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Cell polarity signaling

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Cell polarity is a fundamental entity of living organisms. Cells must receive accurate decisions where to divide and along which plane, along which axis to grow, where to grow structures like flagellum or filopodium and how to differentially respond to external stimuli. In multicellular organisms cell polarity also regulates cell–cell communication, pattern formation and cell identity. In eukaryotes the RHO family of small G proteins have emerged as central regulators of cell polarity signaling. It is by now well established that ROPs, the plant specific RHO subfamily members, affect cell polarization. Work carried out over the last several years is beginning to reveal how ROPs are activated, how their activity is spatially regulated, through which effectors they regulate cell polarity and how they interact with hormonal signaling and other polarity determinants. The emerging picture is that while the mechanisms of cell polarity signaling are often unique to plants, the principles that govern cell polarization signaling can be similar. In this review, we provide an updated view of polarity signaling in plants, primarily focusing on the function of ROPs and how they interact with and coordinate different polarity determinants.

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Introduction

Cell polarity is a fundamental entity of most if not all cells (reviewed in [1–3]). Polarity starts by breaking symmetry, typically characterized by asymmetric distribution of polarity determinants. Some of the core mechanisms of cell polarity are conserved in eukaryotes and include local activation of RHO GTPases, which are known to regulate a diversity of downstream pathways. Plants have a single family of RHO GTPases, known as ROPs (Rho of Plant), which are implicated as central regulators of cell polarity (reviewed in [4–6]).

ROPs are believed to have diverged from the Rac family comprising a unique subfamily [7,8]. In the absence of Cdc42 and Rho subfamilies that exist in fungi and animal cells, ROPs have been suggested to carry out diverse functions. While tempting, such a conclusion should be taken with caution given recent work showing that earlier phylogenetic analysis of the RHO family has been biased by focusing on Opisthokonts (fungi and animal) lineages [8]. Interestingly, no *ROP* genes have been identified in a subgroup of green algae that includes *Chlamydomonas reinhardtii* and *Chlorella variabilis*. In other green algae such as *Ostreococcus* spp. there is one ROP. In the moss *Physcomitrella patens* and the lycophyte *Selginella molendorffii* there are four and two ROPs, respectively [8,9]. The algae and non-seed plant ROPs all terminate with a canonical prenylation CaaX box motif. Seed plants have two types of ROPs: type-I ROPs, which terminate with a C-terminal CaaX box motif, similar to non-seed plants and algae ROPs, and type-II ROPs, which contain a different C-terminal end. The type-II ROPs are not prenylated and are thought to have evolved from type-I ROPs due to insertion of an additional intron at the 3′-end [10,11]. In angiosperms the ROP family has greatly diversified reaching up to 11 members in Arabidopsis, 13 members in poplar and nine members in maize [9]. In Table 1 we have listed the 11 Arabidopsis ROPs and grouped them according to their type and similarity, based upon the most extensive phylogenetic analysis of ROPs available to date [9].

Here we are reviewing the most recent literature on cell polarity signaling in plants with special emphasis on regulation of ROP activity and signaling, membrane heterogeneity, and external cues affecting polarity. In addition we highlight both the commonalities and differences between plants and other eukaryotes and describe some novel plant specific polarity determinants. Due to space limitations, important aspects such as pathogen-induced polarity, and hormone signaling interactions, which deserve reviews in their own right, will not be covered. In addition, we apologize to colleagues whose work we have not cited.

Spatial activation and inactivation of ROPs

Leaf epidermal pavement cells are characterized by diffuse growth that involves spatially and intercellular regulated ROP activity that results in the formation of the characteristic lobes and indentations. Both pollen tubes and root hairs are characterized by unidirectional tip-growth, which requires highly restricted ROP activity at the growing tip. Immunolocalization studies carried with pea pollen tubes, Arabidopsis roots and root hairs, tobacco BY2 cells and maize leaf epidermis showed that similar to fungal and animal RHO proteins, ROPs are

Table 1

Arabidopsis ROPs. Color rectangles indicate high sequence similarity. Division to clades is according to Fowler [9]. Non seed plants: denotes ROPs with highest degree of similarity to *Physcomitrella patens* ROPs

Name	Alternative names	Gene ID	Type	Clade	Non seed plants	Seed plants	Expression in pollen
ROP7	Arac2/AtRAC2	At5g45970	I	1	+	+	
ROP8	Arac9/AtRAC9	At2g44690	I	1	+	+	
ROP1	Arac11/AtRAC11	At3g51300	I	2	–	+	+
ROP3	Arac1/AtRAC1	At2g17800	I	2	–	+	+
ROP5	Arac6/AtRAC6	At4g35950	I	2	–	+	+
ROP2	Arac4/AtRAC4	At1g20090	I	2	–	+	
ROP4	Arac5/AtRAC5	At1g75840	I	2	–	+	
ROP6	Arac3/AtRAC3	At4g35020	I	2	–	+	
ROP9	Arac7/AtRAC7	At4g28950	II	3	–	+	
ROP10	Arac8/AtRAC8	At3g48040	II	3	–	+	
ROP11	Arac10/AtRAC10	At5g62880	II	3	–	+	

primarily localized in the plasma membrane [12•,13–15]. In agreement, it has been shown in numerous studies that translational fusions of ROPs with fluorescent proteins primarily localize at the plasma membrane [5,15,16•,17–20]. Thus, a central question emerges: how is spacial regulation of ROPs achieved?

Like other members of the RHO family, ROPs function as molecular switches that exist in active GTP-bound and inactive GDP-bound states. Several lines of evidence indicate that ROP activation/inactivation cycles are spatially regulated (Figure 1). GDP/GTP exchange is facilitated by GEFs (guanine nucleotide exchange factors). In plants there are two types of GEFs for ROPs: the plant specific PRONE domain GEFs, designated ROPGEFs [21] and the Dock family GEFs, which in Arabidopsis is represented by a single member called SPIKE1 (SPK1) [22]. It has been shown that in pollen tubes and root hairs ROPGEFs are activated by receptor like kinases (RLKs), which phosphorylate and relieve autoinhibition by the C-terminal domain of the ROPGEF [23,24]. In tobacco pollen tubes several Arabidopsis ROPGEFs accumulate at the cell apex [25] where they possibly interact with and are activated by RLK such as PRK2a [23,24]. In root hairs, AtROPGEF1 interacts with the RLK FERONIA (FER) and induces ROP activation [26].

ROPGAPs (GTPase activating protein) enhance GTP hydrolysis and ROP inactivation [27]. Following expression in tobacco pollen tubes AtROPGAP1 localized to the pollen tube shank [28], whereas the ROPGAP REN1 localized subapically below the growing pollen tube tip [29]. Taken together, in the pollen tube tip concentrated restricted ROP activity domain is achieved by spatial distribution of ROPGEFs and ROPGAPs. Likewise, during secondary wall formation in metaxylem cells, both ROPGEF4 and ROPGAP3 are required for reconstitution of active ROP11 domains [30••]. How ROPGEFs, ROPGAPs and RLKs accumulate at specific spatially distributed domains is still an open question.

In addition to GEFs and GAPs, RhoGDIs (Rho GDP Dissociation Inhibitor) are a third group of ROP regulators. Unexpectedly, despite their predicted importance in RHO regulation, knockout mutants of RhoGDI in *Saccharomyces cerevisiae* (*S. cerevisiae*) and mice have very mild phenotypes, indicating that in these organisms RhoGDI function is redundant with other cellular components [31]. In Arabidopsis there are three RhoGDIs designated RhoGDI1, RhoGDI2a, and RhoGDI2b. Mutants of RhoGDI1 also called SCN1 develop root hairs with multiple tips [32] and wavy pollen tubes [33]. These phenotypes may result from the function of RhoGDIs in ROP recycling [34] or from ROP hyper activation [31]. $RhoGDI2a^{RNAi}$ pollen tubes are depolarized similar to pollen tubes overexpressing constitutively active (CA) ROP1. In contrast, overexpression of RhoGDI2a suppresses ROP1-induced depolarization [33]. Taken together, these data show that a delicate balance between ROP and RhoGDI levels is critical for cell polarization in plants.

Modeling of *S. cerevisiae* bud formation shows that polarity can be established by spontaneous polarization of Cdc42 in the absence of spatial cues, via a mechanism that involves a positive feedback loop. Cdc42 spontaneous polarization is actin independent, however it requires the GEF Cdc24 and the scaffold protein Bem1 that interacts with both $Cdc42^{GTP}$ and Cdc24. It was proposed that the GEF activity of Cdc24 converts more Cdc42 molecules to active $Cdc42^{GTP}$, which in turn interact with Bem1. This positive feedback loop creates domains of active Cdc42 at the membrane that determine the site of bud location [35]. Recently, an alternative actin-independent mechanism of Cdc42 polarization was described in [36]. The authors propose existence of distinct pathways for Cdc42 activation and localization,