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Cell Polarity in Plants: The Yin and Yang of Cellular Functions

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Abstract

Spatial organization is fundamental for the performance of living organisms and is reflected in a distinct distribution of structures and molecules down to the subcellular level. In particular, eukaryotic cells harbor a vast range of possibilities for distributing organelles, the cytoskeleton or the extracellular matrix in an active and highly regulated manner. An asymmetric or polar distribution is rather the rule than the exception and often reflects a particular position or orientation of a cell within a multicellular body. Here, we highlight recent insights into the regulation of cell polarity in plants and reveal the interactive nature of underlying molecular processes.

Introduction

The morphology of living organisms is organized in four dimensions and naturally includes symmetric and asymmetric structures. One example is the human body which displays a bilateral symmetry overall but inner organs become asymmetric as early as six weeks after the onset of embryogenesis [1]. As one determinant of breaking initial symmetry, ciliary motility is possibly responsible for the transport of morphogens preferentially to one side of developing organs [1]. In plants, there are highly symmetric body structures, like radial flowers or the bilateral leaves. However, there are also fundamental asymmetric developmental processes which are likewise reflected in polar organization of cellular and subcellular structures. Examples of those are the transition from radial to bilateral embryo organization or the continuous and directional organogenesis in adult plants.

Cell polarity, defined as the asymmetric distribution of any molecular or morphological feature within a single cell, is essential for establishing these structures and for any directional physiological or developmental process. In conceptual terms, cell polarity may depend on a fixed or self-maintaining molecular inhomogeneity within a cell or be constantly adjusted by asymmetric fields of signals present in the cellular environment (Figure 1). This distinction may also be applied to formative cell divisions after which two daughter cells follow different fates. Fate decision either depends on cell polarity already present and carried over from the mother cell (intrinsic) or be established after division based on exposure to a different regime of signals (extrinsic, Figure 1). Thus, cell polarity is not only important for cellular functions but fulfils essential roles in developmental

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processes. In this review, we discuss recent insights into the regulation of cell polarity in plants. Due to space constraints, we focus predominantly on the onset of cell polarity and focus exemplarily on the regulation of polar auxin transport, planar polarity in root hair cells and polar growth of pollen tubes. For further reading, we refer the interested reader to other cases of cell polarity which also have received substantial attention like the inner-outer polarity of the root endodermis or developing stomata [2,3].

Polar Auxin Transport: New Lessons from Pavement Cells

The exceptional dynamics of the distribution of the phytohormone auxin is essential for the initiation, the plasticity and the robustness of developmental programs [4]. The generation of instructive auxin maxima and minima depends on the polar transport of auxin which, in turn, is determined by various groups of auxin transporters. Among them, the group of PIN-FORMED (PIN) auxin exporters have received most of the attention. These efforts have resulted in an immense amount of experimental data [5] associating polar localization of PIN proteins with cellular features like lipid composition of the plasma membrane or co-localization with regulatory proteins [6,7]. Both theoretical models and experimental data strongly suggest that differential distribution of auxin itself acts as an instructive and reinforcing signal for the initial establishment of cell polarity through a positive effect on PIN accumulation and activity [8]. In agreement with a highly dynamic and adjustable system, PIN proteins cycle continuously between the plasma membrane and the endomembrane system, and selective endocytosis by vesicular transport is one feature essential for their polar distribution [9]. As revealed in *Arabidopsis*, endocytosis predominantly depends on the ARF-guanine nucleotide exchange factor (ARF-GEF) family member GNOM which activates small GTPases of the ARF (ADP ribosylation factor) class [10]. However, a concerted role of GNOM and its closest homolog, GNOM-LIKE1 (GNL1), in a secretory trajectory through the Golgi-apparatus has been shown to be important for PIN polarity more recently (Figure 2) [10,11]. As a highly accessible system, the *de novo* polarization of cells in the leaf epidermis, the pavement cells, has been used to investigate the onset of PIN protein polarity. Although a mechanism of non-nuclear auxin perception is currently under heavy debate and certain findings have to be clarified [12], interdigitation of pavement cells is auxin-dependent and involves the rapid activation of the RHO OF PLANTS (ROP) GTPases ROP2 and ROP6. Auxin-dependent ROP activation leads to the local accumulation of cortical actin microfilaments which, in turn, decreases endocytosis of PIN proteins [13,14] (Figure 2). For this effect, plasma membrane-localized transmembrane kinases (TMKs) are required [15]. In *tmk1;2;3;4* quadruple mutants PIN1 localization is altered, interdigitation is defective and auxin-dependent ROP2/6 activation is strongly impaired. Furthermore, membrane distribution of the ROP2 effector ROP INTERACTIVE CRIB MOTIF-CONTAINING4 (RIC4) and microtubule association of the ROP6 effector RIC1 is strongly decreased in *tmk1;2;3;4* plants [14,15]. Thus, a complex and very local auxin-dependent interplay between membrane-localized and cytosolic components including the cytoskeleton seems to determine PIN protein levels and, consequently, overall cell polarity (Figure 2).

As one important feature influencing PIN polarity via directed transport in a GNOM-independent manner, the phosphorylation status of PINs determined by the AGCVIII kinases

PINOID (PID), WAG1 and WAG2 and the antagonistic phosphatase complex PP2A has been identified [16–20]. Although also other AGCVIII kinases, particularly the D6 PROTEIN KINASE (D6PK)-like kinases, localize polarly at plasma membranes and activate PINs via phosphorylation, partly, at the same sites, only PID/WAG-dependent phosphorylation determines PIN localization [7,21] (Figure 2). In fact, PID/WAG-dependent phosphorylation is important for the integration of environmental stimuli into plant growth processes. One striking example is the relocalization of PIN3 during the phototropic bending of the hypocotyl which is fully PID/WAG-dependent [20]. Interestingly, D6PK-dependent but not PID/WAG-dependent phosphorylation is rapidly increased upon auxin treatments [21] suggesting another distinct leverage for auxin to enhance its own polar transport.

A connection between PIN protein regulation and a distinct membrane composition has been revealed when a phosphatidylinositol-4,5-bisphosphate (PtdIns(4,5)P₂) dependence of polar PIN and D6PK localization was discovered [22,23]. Although cause and consequence are difficult to disentangle, mutants lacking two PtdIns4P 5-kinases important for the generation of PtdIns(4,5)P₂, display defects in PIN polarity, auxin distribution and auxin-dependent development [23]. Furthermore, D6PK is found in sterol- and phosphatidylinositol-phosphate-5-kinase 3 (PIP5K3)-rich domains determined for root hair bulging [22]. In fact, D6PK but also PID are able to bind phospholipids directly [22,24] being in line with their function as docking platforms for proteins towards the cytosol. Another connection between membrane composition and AGCVIII kinases, and thus polar auxin transport, is provided by the observation that PID/WAG kinases are activated by 3'-phosphoinositide-dependent protein kinase 1 (PDK1) *in vitro*, a kinase which interacts with PtdIns phosphates via its pleckstrin homology (PH) domain [25,26].

Planar Polarity of root epidermis cells

Comparable to molecular dipoles in magnetic fields, epithelial cells often show a common polarity along their layer which is designated as planar cell polarity (PCP). With the *Drosophila* wing epidermis having received considerable attention [27], *Arabidopsis* root epidermis cells are considered as a case of PCP in plants. As an expression of this polarity, root hairs always emerge from the basal end of epidermis cells arguing for the presence of extrinsic information determining hair cell polarity before hair bulging [28] (Figure 3). In fact, using hair bulging as a morphological marker for epidermis polarity, an auxin gradient across cells has been found to be instructive [29,30]. The gradient depends on a combination of regulated auxin transport and local biosynthesis with ethylene signaling acting upstream and GNOM acting downstream of auxin biosynthesis [29,30]. Interestingly, local accumulation of ROP2, 4 and 6 proteins is among the earliest bulging markers known to date [22,31] and, not surprisingly, the cytoskeleton is essential for the bulging process itself [32,33]. Assisted by *ACTIN2* (*ACT2*), *ACT7* is the main actin gene involved in root hair bulging in *Arabidopsis* [34]. Again, both genes function genetically downstream of ethylene signaling but upstream of polar ROP positioning [34] (Figure 3). Reflecting a possible interaction with the plasma membrane, cortical cytoskeleton reorganization is less pronounced in *sabre* (*sab*) mutants devoid of a mostly plasma membrane-associated protein of unknown function [35]. At the same time, bulging sites are more randomly distributed in *sab* and, at least on the genetic level, the *SAB* locus interacts with the *CLIP170*-

ASSOCIATED PROTEIN (CLASP) gene encoding a protein stabilizing and associating with microtubules. Together with the observation that *SAB* also regulates the direction of CLASP-labelled preprophase band microtubules to guide cell division orientation [35,36], this suggests that SABR is part of a mechanism translating extrinsic information into a distinct cell morphology (Figure 3).

However, as also true for other regulators of basic cellular processes influencing PCP [37], investigating the local translation of molecular into morphological cell polarity is a challenging enterprise. For example, similarly as ROPs, D6PK accumulates at bulging sites (Figure 3) and in *d6pk* mutants root hair cells are hyperpolar [22]. Whether this reflects a role of D6PK directly at the bulging site or an influence of D6PK on local auxin distribution needs still to be determined. In comparison, a rather specific regulator of actin reorganization during hair bulging seems to be the suppressor of PCP, ACTIN INTERACTING PROTEIN1-2 (AIP1-2). Although the AIP1-2 protein interacts with all widely expressed actins, *AIP1-2* expression is strongly associated with root hair cell identity possibly mediating some developmental specificity [34].

Polar growth of pollen tubes

In double fertilizing flowering plants, pollen tubes grow along the pistil after pollination – like in the case of root hairs mediated by tip growth – to deliver the non-motile sperm cells to the female gametes [38]. Neglecting the engulfed sperm cells, the pollen is a unicellular entity and, thus, directional growth of pollen tubes is an extreme case of cell polarity which, again, is regulated by a complex interplay between extrinsic and intrinsic molecular gradients (Figure 4). In addition to a whole spectrum of molecules important for guiding the tube to the ovule [38], polar tube growth itself depends on the local secretion of cell wall components, on membrane-associated ion dynamics and on the control of cytoskeleton and vesicle localization [39,40]. As a reemerging pattern, *Arabidopsis* GNOM contributes also in this case to a vibrant vesicle-based recycling of plasma membrane components, here together with its homolog GNL2 [41], and RIC1 contributes to the local regulation of cytoskeleton dynamics [42]. Consistently, members of the conserved oligomeric golgi (COG) complex important for retrograde trafficking of intra-Golgi vesicles has recently been shown to be essential for pollen tube growth [43]. As highly specific upstream components, tip-localized receptor complexes containing POLLEN RECEPTOR LIKE KINASES (PRKs), MALE DISCOVERER (MDISs), MDIS1-INTERACTING RECEPTOR LIKE KINASES (MIKs) and LOST IN POLLEN TUBE GUIDANCE (LIPs) receptor-like kinases, possibly in various combinations, act as a sensors for ovule-derived LURE peptides [44–46] serving as tube attractants [47,48]. Intracellularly, PRKs interact with pollen-specific ROP GUANINE NUCLEOTIDE-EXCHANGE FACTORS (ROPGEFs), which activate ROPs [44] providing a link to vesicle transport and cytoskeleton regulation. Interestingly, local levels of PRK6 respond fast to a change in the external LURE gradient implying that the LURE ligands themselves promote polar distribution of their own receptor complexes [44].

Not surprisingly, polar and vesicle-based deposition of cell wall material is essential for the tip-growth of cells including pollen tubes [49]. As candidates for providing essential feedback from the cell wall, membrane-bound proteins of the *Catharanthus roseus*

RECEPTOR-LIKE KINASE 1-like (CrRLKs) family have been identified [50]. The CrRLKs ANXUR1 (ANX1) and ANX2 are localized at the pollen tube tip, *anx1;anx2* double mutant pollen tubes burst prematurely [51,52] and ANX-overexpression leads to enhanced exocytosis and cell wall deposition [53]. Furthermore, the cytosolic Ca^{2+} gradient essential for tip growth [54] and which has recently been found to require the Ca^{2+} channel CNGC18 [55], is decreased in *anx1;anx2* pollen [53]. Strikingly, RUPTURED POLLEN TUBE (RUPO), a CrRLK important for pollen tube integrity in rice, interacts directly with potassium transporters [56]. Together with the observation that the mechanosensitive ion channel MSL8 prevents bursting of pollen tubes [57], these findings nicely underline that the polar growth of cells requires a tight and local regulation of the turgor pressure-based cell expansion on multiple levels.

Conclusions

Due to a thorough exploitation of genetic, molecular and optical tools, more and more factors important for plant cell polarity are revealed and gradually the picture becomes more complex. Partly, factors like regulators of vesicular transport or of the cytoskeleton reemerge in various contexts, but others are obviously specific for their respective processes and provide fascinating opportunities for revealing instructive interfaces between developmental programs and cell biology. Due to its interactive character and the sparseness of truly naïve initial states, regulation of cell polarity is, however, difficult to tackle. For example, is any extrinsic gradient the cause or the consequence of cell polarity or is there a constant feedback loop connecting both? To unravel this, not only localization of factors has to be determined with high spatio-temporal resolution and utmost sensitivity [58] but also these factors should be sensed or modulated at specific sites in individual cells [59,60]. Computational models integrating observations from cell biological investigations may be a solution to deal with the expected level of complexity necessary to consider [61]. Nevertheless, the importance of cell polarity for our understanding of the performance of organisms makes it a fascinating and most likely very rewarding enterprise to continue exploring this aspect in a systematic and systemic manner.

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Figure 1. Schematic representation of cell polarity. The asymmetry of intrinsic or extrinsic processes results in polar distribution or properties of subcellular features.

Figure 2. Simplified scheme of the regulation of PIN protein polarity. Originating from the trans-golgi network (TGN), PIN protein distribution depends on regulated vesicular transport and posttranslational protein modification.

Figure 3.

Planar polarity of root hair cells. Planar polarity of root hair cells is reflected by the emergence of hairs at the basal end of cells. The position of bulging depends on transport and local biosynthesis of auxin and involves the reorganization of the cortical cytoskeleton.

Figure 4.

Regulation of polar growth of pollen tubes. A complex interplay between extra- and intracellular components is essential for mediating a very local and directional expansion of the cell.