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Review

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An overview of plant division-plane orientation

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Summary

Plants, a significant source of planet-wide biomass, have an unique type of cell division in which a new cell wall is constructed *de novo* inside the cell and guided towards the cell edge to complete division. The elegant control over positioning this new cell wall is essential for proper patterning and development. Plant cells, lacking migration, tightly coordinate division orientation and directed expansion to generate organized shapes. Several emerging lines of evidence suggest that the proteins required for division-plane establishment are distinct from those required for division-plane maintenance. We discuss recent shape-based computational models and mutant analyses that raise questions about, and identify unexpected connections between, the roles of well-known proteins and structures during division-plane orientation.

I. Introduction

Cell division, a fundamental requirement for life, is carefully regulated in both space and time. Symmetrical proliferative divisions are essential for growth and account for the vast majority of plant cell divisions. When and where proliferative divisions occur along with expansion and differentiation allows formation of the entire plant body. Formative (asymmetrical) divisions are critical for the development of new cell-types. Due to their precise role in development, asymmetrical cell divisions tend to be initiated by specific transcription factors and signaling pathways: readers are directed to recent reviews on asymmetrical division-plane specification and polarization (Kajala *et al.*, 2014; Shao & Dong, 2016). Here, we discuss computational division-plane modeling approaches and our perspective on division-plane establishment and maintenance in plants, whereas recent reviews provide insight into phragmoplast organization and new cell wall formation (Lee & Liu, 2013; Jürgens *et al.*, 2015; Smertenko *et al.*, 2017).

II. Models of plant cell division

Basic patterns of plant cell divisions were originally described in the late 1800s (Hofmeister, 1863; Sachs, 1878; Errera, 1888), and recently revisited (Besson & Dumais, 2014). Divisions typically occur perpendicular to the cell's long axis at positions that minimize the final surface area of the new cell wall, similar to soap-films (Errera, 1888; Flanders *et al.*, 1990). For each cell, multiple division planes represent possible minimal final surface areas (Besson & Dumais, 2014).

Within the past few years, computational modeling was used to predict plant cell division-plane orientation. For simplicity, most models used 2D instead of 3D plant cells. Predicting divisions along the shortest plane through the center of mass accounts for many features of tissues composed of symmetrically dividing cells (Sahlin & Jönsson, 2010; Shapiro *et al.*, 2015). Empirically determined 'stochasticity factors' added variability to shape-based division-plane predictions notably improving their ability to match

in vivo division planes (Dupuy *et al.*, 2010; Besson & Dumais, 2011). More elongated cells tend to divide along the shortest plane, whereas less elongated cells have more division-plane variability (Besson & Dumais, 2011). Importantly, these models emphasize division-plane orientation variability, an idea underappreciated for more than a century (Besson & Dumais, 2014).

Recently, the 3D shape of plant cells has been used to predict division-plane orientations (Yoshida *et al.*, 2014; Martinez *et al.*, 2017a). One method identifies only the shortest division plane through the cell's center-of-mass (Yoshida *et al.*, 2014). Another method generates multiple soap-film minima division predictions (Martinez *et al.*, 2017a) to directly test the hypothesis that division planes mimic soap-film minima (Errera, 1888). Simple 3D geometric properties are sufficient to generate probabilistic division predictions that are often consistent with *in vivo* division planes of epidermal maize cells (Martinez *et al.*, 2017a). It has still not been demonstrated how divisions are specified, but microtubule organization and nuclear positioning contribute: mutants with division-plane specification defects are discussed in the next section.

Cell geometry may account for many *in vivo* division-plane orientations, but other factors, such as local (Asada, 2013; Martinez *et al.*, 2017a) or tissue-level mechanical stresses (Lintilhac & Vesecky, 1981; Louveaux *et al.*, 2016) and developmental cues (Van Damme *et al.*, 2011; Kajala *et al.*, 2014; Yoshida *et al.*, 2014; Walbot & Egger, 2016) can alter division-plane orientation. Indeed, factors that override geometry-based cell divisions are of great interest. Local mechanical stresses likely alter the division plane during avoidance of four-way junctions (Fig. 1a), when the location of the preprophase band (PPB), a structure that indicates the future division plane (discussed in the next section, Fig. 2a), shifts to avoid an adjacent, perpendicular cell wall or a neighboring PPB (Gunning *et al.*, 1978; Flanders *et al.*, 1990; Martinez *et al.*, 2017a). PPB repositioning suggests cell–cell communication potentially mediated by mechanical cues, but this remains to be experimentally addressed. Another example occurs in shoot apical meristem boundary cells (Fig. 1b). These long, thin cells divide more slowly than adjacent cells. Boundary cell divisions occur along the long division plane in higher frequencies than expected based on the 2D Besson–Dumais shape-based model, reflecting division-plane alignment parallel to maximal stress (Louveaux *et al.*, 2016). The observation is consistent with imposed mechanical stresses, such as laser ablation or wounding of adjacent cells causing microtubule arrays and corresponding division planes to realign parallel with maximal stress (Hush *et al.*, 1990; Sampathkumar *et al.*, 2014). In addition, when tobacco cells are plasmolyzed, they divide with higher frequencies along the long plane than would be predicted by the Besson–Dumais model, likely parallel to maximal stress (Asada, 2013). These exceptions indicate an urgent need to compare cell-shape and mechanical models to determine their relative contribution in division-plane selection in different tissues. Although little has been done yet to compare mutants with division-plane defects to model-based predictions (Yoshida *et al.*, 2014), together their feedback will inform both future experiments and model refinements.

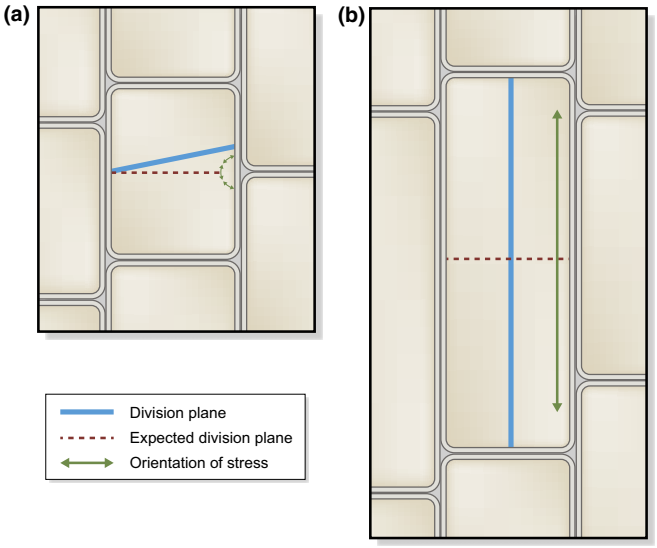

Fig. 1 Local or tissue-level stress alters division planes to favor positions that would not be predicted by cell-shape based modeling. (a) Local stress (green) at four-way junctions may cause divisions (blue) to shift away from the junction. (b) Division (blue) occurs more frequently (5%) parallel to tissue-level stress (green) and across the longitudinal plane than expected using the 2D Besson–Dumais model (Besson & Dumais, 2011; Louveaux *et al.*, 2016).

III. Establishing the division plane

Before the cell divides, several requirements must be met. The cell reaches a minimal size (Jones *et al.*, 2017) and the nucleus migrates toward the center of the cell during symmetrical divisions (Wada, 2017) or to another location in asymmetrical divisions (Rasmussen *et al.*, 2011a; Facette & Smith, 2012; Kimata *et al.*, 2016). Interactions between cell-cycle regulators and proteins required for division-plane establishment (below) have been identified (Hush *et al.*, 1996; Boruc *et al.*, 2010; Spinner *et al.*, 2013; Costa, 2017). In the next sections, we focus on PPB form and function, but note that not all plant cells require a PPB for division-plane orientation. Examples of PPB-independent divisions include meiocytes (Otegui & Staehelin, 2004), endosperm (Brown & Lemmon, 2001) and some moss cells (Doonan *et al.*, 1987; Kosetsu *et al.*, 2017). Many PPB-independent divisions occur in invariant locations suggesting strong positioning cues. Discovering yet unknown positioning mechanisms may identify highly conserved features of plant cell division orientation.

The PPB is a microtubule and actin filament structure that assembles in G2 and aligns with the future division site (Fig. 2a, top left), (Rasmussen *et al.*, 2013). PPB orientation often matches that of interphase microtubules (Gunning & Sammut, 1990). Multiple microtubule-associated proteins co-localize with the PPB (Li *et al.*, 2015). This PPB subtends the cortical division zone (CDZ), a local region of the membrane (Smertenko *et al.*, 2017; Van Damme *et al.* 2007). The CDZ is characterized by increased accumulation of clathrin-coated endocytotic vesicles (Karahara *et al.*, 2009). As the PPB forms, increased interactions occur between actin filaments and microtubules (Takeuchi *et al.*, 2016). Indeed, actin filament disruption by drugs or mutants induces both PPB widening and

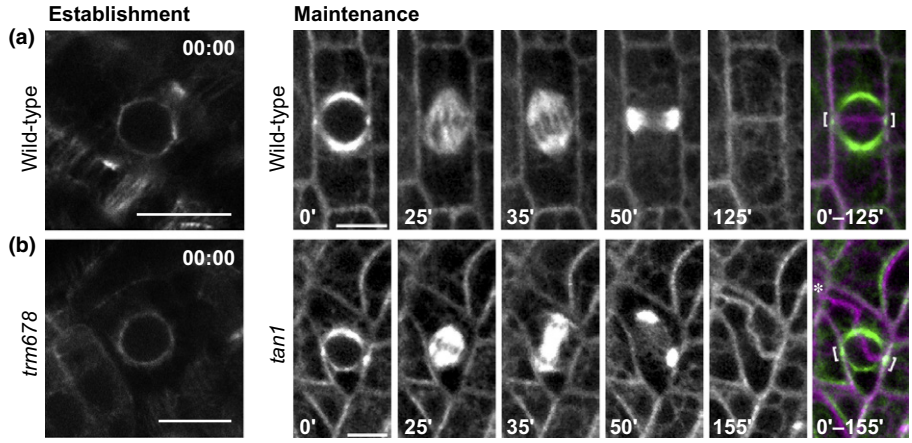

Fig. 2 Division-plane establishment and maintenance. (a) Examples of typical land-plant preprophase band (PPB) of wild-type Arabidopsis (top left) and mitotic microtubule structures in maize (from prophase with a PPB until the new cell wall is formed, top right). (b) Mutants with defects in division-plane establishment lacking a clear PPB (*tonneau1 recruitment motif*, (*trm6,7,8*), bottom left) and maintenance, assessed by time-lapse imaging, when the new cell wall does not return to the location of the PPB (*tangled1 (tan1*) mutant, bottom right). Merged images (far right) show late prophase cell (with PPB in green and indicated with white brackets) and finished cell division (in magenta, asterisk shows misplaced new cell wall). Left panels were modified from (Schaefer *et al.*, 2017) and reprinted with permission from the authors and AAAS. Right panels were modified from (Martinez *et al.*, 2017b) with permission from the authors. Bars, 10 μm.

defects in division-plane orientation (Mineyuki & Palevitz, 1990; McDowell *et al.*, 1996; Sano *et al.*, 2005; Rasmussen *et al.*, 2011a; Vaškebová *et al.*, 2017). PPB actin-microtubule interactions are possibly mediated by actin and microtubule-binding proteins that localize to the PPB, such as formins (Li *et al.*, 2010), Myosin VIII (Wu & Bezanilla, 2014), or kinesins (Buschmann *et al.*, 2011; Klotz & Nick, 2012; Schneider & Persson, 2015; Tian *et al.*, 2015; Walter *et al.*, 2015; Tseng *et al.*, 2017; Yamada *et al.*, 2017). The potential role of microtubule-actin crosslinking proteins in refining division-plane orientation or PPB narrowing is still unknown.

Proper PPB assembly and division-plane establishment requires a complex of conserved type 2A protein phosphatase subunits (PP2A), plant-specific proteins, and those similar to centrosomal proteins, called the TON1/TRM/PP2A (TTP) complex (Figs 3, 4) (Spinner *et al.*, 2013). Key components of the TTP complex are identified by mutants with short, thick 'barrel' stature called *tonneau* (*ton*) (Camilleri *et al.*, 2002; Azimzadeh *et al.*, 2008) and *fass* (Torres-Ruiz & Jürgens, 1994). These mutants have cell elongation defects due to aberrant interphase microtubule array organization (Azimzadeh *et al.*, 2008; Spinner *et al.*, 2010; Kirik *et al.*, 2012). In addition, cells do not form PPBs and have division-plane defects (Camilleri *et al.*, 2002; Azimzadeh *et al.*, 2008). *fass* is allelic to *ton2,* encoding a B″ regulatory subunit of the PP2A (Camilleri *et al.*, 2002). Similar to *fass,* maize *fass* homologs *discordia1* and *alternative discordia1* together are required for PPB formation and their proteins localize to the division site until metaphase, potentially to promote specific protein de-phosphorylation (Wright *et al.*, 2009; Spinner *et al.*, 2013). Other TTP components have conserved domains common to centrosomal proteins encoded by two highly similar genes *tonneau1a (ton1a)* and *ton1b* which together are required for PPB formation and interphase microtubule array organization. TON1 colocalizes with interphase microtubules and PPBs (Azimzadeh *et al.*, 2008). Recently, an interaction between TON1 and many of a 34-member protein family containing a conserved motif named the TON1-recruiting motif (TRM) was identified (Drevensek *et al.*, 2012). Several, but not all, TRM proteins bind microtubules and different TRM proteins interact with TTP proteins (Fig. 3) (Spinner *et al.*, 2013). Specificity may be controlled by TRMs with different binding affinity for TTP members or microtubules. It is still unclear what proteins are de-phosphorylated and how that leads to proper interphase microtubule array organization and PPB formation.

One difficult question is whether interphase microtubule array organization can be functionally separated from PPB formation. Important insight has come from recent analysis of partial-loss-of-function mutants with more severe defects in PPB formation than apparent interphase microtubule array organization. These mutants display almost normal growth and mild division-plane orientation defects (Zhang *et al.*, 2016; Schaefer *et al.*, 2017). The *ton1a* single mutant lacks proper PPBs, yet many divisions were still properly oriented, especially in root cortex cells (Zhang *et al.*, 2016). The triple *trm 6,7,8* mutant lacks proper PPBs but grows well (Fig. 2b, left panel, Schaefer *et al.*, 2017). These three *TRMs* compose a small subfamily and encode about a quarter of TRMs with a probable microtubule-binding motif (Drevensek *et al.*, 2012). Although the PPB does not form normally, Phragmoplast orienting kinesin1 (POK1, discussed in the next section) still localizes at the division site, although less often than in wild-type (WT) cells (Schaefer *et al.*, 2017). The *trm* mutants lacking proper PPBs had aberrant spindle rotation and division-plane defects.

The PPB is thought to promote spindle bipolarity and prevent spindle rotation (Ambrose & Cyr, 2008). When the PPB forms, microtubules accumulate around the nucleus perpendicular to the PPB before metaphase. If the PPB does not form, microtubules accumulate nonspecifically around the nucleus (Camilleri *et al.*, 2002; Chan *et al.*, 2003; Azimzadeh *et al.*, 2008; Schaefer *et al.*, 2017), which delays spindle formation (Chan *et al.*, 2003).

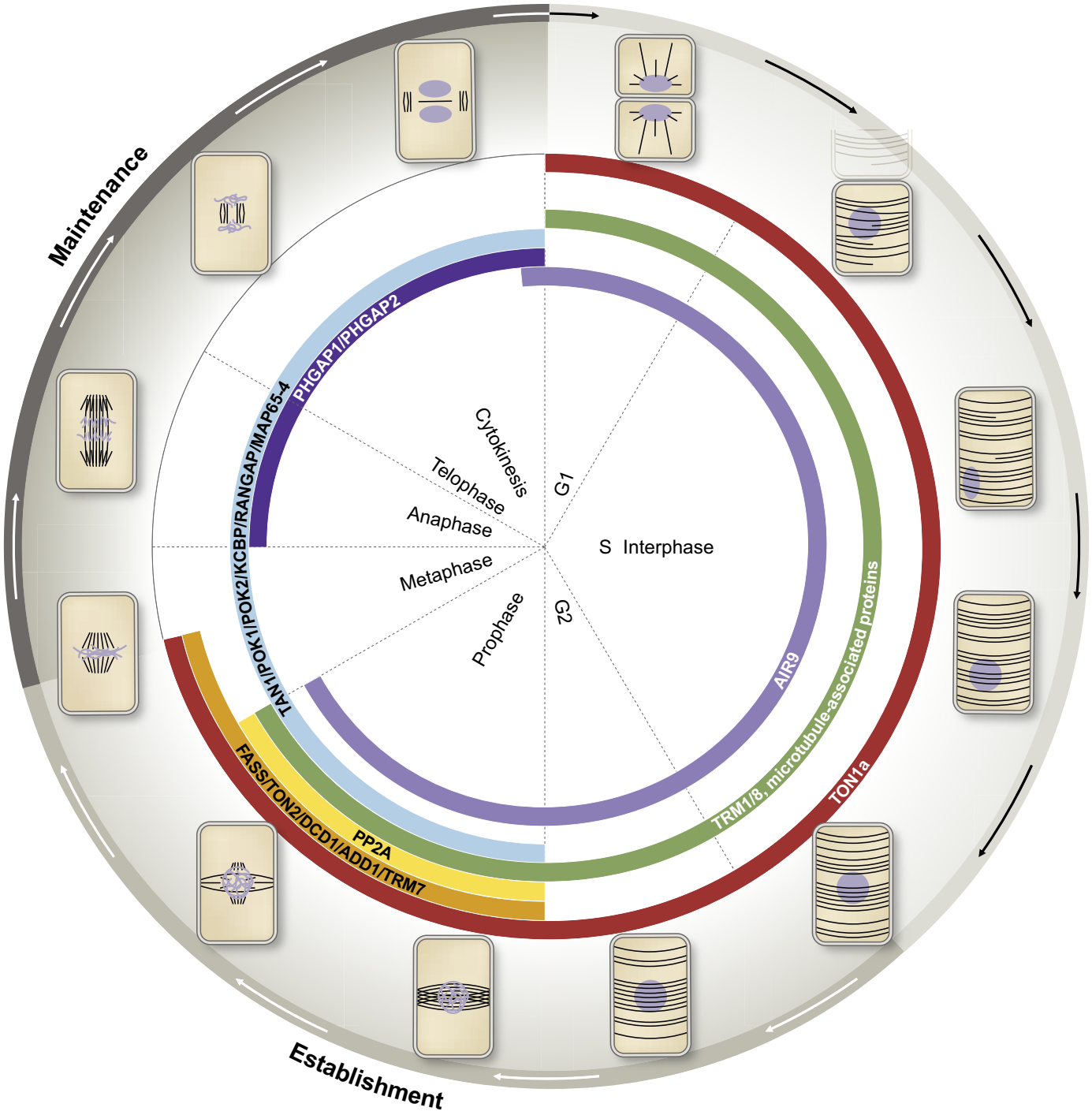

Fig. 3 Accumulation of division site localized proteins required for establishment and maintenance of symmetrical plant cell divisions. This schematic representation of the cell cycle indicates key transitions, not the timing of the transitions. The position of cortical microtubule arrays (black) and DNA (gray) of plant cells is shown together with phases of the cell cycle. The localization of proteins that promote proper formation of the preprophase band (PPB) are listed under Establishment. TON1a (red) localizes to the interphase microtubule array, then the division site during prophase and part of metaphase (Azimzadeh *et al.*, 2008). FASS/TON2/DCD1/ADD1 and TRM7 (orange) localize to the division site from prophase to metaphase (Wright *et al.*, 2009; Spinner *et al.*, 2013; Schaefer *et al.*, 2017). TRM1 and TRM8 (green) localize to the interphase cortical array and the PPB (Drevensek *et al.*, 2012; Schaefer *et al.*, 2017), similar to many microtubule-binding proteins (Li *et al.*, 2015). TAN1, POK1, POK2, KCBP, RAN-GAP and MAP65-4 (blue) localize to the division site from prophase through cytokinesis (Walker *et al.*, 2007; Xu *et al.*, 2008; Lipka *et al.*, 2014; Buschmann *et al.*, 2015; Li *et al.*, 2017; Martinez *et al.*, 2017b). PHGAP1 and PHGAP2 (indigo) localize to the division site from metaphase through cytokinesis (Stöckle *et al.*, 2016). AIR9 (violet) localizes to the division site along the violet track, co-localizing with the interphase microtubule array, then co-localizing with the PPB. AIR9 localizes to the division site when the phragmoplast reaches the cortex (Buschmann *et al.*, 2006).

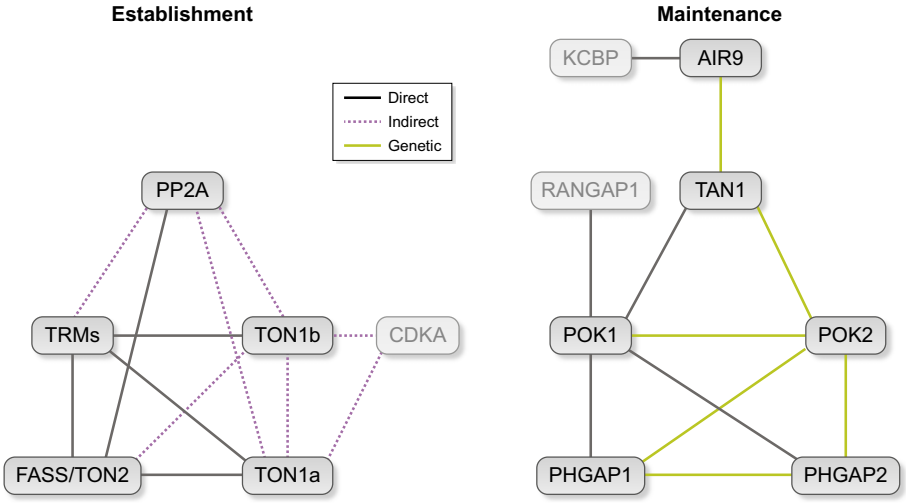

Fig. 4 A schematic of currently known division-plane establishment and maintenance interactions. Potentially indirect protein–protein interactions identified by mass-spectrometry are indicated with dotted magenta lines, direct protein–protein interactions are indicated with black lines, whereas genetic interactions are indicated with green lines. Establishment: the components of the TON1/TRM/PP2A (TTP) complex. TON1a interacts with TON1b (Spinner *et al.*, 2013). FASS/TON2 interacts with TON1a, TON1b and PP2A (Spinner *et al.*, 2013). TRM1 interacts with TON1a via a region of TRM1 containing conserved domain 2 (Drevensek *et al.*, 2012). TON1a interacts with multiple TRMs (2, 3, 7, 11, 14, 19, 20, 21, 22, 25 and 26) (Drevensek *et al.*, 2012). TRM19 interacts with TON1, FASS/TON2 and PP2A (Spinner *et al.*, 2013). TRM1, TRM3 and TRM29 interact with FASS/TON2, probably via interaction with conserved TRM domain 3 (Spinner *et al.*, 2013). CDKA interacts with TON1a (Spinner *et al.*, 2013; Costa, 2017) and TON1b (Van Leene *et al.*, 2007): genetic interactions suggest that speeding up cell-cycle progression worsens division-plane defects of *ton1a* mutants (Costa, 2017). Maintenance: POK1 interacts with TAN1 (Müller *et al.*, 2006; Walker *et al.*, 2007; Rasmussen *et al.*, 2011b), RAN-GAP (Xu *et al.*, 2008) and PHGAP1 and 2 (Stöckle *et al.*, 2016). *tan1 air9* double mutants have a synthetic division-plane orientation defect suggesting genetic interaction (Mir *et al.*, 2018). AIR9 physically interacts with KCBP (Buschmann *et al.*, 2015). CDKA, KCBP and RANGAP1 are labeled in gray to reflect that specific roles in division-plane establishment or maintenance are still unclear. This model reflects our current understanding of division-plane establishment and maintenance but there are likely as-yet-unidentified proteins and interactions between them.

Interestingly, in early gametophytic moss cells that do not make PPBs, spindle bipolarity is still anticipated by bipolar accumulation of cytoplasmic microtubule organizing centers to promote proper division-plane orientation (Kosetsu *et al.*, 2017), similar to cytoplasmic microtubule organizing centers that accumulate before PPB formation in *Marchantia polymorpha* (Buschmann *et al.*, 2016). Although altered spindle positioning may lead to division-plane defects, spindle rotation and other defects occur in many cells without division-plane defects (Rasmussen *et al.*, 2013).

IV. Maintaining the division plane during mitosis and cytokinesis

Once a division plane has been established, information about its location must be maintained until the phragmoplast, a structure that helps direct assembly of the new cell wall (Lee & Liu, 2013; Smertenko *et al.*, 2017), reaches the division site. Defects in division-plane maintenance are identified by comparing the division plane specified by the PPB to the placement of the new cell wall (Fig. 2b, right panel) (Rasmussen, 2016). When the final division occurs outside the PPB location, division-plane maintenance is defective. If the cell naturally does not form a PPB, division-plane maintenance defects can be inferred by comparing developmentally matched WT and mutant cell division patterns (Wu & Bezanilla, 2014; Kosetsu *et al.*, 2017). In moss cells with no PPBs, the *myosin VIII* mutant has division-plane defects. MYOSIN VIII, a motor protein that interacts with both actin and microtubules, localizes to the division site and the phragmoplast, and may promote phragmoplast guidance via actin filaments to the division site (Wu & Bezanilla, 2014).

Two class XII kinesins, POK1 and POK2 localize to the division site throughout mitosis and cytokinesis (Lipka *et al.*, 2014). The *pok1pok2* double mutant has short stature and misplaced cell walls (Müller *et al.*, 2006). Time-lapse indicates that the phragmoplast does not return to the division site specified by the PPB (Lipka *et al.*, 2014). A number of division-site localized proteins required for division-plane maintenance interact directly with POK1 (Fig. 3, discussed below).

A mutant identified in maize, *tan1,* has short stature and aberrant cell wall placement indicative of division-plane defects (Smith *et al.*, 1996). TAN1, a microtubule-binding protein (Smith *et al.*, 2001), localizes to the division site throughout mitosis and cytokinesis, making it the first identified positive division-site marker (Walker *et al.*, 2007). In maize, TAN1-YFP also localizes to mitotic microtubule arrays (Martinez *et al.*, 2017b). TAN1 interacts with POK1 and its division-site accumulation is FASS-, POK1- and PPB- dependent (Walker *et al.*, 2007; Rasmussen *et al.*, 2011b; Martinez *et al.*, 2017b). The maize *tan1* mutant has both division-plane maintenance defects and delays in mitotic progression (Fig. 2b) (Martinez *et al.*, 2017b). A partially rescued TAN1-YFP line, which no longer localized to mitotic microtubule arrays, had significant mitotic progression delays but only minor defects in division-plane orientation. These plants grew normally, suggesting that division-plane orientation is critical for proper growth (Martinez *et al.*, 2017b). TAN1 may have separate functions in microtubule organization and division-plane orientation. It is

unclear whether defects in microtubule organization per se lead to division-plane maintenance defects because many mutants with general microtubule organization defects produce abnormal PPBs (Rasmussen *et al.*, 2013).

Auxin-induced-in-root-cultures 9 (AIR9), a microtubule-binding protein that colocalizes with the PPB, disappears from the division site before metaphase later accumulating at the division site as the phragmoplast touches the cortex (Buschmann *et al.*, 2006). AIR9's contribution to division-plane orientation remained elusive because *air9* mutants have no obvious division-plane defects (Buschmann *et al.*, 2015) similar to very minor division-plane defects in *Arabidopsis thaliana tan1* mutants (Walker *et al.*, 2007). Recently, a function in division-plane orientation was revealed for AIR9 using a *tan1air9* double mutant (Mir *et al.*, 2018). The double mutant displays a synthetic phenotype: short plants with division-plane defects, hypersensitivity to microtubule-depolymerizing drugs, and root cell-file rotation (Mir *et al.*, 2018). Around half of the divisions completed in a location different than the PPB, indicating a significant defect in division-plane maintenance. Surprisingly, *tan1air9* double mutants have unexpected interphase microtubule array organization defects leading to defects in cell elongation and aberrant root cell-file rotation. Although full-length TAN1-YFP rescued the double mutant, a TAN1-YFP protein lacking a domain required for its localization to the PPB (Rasmussen *et al.*, 2011b) rescued everything but the cell-file rotation defect, potentially highlighting this domain's function in interphase microtubule array organization (Mir *et al.*, 2018). TAN1 and AIR9 likely act in parallel pathways to promote division-plane maintenance and organize cortical microtubule arrays but the mechanisms are still unknown.

A pair of putative Rho-of-plants (ROP) GTPase-activating-proteins (GAPs, ROP-GAPs) with pleckstrin homology (PH) domains (PHGAPs) were identified via interaction with POK1. These proteins localize during interphase to the plasma membrane and appear at the division site during metaphase. Double *phgap1 phgap2* mutants have minor defects in division-plane orientation (Stöckle *et al.*, 2016). It is tempting to speculate that ROP proteins generally participate in division-plane orientation, in addition to their role in polarization during asymmetrical divisions (Humphries *et al.*, 2011).

Several other proteins localize to the division site from prophase through cytokinesis (Xu *et al.*, 2008; Buschmann *et al.*, 2015; Li *et al.*, 2017), but obvious roles in division-plane orientation cannot be assigned because mutants do not have division-plane defects. Kinesin-like calmodulin-binding protein (KCBP), a kinesin-14 with microtubule minus-end directed motility (Yamada *et al.*, 2017), localizes to the division site (Buschmann *et al.*, 2015). Another plant-specific microtubule-associated protein, MAP65-4, also localizes to the division site. MAP65-4 plays a semi-redundant function with MAP65-3 in phragmoplast assembly, possibly by crosslinking antiparallel microtubules, but its role in division-plane orientation is unknown (Li *et al.*, 2017). Newly identified proteins with division-site localization suggests that we still have much to learn about the proteins required for division-plane maintenance.

The past few years have led to new insights. Computational modeling approaches can be used to clarify relative contributions of mechanics with geometry in division-plane orientation as well as the nature of defects in known division-plane orientation mutants. New players in division-plane establishment and maintenance (Figs 2–4), in addition to unanticipated connections between known proteins, lead to the hypothesis that establishment and maintenance are regulated by different protein modules. Many more proteins are likely required for division-plane establishment and maintenance, making this an exciting area for future research. Considering the tremendous recent progress, we expect to identify both new players and their interconnections to clarify this fundamental cellular process.

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References

Ambrose JC, Cyr R. 2008. Mitotic spindle organization by the preprophase band. *Molecular Plant* **1**: 950–960.

Asada T. 2013. Division of shape-standardized tobacco cells reveals a limit to the occurrence of single-criterion-based selection of the plane of symmetric division. *Plant & Cell Physiology* **54**: 827–837.

Azimzadeh J, Nacry P, Christodoulidou A, Drevensek S, Camilleri C, Amiour N, Parcy F, Pastuglia M, Bouchez D. 2008. Arabidopsis TONNEAU1 proteins are essential for preprophase band formation and interact with centrin. *Plant Cell* **20**: 2146–2159.

Besson S, Dumais J. 2011. Universal rule for the symmetric division of plant cells. *Proceedings of the National Academy of Sciences, USA* **108**: 6294–6299.

Besson S, Dumais J. 2014. Stochasticity in the symmetric division of plant cells: when the exceptions are the rule. *Frontiers in Plant Science* **5**: 538.

Boruc J, Mylle E, Duda M, De Clercq R, Rombauts S, Geelen D, Hilson P, Inzé D, Van Damme D, Russinova E. 2010. Systematic localization of the Arabidopsis core cell cycle proteins reveals novel cell division complexes. *Plant Physiology* **152**: 553–565.

Brown RC, Lemmon BE. 2001. The cytoskeleton and spatial control of cytokinesis in the plant life cycle. *Protoplasma* **215**: 35–49.

Buschmann H, Chan J, Sanchez-Pulido L, Andrade-Navarro MA, Doonan JH, Lloyd CW. 2006. Microtubule-associated AIR9 recognizes the cortical division site at preprophase and cell-plate insertion. *Current Biology* **16**: 1938–1943.

Buschmann H, Dols J, Kopischke S, Peña EJ, Andrade-Navarro MA, Heinlein M, Szymanski DB, Zachgo S, Doonan JH, Lloyd CW. 2015. Arabidopsis KCBP interacts with AIR9 but stays in the cortical division zone throughout mitosis via its MyTH4-FERM domain. *Journal of Cell Science* **128**: 2033–2046.

Buschmann H, Green P, Sambade A, Doonan JH, Lloyd CW. 2011. Cytoskeletal dynamics in interphase, mitosis and cytokinesis analysed through *Agrobacterium*-mediated transient transformation of tobacco BY-2 cells. *New Phytologist* **190**: 258–267.

Buschmann H, Holtmannspötter M, Borchers A, O'Donoghue M-T, Zachgo S. 2016. Microtubule dynamics of the centrosome-like polar organizers from the basal land plant *Marchantia polymorpha*. *New Phytologist* **209**: 999–1013.

Camilleri C, Azimzadeh J, Pastuglia M, Bellini C, Grandjean O, Bouchez D. 2002. The Arabidopsis *TONNEAU2* gene encodes a putative novel protein phosphatase 2A regulatory subunit essential for the control of the cortical cytoskeleton. *Plant Cell* **14**: 833–845.

Chan J, Calder GM, Doonan JH, Lloyd CW. 2003. EB1 reveals mobile microtubule nucleation sites in Arabidopsis. *Nature Cell Biology* **5**: 967–971.

Costa S. 2017. Are division plane determination and cell-cycle progression coordinated? *New Phytologist* **213**: 16–21.

Doonan JH, Cove DJ, Corke FMK, Lloyd CW. 1987. Preprophase band of microtubules, absent from tip-growing moss filaments, arise in leafy shoots during transition to intercalary growth. *Cell Motility and the Cytoskeleton* **7**: 138–153.

Drevensek S, Goussot M, Duroc Y, Christodoulidou A, Steyaert S, Schaefer E, Duvernois E, Grandjean O, Vantard M, Bouchez D *et al.* 2012. The *Arabidopsis* TRM1–TON1 interaction reveals a recruitment network common to plant cortical microtubule arrays and eukaryotic centrosomes. *Plant Cell* **24**: 178–191.

Dupuy L, Mackenzie J, Haseloff J. 2010. Coordination of plant cell division and expansion in a simple morphogenetic system. *Proceedings of the National Academy of Sciences, USA* **107**: 2711–2716.

Errera L. 1888. Über Zellformen und Siefenblasen. *Botanisches Centralblatt* **34**: 395–399.

Facette MR, Smith LG. 2012. Division polarity in developing stomata. *Current Opinion in Plant Biology* **15**: 585–592.

Flanders DJ, Rawlins DJ, Shaw PJ, Lloyd CW. 1990. Nucleus-associated microtubules help determine the division plane of plant epidermal cells: avoidance of four-way junctions and the role of cell geometry. *Journal of Cell Biology* **110**: 1111–1122.

Gunning BE, Hardham AR, Hughes JE. 1978. Pre-prophase bands of microtubules in all categories of formative and proliferative cell division in *Azolla* roots. *Planta* **143**: 145–160.

Gunning B, Sammut M. 1990. Rearrangements of microtubules involved in establishing cell division planes start immediately after DNA synthesis and are completed just before mitosis. *Plant Cell* **2**: 1273–1282.

Hofmeister W. 1863. Zusatze und Berichtigungen zu den 1851 veroffentlichen Untersuchungengen der Entwicklung hoherer Kryptogamen. *Jahrbucher fur Wissenschaft und Botanik* **3**: 259–293.

Humphries JA, Vejlupkova Z, Luo A, Meeley RB, Sylvester AW, Fowler JE, Smith LG. 2011. ROP GTPases act with the receptor-like protein PAN1 to polarize asymmetric cell division in maize. *Plant Cell* **23**: 2273–2284.

Hush JM, Hawes CR, Overall RL. 1990. Interphase microtubule re-orientation predicts a new cell polarity in wounded pea roots. *Journal of Cell Science* **96**: 47–61.

Hush J, Wu L, John PC, Hepler LH, Hepler PK. 1996. Plant mitosis promoting factor disassembles the microtubule preprophase band and accelerates prophase progression in Tradescantia. *Cell Biology International* **20**: 275–287.

Jones RA, Forero-Vargas M, Withers SP, Smith RS, Traas J, Dewitte W, Murray J. 2017. Cell-size dependent progression of the cell cycle creates homeostasis and flexibility of plant cell size. *Nature Communications* **8**: 15 060.

Jürgens G, Park M, Richter S, Touihri S, Krause C, El Kasmi F, Mayer U. 2015. Plant cytokinesis: a tale of membrane traffic and fusion. *Biochemical Society Transactions* **43**: 73–78.

Kajala K, Ramakrishna P, Fisher A, Bergmann DC, De Smet I, Sozzani R, Weijers D, Brady SM. 2014. Omics and modelling approaches for understanding regulation of asymmetric cell divisions in arabidopsis and other angiosperm plants. *Annals of Botany* **113**: 1083–1105.

Karahara I, Suda J, Tahara H, Yokota E, Shimmen T, Misaki K, Yonemura S, Staehelin LA, Mineyuki Y. 2009. The preprophase band is a localized center of clathrin-mediated endocytosis in late prophase cells of the onion cotyledon epidermis. *Plant Journal* **57**: 819–831.

Kimata Y, Higaki T, Kawashima T, Kurihara D, Sato Y, Yamada T, Hasezawa S, Berger F, Higashiyama T, Ueda M. 2016. Cytoskeleton dynamics control the first asymmetric cell division in Arabidopsis zygote. *Proceedings of the National Academy of Sciences, USA* **113**: 14 157–14 162.

Kirik A, Ehrhardt DW, Kirik V. 2012. *TONNEAU2/FASS* regulates the geometry of microtubule nucleation and cortical array organization in interphase *Arabidopsis* cells. *Plant Cell* **24**: 1158–1170.

Klotz J, Nick P. 2012. A novel actin-microtubule cross-linking kinesin, NtKCH, functions in cell expansion and division. *New Phytologist* **193**: 576–589.

Kosetsu K, Murata T, Yamada M, Nishina M, Boruc J, Hasebe M, Van Damme D, Goshima G. 2017. Cytoplasmic MTOCs control spindle orientation for asymmetric cell division in plants. *Proceedings of the National Academy of Sciences, USA* **114**: E8847–E8854.

Lee Y-RJ, Liu B. 2013. The rise and fall of the phragmoplast microtubule array. *Current Opinion in Plant Biology* **16**: 757–763.

Li Y, Shen Y, Cai C, Zhong C, Zhu L, Yuan M, Ren H. 2010. The type II *Arabidopsis* formin14 interacts with microtubules and microfilaments to regulate cell division. *Plant Cell* **22**: 2710–2726.

Li S, Sun T, Ren H. 2015. The functions of the cytoskeleton and associated proteins during mitosis and cytokinesis in plant cells. *Frontiers in Plant Science* **6**: 282.

Li H, Sun B, Sasabe M, Deng X, Machida Y, Lin H, Julie Lee Y-R, Liu B. 2017. Arabidopsis MAP65-4 plays a role in phragmoplast microtubule organization and marks the cortical cell division site. *New Phytologist* **215**: 187–201.

Lintilhac PM, Vesecky TB. 1981. Mechanical stress and cell wall orientation in plants. II. The application of controlled directional stress to growing plants; with a discussion on the nature of the wound reaction. *American Journal of Botany* **68**: 1222–1230.

Lipka E, Gadeyne A, Stöckle D, Zimmermann S, De Jaeger G, Ehrhardt DW, Kirik V, Van Damme D, Müller S. 2014. The Phragmoplast-Orienting Kinesin-12 class proteins translate the positional information of the preprophase band to establish the cortical division zone in *Arabidopsis thaliana*. *Plant Cell* **26**: 2617–2632.

Louveaux M, Julien J-D, Mirabet V, Boudaoud A, Hamant O. 2016. Cell division plane orientation based on tensile stress in *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences, USA* **113**: E4294–E4303.

Martinez P, Allsman L, Brakke KA, Hoyt C, Hayes J, Rasmussen CG. 2017a. Using the three dimensional shape of plant cells to predict probabilities of cell division orientation. *bioRxiv*: 199885

Martinez P, Luo A, Sylvester A, Rasmussen CG. 2017b. Proper division plane orientation and mitotic progression together allow normal growth of maize. *Proceedings of the National Academy of Sciences, USA* **114**: 2759–2764.

McDowell JM, An YQ, Huang S, McKinney EC, Meagher RB. 1996. The Arabidopsis ACT7 actin gene is expressed in rapidly developing tissues and responds to several external stimuli. *Plant Physiology* **111**: 699–711.

Mineyuki Y, Palevitz BA. 1990. Relationship between preprophase band organization, F-actin and the division site in *Allium*. *Journal of Cell Science* **97**: 283–295.

Mir R, Morris VH, Buschmann H, Rasmussen CG. 2018. Division plane orientation defects revealed by a synthetic double mutant phenotype. *Plant Physiology* **176**: 418–431.

Müller S, Han S, Smith LG. 2006. Two kinesins are involved in the spatial control of cytokinesis in Arabidopsis thaliana. *Current Biology* **16**: 888–894.

Otegui MS, Staehelin LA. 2004. Electron tomographic analysis of post-meiotic cytokinesis during pollen development in *Arabidopsis thaliana*. *Planta* **218**: 501–515.

Rasmussen CG. 2016. Using live-cell markers in maize to analyze cell division orientation and timing. In: Caillaud M-C, ed. *Methods in Molecular Biology. Plant Cell Division*. New York, NY, USA: Springer, 209–225.

Rasmussen CG, Humphries JA, Smith LG. 2011a. Determination of symmetric and asymmetric division planes in plant cells. *Annual Review of Plant Biology* **62**: 387–409.

Rasmussen CG, Sun B, Smith LG. 2011b. Tangled localization at the cortical division site of plant cells occurs by several mechanisms. *Journal of Cell Science* **124**: 270–279.

Rasmussen CG, Wright AJ, Müller S. 2013. The role of the cytoskeleton and associated proteins in determination of the plant cell division plane. *Plant Journal* **75**: 258–269.

Sachs J. 1878. Uber die Anordnung der Zellen in jungsten Pflanzentheilen. *Arb Bot Inst Würzburg* **2**: 46–104.

Sahlin P, Jönsson H. 2010. A modeling study on how cell division affects properties of epithelial tissues under isotropic growth. *PLoS ONE* **5**: e11750.

Sampathkumar A, Krupinski P, Wightman R, Milani P, Berquand A, Boudaoud A, Hamant O, Jönsson H, Meyerowitz EM. 2014. Subcellular and supracellular mechanical stress prescribes cytoskeleton behavior in Arabidopsis cotyledon pavement cells. *eLife* **3**: e01967.

Sano T, Higaki T, Oda Y, Hayashi T, Hasezawa S. 2005. Appearance of actin microfilament 'twin peaks' in mitosis and their function in cell plate formation, as visualized in tobacco BY-2 cells expressing GFP-fimbrin. *Plant Journal* **44**: 595–605.

Schaefer E, Belcram K, Uyttewaal M, Duroc Y, Goussot M, Legland D, Laruelle E, de Tauzia-Moreau M-L, Pastuglia M, Bouchez D. 2017. The preprophase band of microtubules controls the robustness of division orientation in plants. *Science* **356**: 186–189.

Schneider R, Persson S. 2015. Connecting two arrays: the emerging role of actin-microtubule cross-linking motor proteins. *Frontiers in Plant Science* **6**: 415.

Shao W, Dong J. 2016. Polarity in plant asymmetric cell division: division orientation and cell fate differentiation. *Developmental Biology* **419**: 121–131.

Shapiro BE, Tobin C, Mjolsness E, Meyerowitz EM. 2015. Analysis of cell division patterns in the *Arabidopsis* shoot apical meristem. *Proceedings of the National Academy of Sciences, USA* **112**: 4815–4820.

Smertenko A, Assaad F, Baluška F, Bezanilla M, Buschmann H, Drakakaki G, Hauser M-T, Janson M, Mineyuki Y, Moore I *et al.* 2017. Plant cytokinesis: terminology for structures and processes. *Trends in Cell Biology* **27**: 885–894.

Smith LG, Gerttula SM, Han S, Levy J. 2001. Tangled1: a microtubule binding protein required for the spatial control of cytokinesis in maize. *Journal of Cell Biology* **152**: 231–236.

Smith LG, Hake S, Sylvester AW. 1996. The tangled-1 mutation alters cell division orientations throughout maize leaf development without altering leaf shape. *Development* **122**: 481–489.

Spinner L, Gadeyne A, Belcram K, Goussot M, Moison M, Duroc Y, Eeckhout D, De Winne N, Schaefer E, Van De Slijke E *et al.* 2013. A protein phosphatase 2A complex spatially controls plant cell division. *Nature Communications* **4**: 1863.

Spinner L, Pastuglia M, Belcram K, Pegoraro M, Goussot M, Bouchez D, Schaefer DG. 2010. The function of TONNEAU1 in moss reveals ancient mechanisms of division plane specification and cell elongation in land plants. *Development* **137**: 2733–2742.

Stöckle D, Herrmann A, Lipka E, Lauster T, Gavidia R, Zimmermann S, Müller S. 2016. Putative RopGAPs impact division plane selection and interact with kinesin-12 POK1. *Nature Plants* **2**: 16120.

Takeuchi M, Karahara I, Kajimura N, Takaoka A, Murata K, Misaki K, Yonemura S, Staehelin LA, Mineyuki Y. 2016. Single microfilaments mediate the early steps of microtubule bundling during preprophase band formation in onion cotyledon epidermal cells. *Molecular Biology of the Cell* **27**: 1809–1820.

Tian J, Han L, Feng Z, Wang G, Liu W, Ma Y, Yu Y, Kong Z. 2015. Orchestration of microtubules and the actin cytoskeleton in trichome cell shape determination by a plant-unique kinesin. *eLife* **4**: e09351.

Torres-Ruiz RA, Jürgens G. 1994. Mutations in the FASS gene uncouple pattern formation and morphogenesis in Arabidopsis development. *Development* **120**: 2967–2978.

Tseng K-F, Wang P, Lee Y-RJ, Bowen J, Gicking AM, Guo L, Liu B, Qiu W. 2017. The preprophase band-associated kinesin-14 OsKCH2 is a processive minus-end-directed microtubule motor. *bioRxiv*: 232652.

Van Damme D, De Rybel B, Gudesblat G, Demidov D, Grunewald W, De Smet I, Houben A, Beeckman T, Russinova E. 2011. Arabidopsis α Aurora kinases function in formative cell division plane orientation. *Plant Cell* **23**: 4013–4024.

Van Damme D, Vanstraelen M, Geelen D. 2007. Cortical division zone establishment in plant cells. *Trends Plant Sci* **12**: 458–464.

Van Leene J, Stals H, Eeckhout D, Persiau G, Van De Slijke E, Van Isterdael G, De Clercq A, Bonnet E, Laukens K, Remmerie N *et al.* 2007. A tandem affinity purification-based technology platform to study the cell cycle interactome in *Arabidopsis thaliana*. *Molecular & Cellular Proteomics* **6**: 1226–1238.

Vaškebová L, Šamaj J, Ovečka M. 2017. Single-point ACT2 gene mutation in the Arabidopsis root hair mutant der1-3 affects overall actin organization, root growth and plant development. *Annals of Botany* doi: 10.1093/aob/mcx180.

Wada M. 2017. Nuclear movement and positioning in plant cells. *Seminars in Cell & Developmental Biology* doi: 10.1016/j.semcdb.2017.10.001.

Walbot V, Egger RL. 2016. Pre-meiotic anther development: cell fate specification and differentiation. *Annual Review of Plant Biology* **67**: 365–395.

Walker KL, Müller S, Moss D, Ehrhardt DW, Smith LG. 2007. Arabidopsis TANGLED identifies the division plane throughout mitosis and cytokinesis. *Current Biology* **17**: 1827–1836.

Walter WJ, Machens I, Rafieian F, Diez S. 2015. The non-processive rice kinesin-14 OsKCH1 transports actin filaments along microtubules with two distinct velocities. *Nature Plants* **1**: 15111.

Wright AJ, Gallagher K, Smith LG. 2009. discordia1 and alternative discordia1 function redundantly at the cortical division site to promote preprophase band formation and orient division planes in maize. *Plant Cell* **21**: 234–247.

Wu S-Z, Bezanilla M. 2014. Myosin VIII associates with microtubule ends and together with actin plays a role in guiding plant cell division. *eLife* **3**: e03498.

Xu XM, Zhao Q, Rodrigo-Peiris T, Brkljacic J, He CS, Müller S, Meier I. 2008. RanGAP1 is a continuous marker of the *Arabidopsis* cell division plane. *Proceedings of the National Academy of Sciences, USA* **105**: 18 637–18 642.

Yamada M, Tanaka-Takiguchi Y, Hayashi M, Nishina M, Goshima G. 2017. Multiple kinesin-14 family members drive microtubule minus end–directed transport in plant cells. *Journal of Cell Biology* **216**: 1705–1714.

Yoshida S, Barbier de Reuille P, Lane B, Bassel GW, Prusinkiewicz P, Smith RS, Weijers D. 2014. Genetic control of plant development by overriding a geometric division rule. *Developmental Cell* **29**: 75–87.

Zhang Y, Iakovidis M, Costa S. 2016. Control of patterns of symmetric cell division in the epidermal and cortical tissues of the Arabidopsis root. *Development* **143**: 978–982.