



## Review

Calcium/calmodulin-mediated regulation of plant immunity<sup>☆</sup>Cécilia Cheval<sup>\*</sup>, Didier Aldon, Jean-Philippe Galaud, Benoît Ranty

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## ABSTRACT

Calcium is a universal messenger involved in the modulation of diverse developmental and adaptive processes in response to various physiological stimuli. Ca<sup>2+</sup> signals are represented by stimulus-specific Ca<sup>2+</sup> signatures that are sensed and translated into proper cellular responses by diverse Ca<sup>2+</sup> binding proteins and their downstream targets. Calmodulin (CaM) and calmodulin-like (CML) proteins are primary Ca<sup>2+</sup> sensors that control diverse cellular functions by regulating the activity of various target proteins. Recent advances in our understanding of Ca<sup>2+</sup>/CaM-mediated signalling in plants have emerged from investigations into plant defence responses against various pathogens. Here, we focus on significant progress made in the identification of CaM/CML-regulated components involved in the generation of Ca<sup>2+</sup> signals and Ca<sup>2+</sup>-dependent regulation of gene expression during plant immune responses. This article is part of a Special Issue entitled: 12th European Symposium on Calcium.

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## 1. Introduction

In their natural environment, plants are constantly exposed to fluctuating conditions, and they have evolved sophisticated mechanisms to perceive and respond to environmental cues in order to survive and propagate. To process the information perceived, plants use secondary messengers such as the Ca<sup>2+</sup> ion. An increase in free Ca<sup>2+</sup> levels in a cell compartment acts as a signal carrying specific information to be translated into appropriate biological responses by downstream effectors. Many exogenous and endogenous factors including light, temperature, drought and salt stress, pathogen-derived molecules and phytohormones provoke elevations of free Ca<sup>2+</sup> levels in different compartments of plant cells [1]. The Ca<sup>2+</sup> level peaks with spatio-temporal characteristics depending on the nature and the strength of the primary stimulus. These stimulus-specific patterns of Ca<sup>2+</sup> signals, also called Ca<sup>2+</sup> signatures, result from a tight control of the activities of channels and pumps, present on the plasma-membrane and endomembranes, that govern Ca<sup>2+</sup> flux between neighbouring compartments [2]. As plants appear to lack most of the Ca<sup>2+</sup> channels found in animals, the

search for ion channels initiating Ca<sup>2+</sup> elevation in plant cells has been a topic of intense research that has provided evidence for the contribution of cyclic nucleotide gated channels, glutamate-like receptor channels and two-pore channels to Ca<sup>2+</sup> signalling in plants [3–5]. Ca<sup>2+</sup> extrusion systems that restore a basal Ca<sup>2+</sup> level after a Ca<sup>2+</sup> rise are represented by Ca<sup>2+</sup>-ATPase pumps and Ca<sup>2+</sup>/proton exchangers [6,7]. Ca<sup>2+</sup> efflux processes are as important as Ca<sup>2+</sup> influx events in shaping defined Ca<sup>2+</sup> signals, and both processes are subject to complex regulation in order to coordinate their respective activities.

Ca<sup>2+</sup> signatures are recognized by Ca<sup>2+</sup> binding proteins that translate Ca<sup>2+</sup> signals into cellular responses through Ca<sup>2+</sup>-dependent regulation of downstream effectors. Most Ca<sup>2+</sup> sensor proteins possess EF hand motifs, a helix-loop-helix structure that binds one Ca<sup>2+</sup> ion [8]. Upon Ca<sup>2+</sup> binding, Ca<sup>2+</sup> sensors undergo conformational changes that promote either their own catalytic activity or their interaction with target proteins. Plants have a superfamily of EF hand proteins with at least 250 members predicted from the genome of the model plant *Arabidopsis thaliana* [9], and those known to function as Ca<sup>2+</sup> sensors and transducers are mainly represented by three sub-families: calmodulin (CaM) and calmodulin-like proteins (CMLs), Ca<sup>2+</sup>-dependent protein kinases (CPKs), calcineurin B-like proteins (CBLs) and their interacting protein kinases [10]. CaM, a well known Ca<sup>2+</sup> sensor found in all eukaryotes, is highly conserved during evolution, whereas CMLs, CPKs and CBLs appear to be restricted to plants and lower protists [11].

Because Ca<sup>2+</sup> acts as a versatile second messenger in various developmental processes and adaptation responses, progress in our understanding of Ca<sup>2+</sup> signalling systems has emerged from studies performed in various fields of plant biology. In particular, investigations on plant defence strategies against pathogens have greatly contributed

**Abbreviations:** CaM, calmodulin; CML, calmodulin-like; CPK, calcium-dependent protein kinase; CBL, calcineurin B-like; Pst, *Pseudomonas syringae* pathovar tomato; PAMP, pathogen-associated molecular pattern; ETI, effector-triggered immunity; PTI, PAMP-triggered immunity; HR, hypersensitive response; ACA, autoinhibited Ca<sup>2+</sup>-ATPase; CNGC, cyclic nucleotide-gated channel; RSS, RNA silencing suppressor; TF, transcription factor; CAMTA, calmodulin binding transcription activator; SA, salicylic acid; NO, nitric oxide

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to identifying components involved in the generation and processing of  $\text{Ca}^{2+}$  signals, and to demonstrating their roles in plant immunity [12,13]. Because exhaustive reviews on  $\text{Ca}^{2+}$  signalling in plants are regularly published, we will focus here on recent advances in  $\text{Ca}^{2+}$ /CaM-mediated signalling during plant–pathogen interactions with an emphasis on key components involved in the generation of  $\text{Ca}^{2+}$  signals and modulation of gene expression. Readers can also refer to recent articles reviewing the function of other  $\text{Ca}^{2+}$  sensor proteins including CPKs and CBLs, in immune and stress signalling [14–16].

## 2. $\text{Ca}^{2+}$ signals in plant immunity

Plants defend themselves against potential pathogens by using two main strategies [17]. The first strategy, referred as to non-host resistance, is initiated by the recognition of conserved pathogen-associated molecular patterns (PAMPs) by pathogen recognition receptors [18]. Typical examples of PAMPs are flg22 and elf18, two peptides derived respectively from bacterial flagellin and the elongation factor Tu, and fungal chitin. Each of these PAMPs is specifically recognized by a distinct receptor kinase. Perception of PAMPs activates diverse signalling events including the generation of  $\text{Ca}^{2+}$  signals and oxidative burst, the production of hormones and phosphorylation cascades, leading to a broad and non-specific resistance, called PAMP-triggered immunity (PTI). To counteract this basal defence, pathogens can deliver a range of effectors into plant cells that suppress PTI, thus allowing the propagation of pathogens in plant tissue and occurrence of disease. In a second strategy, plants activate another layer of defence, called effector-triggered immunity (ETI), which is initiated by the specific recognition of a pathogen effector by the corresponding plant resistance protein. ETI is a robust and specific resistance that often leads to the hypersensitive response (HR). The HR is a programmed cell death of plant cells surrounding the site of infection, which is believed to prevent further spread of the pathogen in plant tissue [19].

One of the earliest signalling events observed after the recognition of a pathogen is ion fluxes across the plasma membrane including influx of

$\text{Ca}^{2+}$  into the cytosol [12]. Transformed plants expressing aequorin, a  $\text{Ca}^{2+}$  sensitive luminescent protein, have been used to monitor changes in intracellular  $\text{Ca}^{2+}$  levels after pathogen inoculation or application of PAMPs. Thus, distinct cytosolic  $\text{Ca}^{2+}$  signatures have been described in *Arabidopsis* leaves after infiltration with various strains of the bacterial pathogen *Pseudomonas syringae* (*Pst*) [20]. All strains produce a rapid and transient rise in cytosolic  $\text{Ca}^{2+}$  concentrations with a maximum peaking at around 10 min after pathogen challenge. In addition, avirulent strains of *Pst* which trigger the HR, elicit a second and sustained increase in cytosolic  $\text{Ca}^{2+}$  levels, whereas virulent strains do not. Interestingly, preventing the  $\text{Ca}^{2+}$  influx with  $\text{LaCl}_3$ , a general  $\text{Ca}^{2+}$  channel blocker, results in the suppression of the HR, suggesting a crucial role of  $\text{Ca}^{2+}$  in ETI. Similar studies have been performed after plant treatment with PAMPs such as flg22 and elf18, or other elicitors of plant defence, to show that different PAMPs and elicitors induce distinct cytosolic  $\text{Ca}^{2+}$  signatures [21]. Moreover, transgenic plants expressing aequorin targeted to different cellular compartments have revealed that PAMPs and elicitors can induce  $\text{Ca}^{2+}$  signatures not only in the cytosol, but also in the nucleus, mitochondria or chloroplasts, suggesting the integration of all organelles in plant defence systems [22,23].

Little is known about the channels and pumps controlling  $\text{Ca}^{2+}$  transport in plant cells [24]. Recently, a collection of mutants obtained by a chemical mutagen treatment of transgenic aequorin plants, has been used to isolate mutated plants exhibiting a disordered  $\text{Ca}^{2+}$  signal in response to flg22 treatment [25]. Interestingly, some mutants show differential phenotypes induced by various PAMPs, and further characterization of these plants will likely lead to the discovery of key actors required for the generation and/or regulation of  $\text{Ca}^{2+}$  signals during PAMP signalling. Other genetic approaches performed to isolate mutants with impaired pathogen resistance, have recently revealed the essential roles of  $\text{Ca}^{2+}$  permeable channels, such as cyclic nucleotide-gated channels (CNGCs), and  $\text{Ca}^{2+}$  pumps, like autoinhibited  $\text{Ca}^{2+}$ -ATPases (ACAs), in plant immunity (Fig. 1). CNGCs are non-selective cation channels that were shown to conduct  $\text{Ca}^{2+}$  through the plant cell plasma-membrane [26]. Disruption of *CNGC2* or *CNGC4* genes in *Arabidopsis* results in an

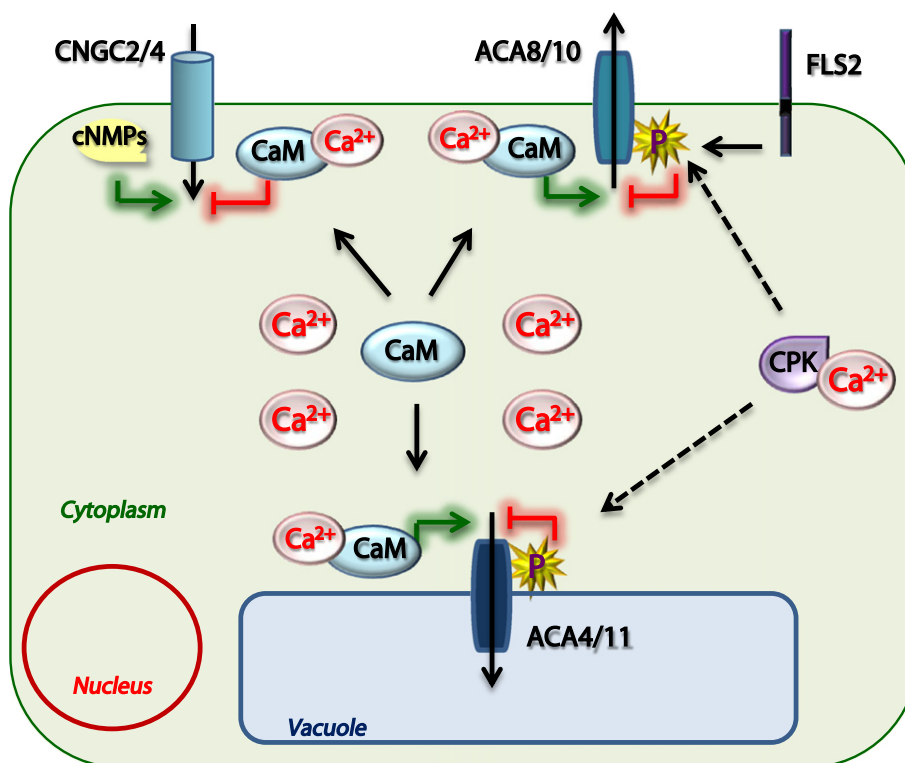


Fig. 1. Role of  $\text{Ca}^{2+}$  and CaM in regulating the activities of  $\text{Ca}^{2+}$  influx/efflux systems involved in plant immunity. Details are given in the text.

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