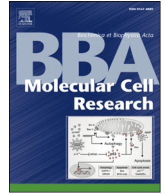
ARTICLE IN PRESS
BBAMCR-17514; No. of pages: 5; 4C: 2
Biochimica et Biophysica Acta xxx (2015) xxx–xxx

Contents lists available at ScienceDirect
Biochimica et Biophysica Acta
journal homepage: www.elsevier.com/locate/bbamcr



Review

Calcium is an organizer of cell polarity in plants☆

Ellie Himschoot [a,b], Tom Beeckman [a,b], Jiří Friml [c], Steffen Vanneste [a,b,*]

[a] Department of Plant Biotechnology and Bio-informatics, Ghent University, Technologiepark 927, B-9052 Ghent, Belgium
[b] Department of Plant Systems Biology, VIB, Technologiepark 927, B-9052 Ghent, Belgium
[c] Institute of Science and Technology Austria (IST Austria), Am Campus 1, 3400 Klosterneuburg, Austria

ARTICLE INFO

Article history:
Received 26 January 2015
Received in revised form 5 February 2015
Accepted 17 February 2015
Available online xxxx

Keywords:
Calcium
Polarity
Trafficking
GTPase
Tension
Arabidopsis

ABSTRACT

Cell polarity is a fundamental property of pro- and eukaryotic cells. It is necessary for coordination of cell division, cell morphogenesis and signaling processes. How polarity is generated and maintained is a complex issue governed by interconnected feed-back regulations between small GTPase signaling and membrane tension-based signaling that controls membrane trafficking, and cytoskeleton organization and dynamics. Here, we will review the potential role for calcium as a crucial signal that connects and coordinates the respective processes during polarization processes in plants. This article is part of a Special Issue entitled: 13th European Symposium on Calcium.

© 2015 Elsevier B.V. All rights reserved.

1. Introduction to polarity and plant development

At its simplest level, polarity can be defined as an asymmetric distribution of components along one or more axes, thereby breaking symmetry [1]. The most basic type of polarity involves establishing a single polar domain and can be found in a wide range of biological processes in unicellular as well as in multicellular organisms, ranging from asymmetric cell divisions, polarized axon growth, directional movement of motile cells, pollen tube and root hair formation in plants, zygote polarization in algae, etc. In each of these examples, the polarity is defined by the local accumulation of cellular components to one side of the cell.

In multicellular organisms, cells are often embedded in a three-dimensional tissue context, requiring additional dimensions of polarity. Hitherto, molecular markers exist defining apical and basal polarity (reflecting position along the embryonic axis), as well as inner- and outer-lateral polar domains (radial polarity) that can coexist within a single plant cell [2]. In addition to these four polar domains, specialized cell types have the capacity to develop additional polar features, superimposed on or across other polar domains, such as in the endodermis that develops casparian strips that encircle the cells [3] and root hairs that develop at a discrete positions in the outer-lateral domains of root epidermal cells [4]. Another complex manifestation of polarity in plants is seen during the morphogenesis of leaf epidermal cells in dicotyledons that is characterized by interdigitation of adjacent cells via the coordinated formation of lobes and indentations [5].

How plants can generate such complex polarity patterns remains poorly understood. Yet, several of the mechanisms underlying generation and maintenance of polarity become identified step by step. Two important cellular processes control polarity: 1) anisotropic membrane trafficking by local delivery or removal of specific membrane proteins and lipids, and 2) the polar organization and dynamics of the cytoskeleton. These cellular processes are believed to be controlled by signals derived from the local activity of small GTPases (ROPs) and from cellular mechanosensing mechanisms. These different aspects of polarity are tightly interconnected, making it difficult to assess their individual contribution to polarity and how they are coordinated to generate and maintain polarity.

In this review, we will focus on the mechanisms by which the second messenger Ca^{2+} is connected to each of the aforementioned polarity processes and signaling cascades and we elaborate on how Ca^{2+} could serve as a general coordinative and integrative signal for plant polarity, a principle that we propose not to be restricted to tip-growing cells (Fig. 1).

2. Calcium hallmarks polarity

Calcium is an elusive second messenger because it can be triggered by a wide range of signals and is transient in nature [6]. Therefore, it is commonly described in terms of Ca^{2+} signatures that can be very

☆ This article is part of a Special Issue entitled: 13th European Symposium on Calcium.

* Corresponding author at: Department of Plant Biotechnology and Bio-informatics, Ghent University, Technologiepark 927, B-9052 Ghent, Belgium.
E-mail addresses: elhim@psb.vib-ugent.be (E. Himschoot), tobee@psb.vib-ugent.be (T. Beeckman), jiri.friml@ist.ac.at (J. Friml), stnes@psb.vib-ugent.be (S. Vanneste).

http://dx.doi.org/10.1016/j.bbamcr.2015.02.017
0167-4889/© 2015 Elsevier B.V. All rights reserved.

Please cite this article as: E. Himschoot, et al., Calcium is an organizer of cell polarity in plants, Biochim. Biophys. Acta (2015), http://dx.doi.org/10.1016/j.bbamcr.2015.02.017

ARTICLE IN PRESS

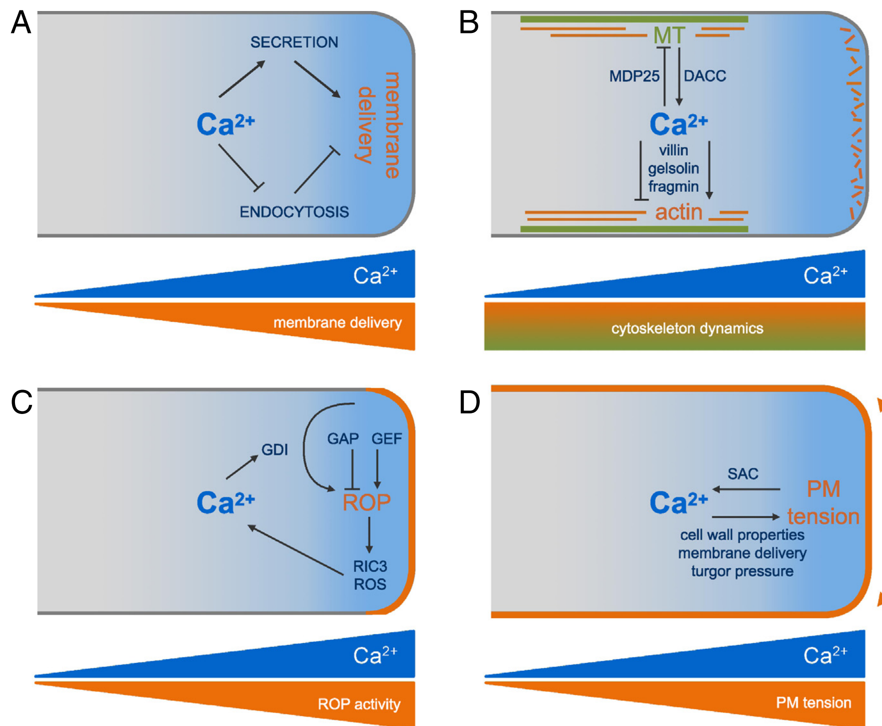


Fig. 1. Interconnection between Ca^{2+} and polarity components. A. A Ca^{2+} gradient spatially coordinates membrane trafficking. High Ca^{2+} concentrations to one side of a cell locally stimulate secretion while reducing (clathrin-mediated) endocytosis thereby locally promoting membrane delivery. The blue and orange color represent the gradients in Ca^{2+} and membrane delivery respectively. B. A Ca^{2+} gradient differentially controls cytoskeleton dynamics. Ca^{2+} controls F-actin dynamics and organization through Ca^{2+}-dependent actin regulating proteins of the villin/gelsolin/fragmin superfamily, regulating actin organization and dynamics. Via MICROTUBULE-DESTABILIZING PROTEIN25 (MDP25) Ca^{2+} can destabilize cortical microtubules (MT). In turn, MTs can stabilize Ca^{2+} signaling via controlling depolarization-activated Ca^{2+}channels (DACC). The blue color represents the Ca^{2+} gradient and the orange/green color the actin/MT dynamics respectively. C. Interaction between Ca^{2+} and ROP signaling to generate and maintain cell polarity. Polarized ROPs (orange gradient) locally stimulate Ca^{2+} entry through the ROP effector RIC3 and ROP-induced reactive oxygen species (ROS) production. ROP activity is positively or negatively regulated by GEFs or GAPs respectively. Polar localization of ROPs to the apex is maintained by GDI which in turn can be controlled by Ca^{2+}. The blue and orange color represent the gradients in Ca^{2+} and ROP activity respectively. D. Interplay between Ca^{2+} and PM tension. The plant cell wall and local differences in plasma membrane (PM) tension both contribute to cell polarization. Upon cellular growth, increased PM tension results in opening of stretch-activated Ca^{2+}channels (SACs) resulting in local Ca^{2+} influx. Ca^{2+} itself can control cell wall rigidity and membrane delivery and turgor pressure to regulate PM tension. The blue and orange color represent the Ca^{2+}gradient and locally high PM tension respectively.

local and short-lived, making it often difficult to detect reliably. Under these limitations, a sharp Ca^{2+} gradient can be detected in the tip of growing pollen tubes and root hairs, that is essential for polar growth [7,8]. In addition, local Ca^{2+} signaling is also central to polarity establishment in fucoid algal zygotes [9]. Importantly, manipulations that refocus Ca^{2+} signals are sufficient to reorient polarity of tip growth, not only in pollen tubes [10], but also in root hairs [11] demonstrating the potential of Ca^{2+} gradients as instructive signals for polarity. The role of Ca^{2+} as a regulator of polarity is mainly derived from studies on tip growth in pollen tubes, a cell type that is easily accessible, and expresses only a relatively small subset of the Ca^{2+} toolkit. However, it must be noted that Ca^{2+} levels were also found to impact on apical–basal polarity in root cells [12], suggesting that the role of Ca^{2+} in plant polarity is not restricted to tip growth.

At least four distinct Ca^{2+} channels contribute to the Ca^{2+} gradient that exists at the pollen tube tip. The first, and most important Ca^{2+} channels for the tip-focused Ca^{2+} gradient, are stretch-activated Ca^{2+} channels (SAC) that open in response to plasma membrane strain, such as the strain associated with rapid growth [13]. However, the underlying molecular nature of these channels remains completely unknown. Secondly, members of the GLUTAMATE RECEPTOR-LIKE (GLR) family, AtGLR1.2 and AtGLR3.7 have been demonstrated to form Ca^{2+} channels in pollen tubes in response to D-Serine derived from the pistil to guide pollen tube growth [14]. Thirdly, several *CYCLIC NUCLEOTIDE GATED CATION CHANNEL* (*CNGC*) genes have been implicated in pollen tube growth [7]. Among them, CNGC18 displays a clear apical localization, with its strongest localization just behind the apex, a position that would allow to refocus the Ca^{2+} maximum in response to directional cues [15]. A fourth family of Ca^{2+} channeling proteins that could contribute to tip-focused Ca^{2+} gradients are the ANNEXINs, that can generate Ca^{2+} permeable channels in response to hydroxyl radicals [16]. Whereas these Ca^{2+} channels reflect mechanisms by which Ca^{2+} enters the cell through the plasma membrane, Ca^{2+} ATPases are continuously active to move Ca^{2+} from the cytosol into adjacent cellular compartments or the apoplast. These mechanisms can contribute to shaping the Ca^{2+} signal [7]. Several of these Ca^{2+} ATPases, such as ACA9, do not show polar localization [17], but are instead activated by local high Ca^{2+} concentrations, acting to dissipate Ca^{2+} signals.

Given that Ca^{2+} carries no structural information, the information embedded in Ca^{2+} gradients and temporal signatures needs to be decoded and translated into a cellular response. This can be achieved by a complex set of Ca^{2+} binding proteins (>250 in *Arabidopsis*) [18] that represent Ca^{2+} sensors with enzymatic activity (Ca^{2+} sensor responders; Ca^{2+}-dependent protein kinase/CPK) or without enzymatic activity (Ca^{2+} sensor relays; calmodulin/CaM, calmodulin-like/CML, calcineurin B-like/CBL). Strong polarity defects in pollen tubes have thus far only been reported for overexpression of CPKs [19], supporting the importance of local CPK activity in directing pollen tube polarity [20]. Many known targets of CPKs are ion channels, allowing to regulate osmotic pressure and membrane potential in the context of Ca^{2+} signals [6]. Moreover, it was recently found that CPK32 directly contributes to the tip-focused Ca^{2+} gradient by activating the Ca^{2+} permeability of CNGC18 [21]. Moreover, CNGC activity can be further modulated by

Please cite this article as: E. Himschoot, et al., Calcium is an organizer of cell polarity in plants, Biochim. Biophys. Acta (2015), http://dx.doi.org/10.1016/j.bbamcr.2015.02.017

Download English Version:

https://daneshyari.com/en/article/10801903

Download Persian Version:

https://daneshyari.com/article/10801903

Daneshyari.com