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Cell polarity: compassing cell division and differentiation in plants

Ying Zhang[1] and Juan Dong[1,2]

Protein polarization underlies directional cell growth, cell morphogenesis, cell division, fate specification and differentiation in plant development. Analysis of *in vivo* protein dynamics reveals differential mobility of polarized proteins in plant cells, which may arise from lateral diffusion, local protein–protein interactions, and is restricted by protein–membrane–cell wall connections. The asymmetric protein dynamics may provide a mechanism for the regulation of asymmetric cell division and cell differentiation. In light of recent evidence for preprophase band (PPB)-independent mechanisms for orienting division planes, polarity proteins and their dynamics might provide regulation on the PPB at the cell cortex to directly influence phragmoplast positioning or alternatively, impinge on cytoplasmic microtubule-organizing centers (MTOCs) for spindle alignment. Differentiation of specialized cell types is often associated with the spatial regulation of cell wall architecture. Here we discuss the mechanisms of polarized signaling underlying regional cell wall biosynthesis, degradation, and modification during the differentiation of root endodermal cells and leaf epidermal guard cells.

Addresses
[1] Waksman Institute of Microbiology, Rutgers, The State University of New Jersey, Piscataway, NJ 08854, USA
[2] Department of Plant Biology, Rutgers, The State University of New Jersey, Piscataway, NJ 08901, USA

Corresponding author: Dong, Juan (dong@waksman.rutgers.edu)

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Introduction

Cell polarity is fundamental to cell functions in all living organisms. How proteins are asymmetrically distributed in a cell and how polarized proteins regulate a diverse array of cellular events have been fascinating questions for biologists.

In animal systems, many polarized proteins, for example, Ste5 [1] and Bem1 [2] in yeast and PAR3/6 in *Caenorhabditis elegans* [3], are scaffold proteins that convene multiple components to ensure concerted interaction for signaling specificity and fidelity. Homologs of these conserved polarity proteins are not encoded in plant genomes. The plant-specific protein BREAKING OF ASYMMETRY IN THE STOMATAL LINEAGE (BASL) represents a polarity factor [4] that scaffolds a mitogen-activated protein kinase (MAPK) signaling cassette in Arabidopsis stomatal lineage cells [5]. How BASL is associated with the plasma membrane (PM) and how BASL polarity is maintained remain unknown.

In plants, protein polarization provides mechanisms for polar cell expansion (thus morphogenesis), asymmetric cell division and functional differentiation. A number of cell types produce daughter cells with unequal sizes and distinct cell fates. Such asymmetric cell divisions are often preceded by protein polarization that presumably leads to the specification of division plane orientation and/or differential cell fates [4,6,7]. What the polarity cue is and how this cue controls subsequent divisional asymmetries (size and fate) are fundamental questions in biology. Using stomatal lineage divisions in maize and Arabidopsis as model systems, we discuss how cell polarity might be instructive to division plane orientation in plants.

In multicellular organisms, cell differentiation typically manifests unique cell morphology and structures for specific physiological roles. One prominent example is that plant cells utilize localized cell wall modification to diversify cell form and function. The differentiation of root endodermal cells and leaf guard cells exemplifies the elaborate spatial regulation of cell wall architecture. Exciting progress has been made towards elucidating the formation of Casparian strip, a lignin band structure in Arabidopsis roots (reviewed in [8]), at a polarized cel signaling level [9]. The differentiation of stomatal guard cells requires spatiotemporally dynamic cell wall deformation and modification that may also require polarized cell signaling.

Protein dynamics and polarity regulation at the plasma membrane

Protein dynamics are critical for their cellular functions. Characterization of protein dynamics and how these dynamics relate to a protein's physiological roles *in vivo* is enabled by advanced microscopy techniques, for

example, FRAP (fluorescence recovery after photobleaching) and photoactivation [10], which have greatly enlightened our understanding of the mechanisms underlying the regulation of cell polarity.

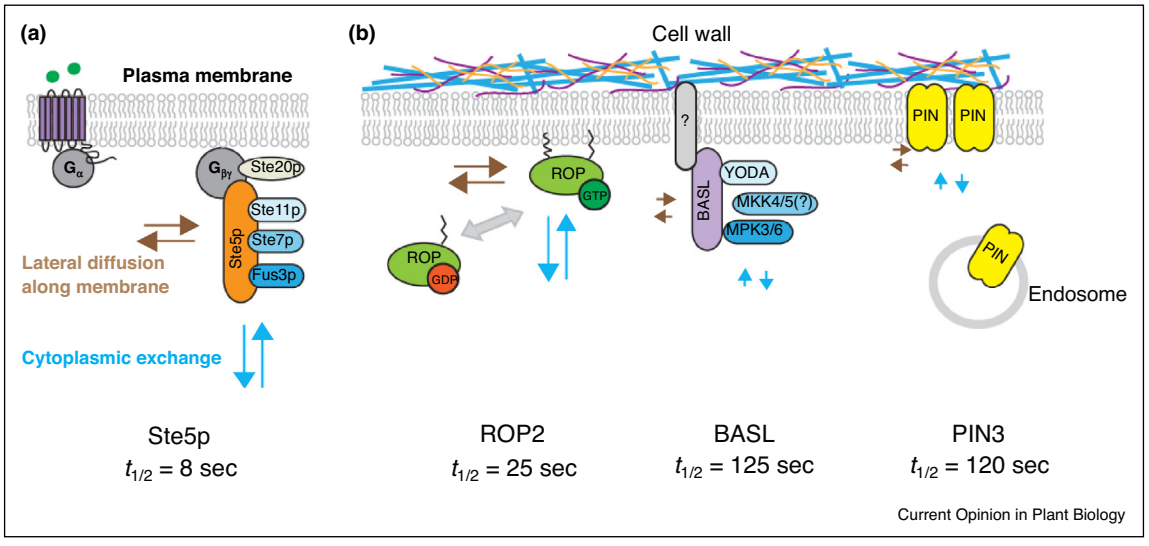
In the establishment and maintenance of cell polarity in eukaryotic organisms, scaffold proteins were commonly found to assemble various signaling components in the cytoplasm and at the PM to a polar site [11]. For example, Ste5 scaffolds a MAPK cascade in budding yeast to activate the mating-specific MAPK Fus3p [11] (Figure 1a). Yeast Bem1 organizes a feedback loop to generate localized activation of the small GTPase Cdc42 to ensure bud polarity axis establishment [12]. In *C. elegans* embryos, the PAR3 (partitioning defective 3) and PAR6 scaffolds organize the anterior and posterior polarity complexes to regulate asymmetric cell division [13].

Scaffold proteins, due to their functions in the assembly of protein complexes, were thought to be stable, but emerging evidence suggests that they are often surprisingly dynamic. Based on FRAP data, the recovery rates, t_{half} or $t_{1/2}$ (the time point when half of the final recovered intensity is reached), suggested rapid movement of polarity factors: Ste5 $t_{1/2}$ = 8 s at the mating tip [14], Bem1 $t_{1/2}$ = 2.37 s at the bud site [15], and cortical PAR6 reached nearly full fluorescence recovery in 1 min [16]. The dynamic features of scaffold proteins suggest that they are under intricate regulation and might confer quick adjustment of the cell polarity machinery in response to external cues and to ensure signaling specificity [17,18].

FRAP analyses were also performed in plant cells to characterize polarity protein dynamics. The available studies examined the membrane-embedded PIN-FORMED (PIN) auxin efflux carriers [19••], ABCG transporters [20], and boron transporters in root cells [21]. In addition, the membrane-associated small GTPase ROPs [22,23] and the MAPK scaffold protein BASL have also been analyzed by FRAP. Interestingly, except for ROP2 ($t_{1/2}$ = 25 s), all other polarity proteins were found to be relatively immobile, for example, PIN3 ($t_{1/2}$ = 120 s) and BASL ($t_{1/2}$ = 125 s), and neither of them reached plateau in 5 min in leaf epidermal cells [24••] (Figure 1b).

The PIN auxin effluxers are fundamental players in the regulation of directional auxin flow. The maintenance of PIN polarity domains mainly depends on three membrane-based mechanisms: polar secretion, endocytosis and endocytic recycling, and lateral diffusion (reviewed in [25,26]). The stabilization of PINs in the PM is

Figure 1



Differential dynamics of polarity proteins in yeast and plants. **(a)** Ste5p scaffolds the MAPKKK Ste 11p, MAPKK Ste7p to activate the mating-specific MAPK Fus3p in yeast. Ste5p is highly mobile at the plasma membrane, where it binds to beta-gamma subunits of G-protein to create a lattice for activating the Ste5p–MAPK cascade protein complex. **(b)** Three polarized proteins in plants: ROP2, a lipid-modified protein for cell polarity; BASL, a scaffold protein for the YODA MAPK cascade; PIN3, a transmembrane auxin transporter. ROP2 rapidly switches between a GTP-bound and GDP-found forms. BASL and PIN3 show similarly slow protein mobility. A hypothetical BASL partner (grey with question mark) was predicted to be membrane-embedded or tightly associated with the plasma membrane. The PIN polarity is mediated by the membrane-trafficking system, and plant cell walls exert constraints for lateral diffusion. FRAP measures the recovery rates ($t_{1/2}$) of the designated PM proteins, which are mainly determined by lateral diffusion along the PM and cytoplasmic exchange (dynamic protein–protein interaction and bulk transport). Brown arrows: long ones show fast lateral diffusion and short ones show slow lateral diffusion. Light blue arrows: long ones show fast cytoplasmic exchange and short ones show slow cytoplasmic exchange. Recovery rates $t_{1/2}$ of the respective polarity proteins (the time point when half of the final recovered intensity is reached) are specified at the bottom.