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

Michelle R Facette[1,3], Carolyn G Rasmussen[2,3] and Jaimie M Van Norman[2,3]

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.

Addresses
[1] Department of Biology, University of Massachusetts, Amherst, MA, United States
[2] Department of Botany and Plant Sciences, Center for Plant Cell Biology, Institute of Integrative Genome Biology, University of California, Riverside, CA, United States

Corresponding authors: Facette, Michelle R (mfacette@umass.edu), Rasmussen, Carolyn G (carolyn.rasmussen@ucr.edu), Van Norman, Jaimie M (jaimie.vannorman@ucr.edu)
[3] Equal contribution names submitted in alphabetical order.

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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

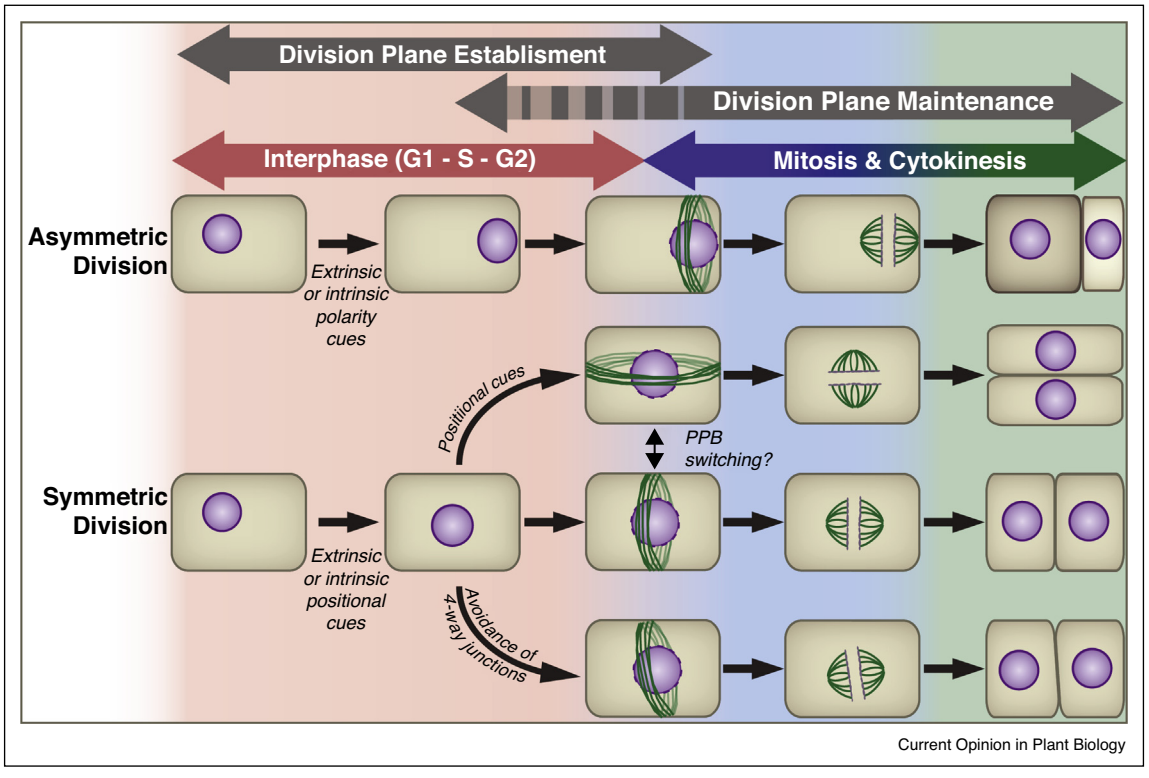
G2 [23]. The single *ton1a* mutant shows misoriented symmetric division planes [24]. This weak mutant can be partially rescued by slowing the G1 to S transition, by generating a *ton1a cycd2;1* double mutant or by chemically blocking DNA synthesis [22•]. Conversely, overexpressing *CYCD2;1* speeds up 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.

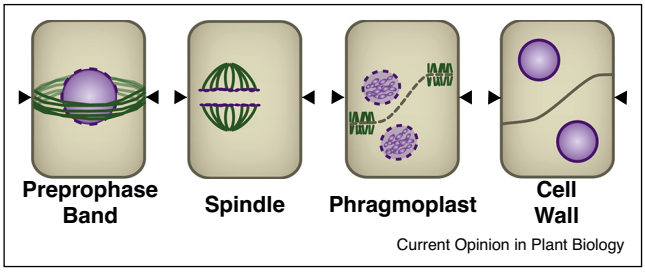
In many land plants, the PPB is formed in late G2 and demarcates the precise location where the future cell wall will meet the existing cell walls after cytokinesis (Figure 1). The cell membrane underlying the PPB or cortical division zone (CDZ) [7], accumulates endocytotic vesicles [35] and many specific 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].

Figure 2



Division plane defects that occur after the PPB disassembles result in placement of the new cell wall outside of the PPB-specified division site.
The PPB coalesces in G2 around the nucleus (left panel). The division site (demarcated with arrowheads throughout mitosis until the cell plate fuses with the mother cell) is labeled by proteins that accumulate before PPB breakdown, or later in mitosis [43,98,99,100•,101,103,105–107,118]. In mutants with division plane defects, the phragmoplast fails to return to the division site, promoting development of the new cell wall in a different location than the division site (see phragmoplast and cell wall panels).

Box 1 After preprophase band disassembly, cell division plane orientation is maintained to position the new cell wall at the specified division site

In some division plane orientation mutants, the new cell wall forms outside the PPB-specified division site, which is described as defective phragmoplast guidance or division plane maintenance [98,99,100•,101,102•], (Figure 2). Some of the corresponding proteins localize to the future division site during PPB formation and are maintained at that position even after PPB disassembly [43,98,99,100•,101,103–107]. Other proteins with yet unknown functions in division plane orientation also localize to the future division site after PPB disassembly [103,106,107]. Two related kinesins, PHRAGMOPLAST ORIENTING KINESIN1 (POK1) and POK2 localize to the division site, interact with other proteins required for division plane maintenance, and are themselves required for division plane maintenance [98,99,104,107,108]. POK2 additionally localizes to the phragmoplast midzone and interacts with several MAP65 microtubule-associated proteins [109•]. POK1 interacts with two closely related putative RHO-OF-PLANTS small monomeric GTPase Activating Proteins (RHO-GAPs) that promote proper division plane orientation [98] and with the microtubule-binding protein TANGLED1 (TAN1) [99,104]. In maize, *tan1* mutants have significant division plane defects and mitotic progression delays [100•,110], which results in growth defects. Although the *tan1* mutant in *A. thaliana* has only minor defects division plane orientation [99], combining *tan1* and a mutant with no detectable abnormal phenotype, *auxin-induced-in-root-cultures 9* (*air9*) [106], causes a synthetic division plane orientation and root growth defects [102•]. Thus, the function of TAN1 and AIR9, two unrelated microtubule-binding proteins, in division plane orientation, suggests multiple pathways converge on this process in *A. thaliana*.

forms the small generative and larger vegetative cells. Two related proteins, SIDECAR POLLEN/LATERAL ORGAN BOUNDARY 27 (SCP/LBD27) [44] and LBD10 [45] are required for pollen development and for maintaining division asymmetry. PPB-independent division plane orientation requires microtubule structures organized by gamma–tubulin [46] and actin–microtubule interactions mediated by MYOSINVIII [47] in moss. Thus, the PPB, while important for orienting many cell divisions, is not required in the presence of other orienting cues. After PPB disassembly, division plane orientation is maintained until cytokinesis completes to properly position the new cell wall (Box 1).

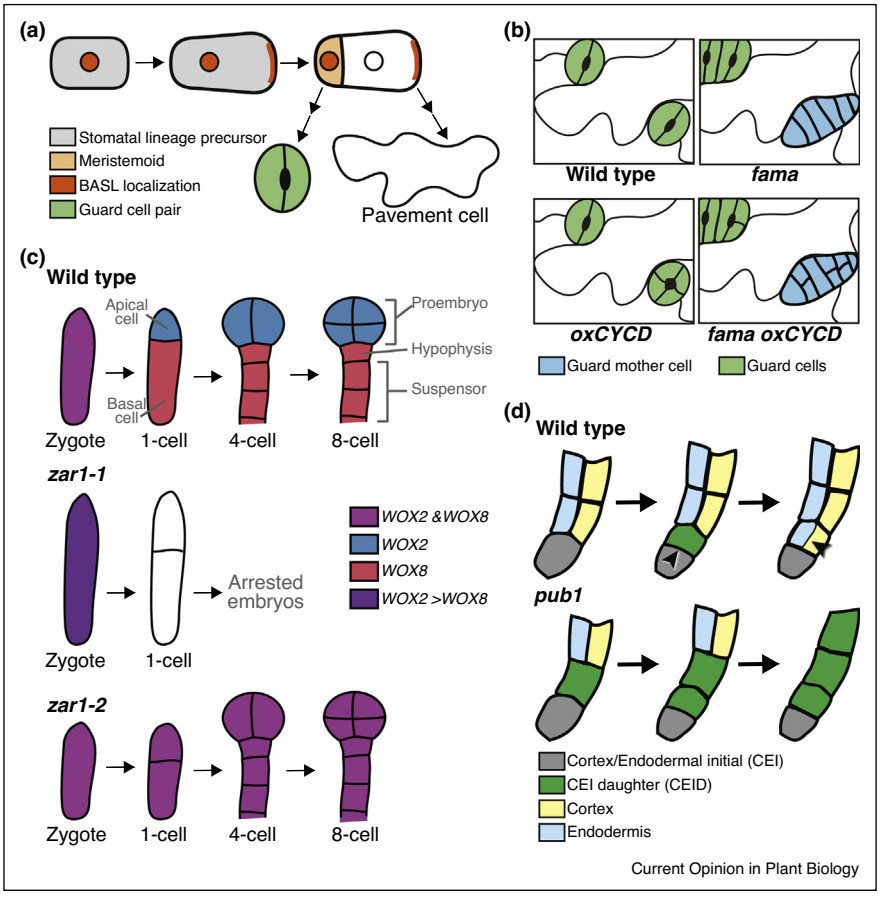
Intrinsic cues informing the timing and orientation of plant cell division

Intrinsic cues originate within the cell. Proteins can respond to or act as intrinsic cues. Two dynamically localized proteins, Breaking Asymmetry in the Stomatal Lineage (BASL) [48] and POLAR [49], exhibit polar localization and have roles in the oriented cell divisions that give rise to the stomata in *Arabidopsis thaliana*. After asymmetric division, differential inheritance of BASL and associated MAPK activity in one daughter cell reduces expression of a key stomatal lineage transcription factor, thereby promoting pavement cell fate (Figure 3a) [50,51]. This suggests that epidermal cell fate may be determined by inheritance of repressive factors; whether this type of mechanistic control over daughter cell fate can be applied to other plant asymmetric cell divisions remains unknown.

Aurora kinases have conserved eukaryotic functions in mitosis and appear to function as intrinsic cues. In plants, α-AURORA kinases are necessary for orientation of many asymmetric cell divisions, including those that occur in lateral root initiation, stomatal development, and the root stem cell niche [52]. Although most AURORA kinase targets remain unknown, AURORA kinases phosphorylate MICROTUBULE-ASSOCIATED-PROTEIN 65-1 (MAP65-1) which promotes cell-cycle progression [53]. Puzzlingly, the AUR1-GFP fusion is not asymmetrically localized. Instead, it co-localizes with MTs around the nuclear envelope and spindle, but does not strongly accumulate on the PPB [52,53]. Cell division orientation and AURORA kinase function may be linked by phosphorylation of microtubule-associated proteins that alter MT organization, but it is not yet clear how AURORA kinases promote orientation of specific asymmetric divisions.

Protein degradation and modification has recently emerged as another type of intrinsic cue necessary for plant asymmetric cell divisions. In maize, a Meprin-Associated-Traf-Homolog Bric-à-Brac/Tramtrack/Broad complex (MATH-BTB) protein, MAB1, is essential for chromosome segregation and asymmetric cell division positioning in germ-line and zygotes by a yet unknown mechanism [54]. MAB1 interacts with an E3 ubiquitin ligase and likely provides substrate specificity. An E3 ubiquitin ligase, PLANT U-BOX4 (PUB4) [55], has a role in the timing and orientation of asymmetric cell divisions

Figure 3



Examples of oriented asymmetric cell divisions in *A. thaliana* development and select mutants with defects in those divisions. **(a)** In stomatal lineage precursors, BASL is initially nuclear localized, but upon MAPK-mediated phosphorylation BASL becomes polarly localized [50]. Asymmetric cell division of the stomatal lineage precursor is oriented away from membrane-associated BASL, producing a smaller meristemoid cell that can divide iteratively or produce a guard mother cell that ultimately forms guard cells [48]. The larger cell that inherits membrane-associated BASL becomes a pavement cell. **(b)** In wild-type, stomatal pores form from a single, oriented symmetric division of a guard mother cell to produce a guard cell pair. In plants overexpressing specific *CYCLIN D* (*CYCD*) isoforms, guard cells undergo additional cell divisions along the shortest path resulting in distorted stomata [18••,19••]. In contrast, *fama* mutant guard mother cells undergo iterative cell divisions along the longest path and guard cells are not formed [20]. Interestingly, when *CYCD* isoforms are overexpressed in a *fama* mutant background, divisions also occur along the shortest path. **(c)** Embryo development begins with an oriented, asymmetric zygotic division, which results in specification of the apical (shootward) and basal (rootward) cell fates. The dominant negative *zar1-1* mutation results in a longer zygote that divides more symmetrically, failure to specify apical and basal cell fate as signified by altered expression of WOX transcription factors, and, ultimately, embryo arrest. In contrast, loss-of-function *zar1-2* mutants have minor defects in the zygotic division and in specification of embryonic axes, however, these defects are non-lethal and embryos typically develop normally [80]. **(d)** The ground tissue cell types are formed during a series of oriented asymmetric cell divisions in roots. The cortex/endodermis initial daughter (CEID) cell undergoes a periclinal cell division to produce endodermis towards the inside and cortex towards the outside. In *pub4* mutants, delayed periclinal division of the CEID and later the endodermis results in apparent initial cell proliferation [56].

in *A. thaliana* roots [56], (Figure 3d). Additionally, the calcium-sensing calpain protease DEFECTIVE KERNEL1 (DEK1) plays a critical role in division plane orientation in multiple land-plant lineages, including cells lacking PPBs [57,58] potentially by activating a mechanosensitive calcium channel [59]. Division plane defects may be influenced by alterations in *dek1* mutant cell wall composition [60]. These examples provide evidence that degradation of specific, but yet unknown, targets is important for modulating the precise timing and orientation of various plant cell divisions.

DiSUMO is an unusual form of a ubiquitin-like modifier that is required for cell cycle progression across multiple kingdoms [61]. Knocking down *DiSUMO* results in female gametophyte lethality where nuclei in the syncytium are not properly positioned or separated and in hemizygous zygotes the first asymmetric division

undergoes karyokinesis, but not cytokinesis [61,62]. Interestingly, DiSUMO (but not SUMO) was often polarized in interphase cells and then later localizing between chromosomes and the cell plate during division. DiSUMO is conjugated with cell regulators, cell plate assembly regulators, and RNA stability factors. A specific role for DiSUMO in division plane orientation is masked by severity of the phenotype, but polarized localization during interphase invites speculation about its potential role in integrating cell cycle timing and intrinsic division plane orienting cues [62]. In summary, unique intrinsic mechanisms-based on protein degradation or modification may orient plant cell divisions, yet these modifications may also amplify or 'lock-in' a program initiated by an extrinsic cue.

Extrinsic mechanical cues informing the orientation of plant cell division

Extrinsic cues alter the probabilities of division plane orientation in symmetric divisions and specify the location of asymmetric divisions. Extrinsic cues that alter the division plane are potentially based on altered local or tissue-level mechanical stresses. Mechanical stresses can be critical for proper morphogenesis, such as during lateral root development [63]. What factors perceive mechanical stresses remain unknown, although dynamic microtubule responses [64], nuclear positioning [30], or a combination may be sufficient. Microtubules respond dynamically to local mechanical stimuli by aligning parallel to maximal stress after wounding [65], application of external pressure [66], plasmolysis [67], or in specific developmental contexts [68,69]. On a subcellular level, PPBs shift away from adjacent neighboring cell walls or cell division structures [70,71] (Figure 1), potentially by responding to local differences in cell wall stresses. Mechanosensors also likely play a role in responding to mechanical cues [59,72–74]; in at least two cases, intact microtubules are irrelevant for protein polarization in response to mechanical cues [75,76••]. During stomatal development, the intrinsic polarity protein BREVIS RADIX-LIKE2 (BRXL2) responds to local and tissue-level mechanical stresses, such as ablation, by localizing towards the ablation site, even without functional microtubule arrays. BRXL2 localization predicts later tissue-level growth patterns [76••] possibly reflecting the cell expansion function of its binding partner, BASL [48]. Despite population-level mechanical response, local extrinsic cues override mechanical cues because proper stomatal spacing still occurs, as reviewed [77].

Extrinsic peptide cues perceived by receptors

Another essential extrinsic cue in division plane orientation uses signaling modules composed of a diffusible signal, often a peptide, generated by one cell (or cell-type) that is recognized by the extracellular domain of leucine-rich repeat receptor-like kinases (LRR-RLKs) in adjacent cells. Perception is followed by activation of downstream targets. Despite apparent simplicity in peptide-ligand modules, mounting evidence suggests complex genetic and physical interactions within LRR-RLK mediated signaling pathways, raising questions about how specificity is achieved [78–80].

Here, we briefly discuss several developmentally important asymmetric cell divisions where extrinsic cues play a prominent role. During vascular development, the procambium undergoes periclinal divisions to produce xylem and phloem. These specific periclinal divisions are modulated by a phloem-produced peptide [81] that directly binds the LRR-RLK PHLOEM INTERCALATED WITH XYLEM (PXY) [82] expressed in procambium cells [83]. Interactions between PXY and other LRR-RLKs suggest multiple inputs [84–86]. In *A. thaliana* embryo development, a cysteine-rich peptide, EMBRYO SURROUNDING FACTOR 1 (ESF1), is expressed in embryo-surrounding cells and positively regulates suspensor elongation and subsequent suspensor cell divisions [87]. How the embryo perceives ESF1 is unknown, but is upstream of YODA, a Mitogen-activated protein kinase kinase kinase (MAPKKK) required for asymmetric zygote divisions [88], and has a synergistic phenotype with another LRR-RLK mutant *short suspensor (ssp)* mutants [87]. A recently identified LRR-RLK, ZYGOTIC ARREST 1 (ZAR1), may perceive ESF1, however broad *ZAR1* expression and unknown protein localization make it unclear how this putative receptor-ligand pair would specifically modulate zygotic cell divisions [80]. Mutations in genes encoding the peptide or ligand components of either of these modules result in altered patterns of cell division and altered cell fate in the vasculature or embryo (Figure 3c), respectively.

An elegant, but incomplete, pathway promotes asymmetric divisions of maize subsidiary cells. BRICK (BRK) proteins regulate branched actin nucleation and are the earliest required proteins for polarization of the subsidiary cells before asymmetric division. BRK proteins polarize during G1, and are required for polar accumulation of the catalytically inactive LRR-RLKs PANGLOSS2 (PAN2) and PAN1 at the subsidiary-cell/guard-cell interface [89•,90,91]. PAN1 activates monomeric GTPase RHO-OF-PLANTS to promote local actin accumulation [92]. LRR-RLK polar accumulation suggests that perception of an extrinsic cue may be important for subsidiary cell division orientation. Subsidiary cell division mutant combinations have synergistic phenotypes, suggesting that, instead of a linear pathway, several parallel or interconnected pathways may converge to promote asymmetric subsidiary cell divisions.

In an interesting twist, extrinsic control of division plane orientation control during maize anther development was demonstrated using the pathogenic fungus *Ustilago maydis* to secrete a maize peptide. Fungus-secreted apoplastic

ZmMAC1 (MULTIPLE ARCHESPORIAL CELLS 1) rescued periclinal cell divisions and cell fate specification in the *mac1* mutant, demonstrating that MAC1 has limited movement and is an extrinsic cue [93••] perceived by a conserved LRR-RLK receptor [93••,94–96]. A similar 'Trojan Horse' method is employed to create a nematode feeding site in *A. thaliana*: nematodes secrete a peptide that mimics an endogenous plant peptide hijacking asymmetric cell division pathways [97]. These results indicate that extrinsic cues, even those supplied by different species, can promote oriented plant cell divisions.

Final thoughts

Many mutants have potential division plane defects (often in specific tissues or cell types), however, a mechanistic understanding of the division plane defect is typically not intensively pursued. Important insight into these mechanisms may be obtained by determining whether the division plane defect reflects a failure to: firstly properly promote, prevent, or time initiation of cell division, secondly position the division plane, thirdly maintain division plane orientation, or fourthly properly direct cell expansion. Advances in methods, such as live-cell imaging of dividing and differentiating cells, will aid in obtaining a more complete understanding of existing mutants. In addition, although recent connections and breakthroughs have been made, discovering how extrinsic and intrinsic cues are coordinated and how they directly modulate division plane orientation machinery is far from understood.

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