



A plane choice: coordinating timing and orientation of cell division during plant development

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Development requires precise cell positioning and tissue organization to generate functional organs and viable organisms. Plant development depends on precisely oriented cell divisions, which are typically classified as either asymmetric or symmetric. Asymmetric (formative) cell divisions give rise to cells with two distinct fates; resulting daughter cells often have different sizes or shapes. Symmetric (proliferative) cell divisions give rise to two identical daughter cells. The orientation of the division plane in both symmetric and asymmetric cell divisions is tightly controlled by a combination of cues both intrinsic, occurring within the cell; and extrinsic, originating outside the cell.

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There are many inputs into plant cell divisions, for recent reviews of hormone signaling in asymmetric division see Pillitteri *et al.* (2016) [1]; for cell fate specification during asymmetric divisions see Zhang and Dong (2018) [2], Kajala *et al.* (2014) [3], Van Norman (2016) [4], Hepworth *et al.* (2018) [5], for an overview of symmetric division plane orientation see Rasmussen and Bellinger (2018) [6], and plant cytokinesis see Smertenko *et al.* (2017) [7] and Smertenko (2018) [8]. Division plane orientation is established before mitosis, and must be maintained throughout mitosis and cytokinesis. The preprophase band (PPB), a microtubule and microfilament structure, marks the

division plane before mitosis, although intrinsic and extrinsic cues including polarized proteins, secreted ligands and cognate receptors, as well as mechanical forces all influence the choice of division plane in interphase. This review focuses on cues that influence division plane orientation in both symmetric and asymmetric cell division and highlights synergistic genetic interactions that reveal multiple interconnected pathways.

Cell-cycle regulators as intrinsic factors in cell division orientation (the right place at the right time)

Once a cell achieves a minimum size [9], receives a specific developmental cue, and/or reaches a critical cell-cycle checkpoint [10], the cell divides. Cell-cycle regulators such as cyclins, cyclin-dependent kinases, Retinoma Blastoma Related (RBR) and E2F regulate the timing of the cell cycle [11,12]. Coordinating cell-cycle timing with polarity and positional cues is necessary to establish division plane orientation. Cell fate regulators and cell-cycle regulators directly interact to balance the timing of fate acquisition and division. For example, in the root ground tissue, transcription of a specific cell cycle regulator, CYCLIND6;1 is directly activated by cell fate-determining transcription factors [13]. Reciprocally, RBR, which suppresses cell cycle progression from G1 to S, physically interacts with transcriptional fate regulators and regulates cell fate independent of cell cycle [14,15]. Cell-cycle regulation and cell fate are often intimately linked [16,17].

Division plane establishment is often thought to occur when the PPB forms in G2. However, it is likely that earlier cues feed into the determination of the division plane. Accelerating the G1/S transition can cause or enhance division plane defects, suggesting that a division plane orienting cue is established or perceived in G1. Overexpression of CYCLIN D isoforms, which promote G1/S progression, results in increased cell division along the short plane during stomatal development [18[•],19[•]]. This increase in cell division is distinct from *fama* or *fourlips* mutants, where multiple divisions occur along the long plane [20,21] (Figure 3b). Further evidence suggesting cues perceived in G1 are important for division plane orientation comes from analysis of *tonneau1* (*ton1a*) *cyclind2;1* mutants [22[•]]. TON1a, TON1b, FASS/TON2/DCD1/ADD1 are part of a protein complex that organize interphase microtubules and PPB formation in

G2 [23]. The single *ton1a* mutant shows misoriented symmetric division planes [24]. This weak mutant can be partially rescued by slowing the G1 to S transition, by generating a *ton1a cycd2;1* double mutant or by chemically blocking DNA synthesis [22*]. Conversely, overexpressing *CYCD2;1* speeds up cell-cycle progression and results in a more severe division plane defect in *ton1a*. Together these results suggest that cues perceived in G1, before PPB formation in G2, influence division plane orientation (Figure 1).

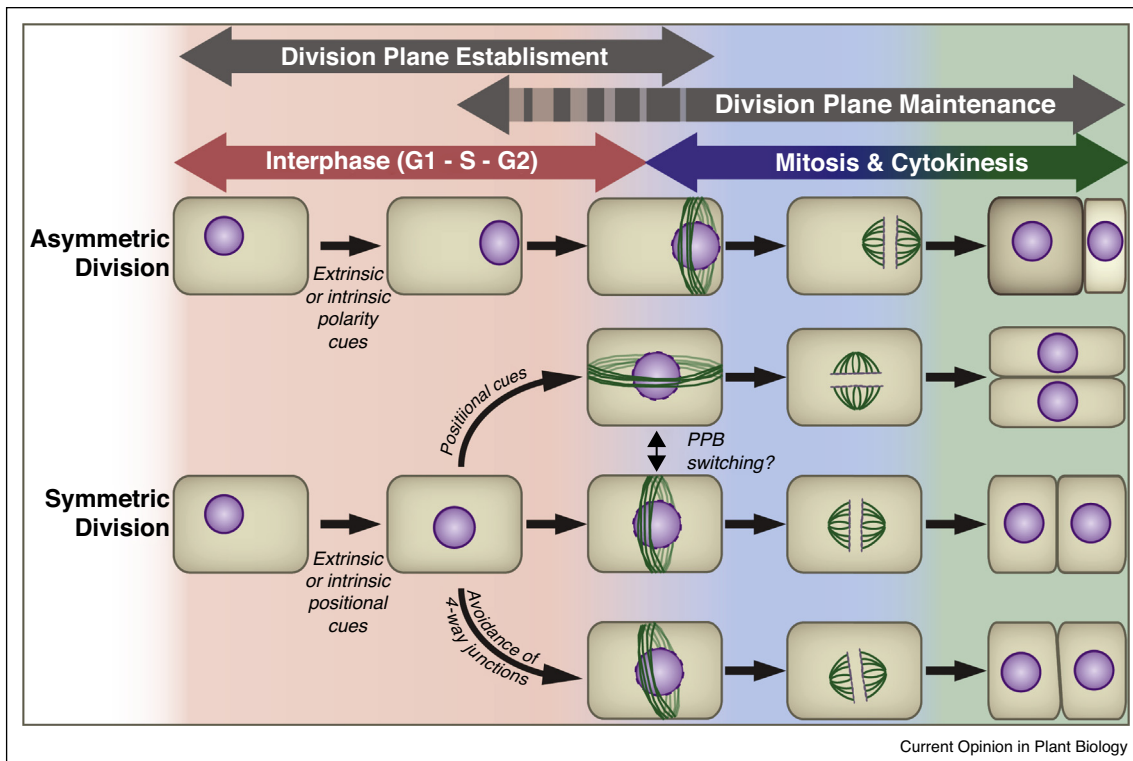
Early division plane positioning

Another critical G1 activity is nuclear movement towards the future division site. Nuclear movement in G1 is driven by actin and actin-binding motor proteins (myosins) and their interactions with nuclear envelope proteins [25–30]. Mechanical stimulation [31] and light [32] also promote nuclear movement. A minus-end directed kinesin is required for both nuclear positioning and timely cell-cycle progression [33,34*]. While nuclear movement is an obvious PPB-independent factor important for division-plane orientation (Figure 1), other as yet unknown

mechanisms acting in G1 or S also likely influence the final position of the division plane. Tying extrinsic and intrinsic cues directly to these G1 activities is critical for understanding division plane choice.

In many land plants, the PPB is formed in late G2 and demarcates the precise location where the future cell wall will meet the existing cell walls after cytokinesis (Figure 1). The cell membrane underlying the PPB or cortical division zone (CDZ) [7], accumulates endocytotic vesicles [35] and many specific proteins, as recently reviewed [6,36,37]. A complex composed of a protein phosphatase type 2A (PP2A), centrin-like proteins, and microtubule-binding proteins are required for PPB formation and organization of the interphase microtubule array [23,24,38–43]. Whether fully developed PPBs are required for division plane specification is under debate due to two mutants that do not make obvious PPBs, but grow well and have relatively minor division plane defects (Zhang *et al.* [24]; Schaefer *et al.* [38]). In addition, there are examples of properly oriented, but PPB-independent divisions. During pollen mitosis I, a PPB-independent asymmetric cell division

Figure 1



Cell division planes are oriented before cytokinesis.

Examples of symmetric and asymmetric cell divisions. Polarity cues or polarized growth may promote specific division plane orientation. Nuclear migration in G1 precedes PPB establishment and influences the future division plane in asymmetric (row 1) and symmetric (row 2) divisions. Local cell wall modifications sometimes occur near the future division site [111–114]. Symmetric cell divisions often occur along one of the shortest planes (row 2), however, these divisions may also be oriented along the long axis of the cell (row 3), such as observed in symmetric division of guard mother cells or longitudinal epidermal divisions [71,115]. PPB shifting can occur to avoid 4-way junctions resulting in 'adjusted' symmetric division planes (row 4) [71,116,117].

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