ca²⁺ influx following the binding of β-1,3/1,4 glucans and glucan-derived oligosaccharides (Martín-Dacal et al., 2023; and Rebaque et al., 2021). However, the downstream signaling mechanisms of the associated PRR have not yet been fully elucidated. Despite evidence that several *CrRLK1*Ls serve as

sensors of CW integrity (Shimizu et al., 2010), the precise intracellular targets of this class of proteins, along with the signaling pathways involved, remain incompletely understood. As such, extensive experimental data is needed to better illuminate cell wall remodeling following exposure to both biotic and abiotic stressors. Moreover, further investigation of the signaling network (s) through which the newly identified CW integrity sensors transmit information across the cell wall is needed (Table 1). The comprehensive characterization of FER exemplifies how cell-specific Ca^{2+} signals are triggered, and underscores the need for further research, which could potentially lead to the identification of additional cell-specific receptors and the associated Ca^{2+} signatures.

In another study, *Arabidopsis* plant tissue was treated with CW fragments, and the results demonstrated how exposure to cellobiose elicited the strongest cytosolic Ca^{2+} spike. Interestingly, separate treatment with the MAMP-peptide flg22 and cellobiose (DAMP) returned distinct calcium spikes, both of which had a quantifiable pattern (Souza et al., 2017). This finding suggests that CW damages perception and PAMP recognition might operate synergistically, even if the responses exhibit distinct Ca^{2+} signatures; nevertheless, the evidence suggests that either can induce an immune response when activated alone. This novel perspective warrants further exploration of the intricacies of CW damages perception and PTI, as the conventional focus on individual elicitors might not comprehensively reflect all of the simultaneous environmental interactions that occur in plants following an attack by a pathogen.

In summary, numerous PRRs/RLKs demonstrate distinct and precise Ca^{2+} spikes (Figure 1), frequently transmitted through CDPKs, when activated; this knowledge suggests that these receptors have a pivotal role in calcium-mediated signaling within plants. Deciphering which calcium-dependent signaling pathways are activated by distinct RLKs following damage perception has the potential to offer invaluable insight for the field of plant immunity.

Decoding Ca^{2+} signaling in plant immunity

Upon pathogen detection at the CW, diverse PRR signaling pathways coincide with rapid Ca^{2+} influx into the cytoplasm (Figure 1; Clapham, 2007; Boller and Felix, 2009; Yu et al., 2017; DeFalco and Zipfel, 2021). Ca^{2+} serves as a universal secondary messenger, yet can also exhibit specific concentration patterns which plant cells decode to adequately activate the immune response. Termed Ca^{2+} signatures, these transient fluctuations in Ca^{2+} levels depend on factors like duration and amplitude (Knight, 1996). Ca^{2+} signaling comprises three stages: (1) encoding a specific trigger via Ca^{2+} flux magnitude and duration; (2) decoding of these signals by specific sensor proteins; and (3) initiation of downstream responses (Köhler et al., 1999; Bhar et al., 2023; Köster et al., 2022). Ca^{2+} signature features can be determined by the type of PAMPs/MAMPs and their concentration (Yu et al., 2017). A Ca^{2+} influx primarily involves CYCLIC NUCLEOTIDE-GATED CHANNELS (CNGCs) (Köhler et al., 1999), GLUTAMATE RECEPTOR-LIKE CHANNELS (GLRs) (Lam et al., 1998; Wudick et al., 2018; Alfieri et al., 2020), and REDUCED HYPEROSMOLARITY INDUCED

Ca^{2+} INCREASE (OSCA1) (Yuan et al., 2014). The efflux of calcium ions involves $\text{Ca}^{2+}/\text{H}^{+}$ exchangers (CAXs) and autoinhibited Ca^{2+} -ATPases (ACAs) (Geisler et al., 2000; Shigaki and Hirschi, 2000; García Bossi et al., 2020). PRRs can induce transient Ca^{2+} increases via three mechanisms: the generation of signaling molecules like ROS or cyclic nucleotide monophosphate (cNMP); direct activation of ion channels by binding to, and activating, Ca^{2+} pumps or channels; and the stimulation of downstream RLCKs to trigger ROS production and Ca^{2+} influx. For example, in *Arabidopsis*, during PAMP-induced signalling, two genes encoding the Ca^{2+} channels CNGC2 and CNGC4 are required (Ma et al., 2012; Tian et al., 2019). CNGC2 and CNGC4 can form a channel that is phosphorylated by the effector-kinase BIK1, thus triggering Ca^{2+} influx into the cytosol (Tian et al., 2019). Studies also reported that PEPR/Pep-signalling during DAMP-triggered immunity generates Ca^{2+} burst through activation of CNGC2 and act synergistically with PAMP-receptor FLS2 (Ma et al., 2012). Hence, the CNGC-mediated calcium influx establishes a crucial connection between the calcium-dependent immunity during PAMP-triggered immunity signalling pathways and PRR complex. Interestingly, it was also shown that the MRLK FER, involved in CW damages perception and CW integrity maintenance, can induce cell-specific calcium burst upon salt stress (Feng et al., 2018).

These changes in cytosolic Ca^{2+} levels are sensed by Ca^{2+} SENSOR PROTEINS (CSPs), which relay information through downstream cascades (Figure 1; Ranty et al., 2016). CSPs encompass CALMODULIN (CaM), CaM-LIKE PROTEINS (CMLs), CALCINEURIN B-LIKE PROTEINS (CBLs), and CALCIUM-DEPENDENT PROTEIN KINASES (CDPKs; CPKs in *Arabidopsis*) (Cheng et al., 2002; Yang and Poovaiah, 2003; Luan, 2009; Batistič and Kudla, 2012; Delormel and Boudsocq, 2019). CBLs interact with CBL-INTERACTING KINASES (CIPKs), while CDPKs are well-documented Ca^{2+} sensors that include phosphorylation sites within the CaM binding domain (Larrainzar et al., 2007; Xie et al., 2012). In response to changes in Ca^{2+} levels, CDPKs activate the kinase domains of downstream signaling molecules (Harmon et al., 1994; Harper et al., 1994; Yoo and Harmon, 1996; Schulz et al., 2013). As such, CIPKs/CDPKs transform pathogen-induced Ca^{2+} signals into phosphorylation events (Seybold et al., 2014; Delormel and Boudsocq, 2019). CDPKs directly influence ROS production, Ca^{2+} influx and transcriptional reprogramming (Kobayashi et al., 2007; Boudsocq and Sheen, 2013; Dubiella et al., 2013; Shinya et al., 2014). In *Arabidopsis*, AtCPK4, AtCPK5, AtCPK6 and AtCPK11 are described as early transcriptional regulators in MAMP-signalling pathway (Boudsocq et al., 2010). In *Solanum tuberosum* (*St*), StCDPK4/5 (*At* homologues: AtCPK5/6) induce ROS production by direct phosphorylation of the NADPH oxidase RBOHB (Kobayashi et al., 2012). Although many studies and advances put CDPKs as a central regulator of Ca^{2+} -mediated stress and immune responses, further research, particularly studies involving elicitor treatment, is needed if we are to comprehensively understand the myriad roles of CDPKs in the immune response.

Well-documented Ca^{2+} sensors, like CCaMK, possess multiple phosphorylation sites (Larrainzar et al., 2007; Xie et al., 2012). This means that Ca^{2+} sensors could participate in various signaling pathways, and more research in *Arabidopsis* is needed to clarify the roles of these sensors in immunity, such as decoding the Ca^{2+}

spikes that arise following DAMP release and perception. While the role of Ca^{2+} influx in plant immunity is already quite well understood, clarifying the specific targets of various Ca^{2+} signatures remain an understudied aspect of the response to pathogens. This is especially relevant for differences in Ca^{2+} influx signatures are particularly relevant during ETI and HR.

Conclusion

Recent research has unveiled the intricate interplay between calcium-mediated signaling and the triggering of immune responses by the perception of pathogens and CW damage. Despite advancements in the field, a comprehensive understanding of how distinct Ca^{2+} signaling patterns correspond to specific elicitors, as well as how these patterns translate into effective immune reactions against pathogens, is lacking. To address these knowledge gaps, future research should apply the latest conceptual frameworks and analytical tools. High-resolution techniques, which could be used to monitor transient Ca^{2+} fluxes, are imperative for locating the subcellular sites at which cytosolic calcium fluxes occur. Furthermore, unraveling the intricate networks involving Ca^{2+} receptors could provide insight into how distinct Ca^{2+} signatures correspond with certain target proteins. In addition, understanding the interactions between Ca^{2+} and EF-hand domains in Ca^{2+} sensors could clarify the underlying mechanisms of these signaling proteins.

RLKs, particularly PRRs, are inducing Ca^{2+} bursts after activation and then modulate the downstream signalling necessary for PTI. However, the specific Ca^{2+} signatures induced by each specific PRRs remain enigmatic. Investigating calcium pumps at the single-cell level, could offer valuable insight into the dynamics of Ca^{2+} fluxes and the respective targets of this form of signaling. Ca^{2+} signaling has been shown to influence cell wall perception and modification, both of which are crucial aspects of plant defense against pathogen infection. More specifically, Ca^{2+} signaling regulates the activities of CWDE and the deposition of reinforcing components. This intricate interplay results in the finely tuned cell wall modifications that are pivotal to defense mechanisms in plants. In this way, plants can stimulate specific signaling pathways to fortify cell walls in a bid to hinder pathogen entry and constrain pathogen proliferation. In summary, exploring Ca^{2+} signaling in the context of plant immunity, especially the early detection of pathogens via cell wall damage perception, is critical to advancing our understanding of plant resilience.

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Author contributions

JG: Figure design, Writing – original draft. PM: Writing – original draft, Funding acquisition, Supervision, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author(s) PM declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

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