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# Redundant mechanisms in division plane positioning

Aimee N. Uyehara [1], Carolyn G. Rasmussen [2,*]

*Department of Botany and Plant Sciences, Center for Plant Cell Biology, University of California, Riverside, USA*

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ABSTRACT

Redundancies in plant cell division contribute to the maintenance of proper division plane orientation. Here we highlight three types of redundancy: 1) Temporal redundancy, or correction of earlier defects that results in proper final positioning, 2) Genetic redundancy, or functional compensation by homologous genes, and 3) Synthetic redundancy, or redundancy within or between pathways that contribute to proper division plane orientation. Understanding the types of redundant mechanisms involved provides insight into current models of division plane orientation and opens up new avenues for exploration.

## 1. Summary of current mechanisms in cell division

Cell division is a fundamental process where a cell divides into two new daughter cells. Cell division is essential for survival in all organisms and plays a vital role in plant growth and development. Plant cells do not migrate and instead control the location of new cells by positioning the division plane. Plant division plane orientation is established, maintained, and completed through the coordination of microtubule and actin arrays with division site proteins. A short description of the microtubule arrays and DNA structures observed in typical symmetric land plant divisions is shown in Fig. 1. Symmetric cell divisions generate the same cell type while asymmetric divisions generate new cell types. For more on division plane determination in symmetric and asymmetric divisions, see reviews (Buschmann and Müller, 2019; Livanos and Müller, 2019; Rasmussen and Bellinger, 2018; Yi and Goshima, 2022). For a synthesis of developmental and cell biological frameworks that modulate division plane orientation, please see (Glanc, 2022; Facette et al., 2019; Yi and Goshima, 2022; Herrmann and Torii, 2021; Zhang et al., 2023).

A number of proteins and processes relevant to plant division plane orientation occur with some level of redundancy. Similar to other systems where redundancy is present, redundancies may contribute to the robustness of maintaining proper division plane positioning (Láruson et al., 2020). Open questions remain about why some processes are reinforced through redundant mechanisms and whether redundancy in division plane orientation contributes to phenotypic plasticity. Typical model systems used to understand division plane positioning include the dicot model *Arabidopsis thaliana* (Arabidopsis), monocots *Zea mays* (maize) and *Brachypodium distachyon*, and non-flowering models *Physcomitrium patens* (*P. patens)* and *Marchantia polymorpha* (*M. polymorpha*) although important discoveries have been found in other plants. This review focuses on genetic and non-genetic redundancies that contribute to proper division plane orientation.

1) The interphase cortical microtubule array: During interphase, microtubules at the cell cortex, the region just underneath the plasma membrane, form a variety of cortical microtubule array organizations. Rapidly elongating cells form ordered arrays perpendicular to the growth axis while isotropically expanding cells tend to form more disordered microtubule arrays. These cortical interphase arrays contribute to positioning cellulose synthase complexes and generating new cell wall material. Therefore, the orientation of the interphase cortical microtubule array influences the direction of cell elongation (Dixit and Cyr, 2004; Oda, 2015). Orientation of the interphase cortical microtubule array often, but not always, precedes orientation of the preprophase band (PPB), described below (Gunning and Sammut, 1990).
2) The preprophase band (PPB): Increased microtubule dynamicity precedes the formation of the PPB ring at the cell cortex during the last part of the G2 phase in the cell cycle (Vos et al., 2004). The PPB surrounds the nucleus (purple) and accurately predicts the future division site and cell plate insertion site (Mineyuki, 1999;

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* Corresponding author.
*E-mail address:* crasmu@ucr.edu (C.G. Rasmussen).
[1] ORCID 0000-0003-4010-4771
[2] ORCID 0000-0002-4354-6295

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Pickett-Heaps and Northcote, 1966; Smertenko et al., 2017). While the PPB is disassembling, microtubules accumulate around the nuclear envelope to coalesce into an acentrosomal spindle. The cortical division zone, however, remains marked by division-site-localized proteins (pink) even though the PPB is no longer present.

3) The spindle: The spindle captures and separates chromosomes (purple) during metaphase and anaphase. Spindle formation is reviewed in Liu and Lee (2022); Zhang and Dawe (2011). After chromosome separation in anaphase, the spindle disassembles to form a plant specific structure called the phragmoplast.
4) The phragmoplast: The phragmoplast directs the formation of the cell plate. The cell plate transitions into the new cell wall after the completion of cytokinesis, reviewed in Gu and Rasmussen (2022); Lee and Liu (2019); Smertenko et al., (2018, 2017).
5) The cortical-telophase microtubule array: The cortical-telophase microtubule array contributes to positioning the phragmoplast. Cortical-telophase microtubules are added into the phragmoplast at the cortex to direct phragmoplast expansion at the division site (Bellinger et al., 2023). As the phragmoplast disassembles at the cell plate fusion site, the cell plate fuses with the mother cell plasma membrane to form the new cell wall.

Cell shape, size, and nuclear movement are closely intertwined with the onset of mitosis and division plane positioning. Plant cells grow to a certain size before they enter mitosis (Gutierrez, 2022). After asymmetric divisions generate small cells, S phase is delayed until cells reach a certain size (D'Ario et al., 2021). Prior to mitosis, the nucleus moves to the future division plane in both symmetrically and asymmetrically dividing cells through the coordinated action of microtubule and actin motor proteins (Facette et al., 2019; Frey et al., 2010). Proteins connecting the nucleus and the cytoskeleton are critical for positioning the PPB (Arif Ashraf et al., 2022). PPB positioning defects may result from errors in nuclear positioning but also reflect combinations of defective cell elongation, disorganized microtubule arrays, or failures in establishing polarity prior to asymmetric division (Pietra et al., 2013; Zhang and Ambrose, 2022). Some mutants discussed below have defects in cell elongation or microtubule orientation in interphase, which may influence the position of the division plane and subsequently alter organ shape. Indeed, cell elongation prior to division typically favors a division bisecting the long axis of the cell (Martinez et al., 2018). The relationship between division plane orientation and cell shape is discussed in more detail in (Laruelle et al., 2022; Louveaux et al., 2016; Martinez et al., 2018; Moukhtar et al., 2019; Rasmussen and Bellinger, 2018). Identifying mutants that only alter PPB formation or positioning (some of which are discussed below) but do not seriously alter interphase microtubule orientation, polarity cues, or cell shape provide exceptionally valuable insight e.g. Schaefer et al. (2017).

## 2. Temporal redundancy

Cell division positioning is buffered through temporal redundancy. We use temporal redundancy to describe situations where alterations to division plane orientation are corrected later by another independent mechanism. Two examples of temporal redundancy discussed below are: 1) when defects in proper organization or positioning of mitotic structures (Fig. 2), such as the spindle, does not alter the proper localization of the final division and 2) when protein recruitment to a specific location earlier in the cell cycle partially abrogates the need for that protein to be recruited later (Fig. 3).

The inner ring (clockwise starting from interphase) illustrates normal symmetric divisions with typical land-plant mitotic structures from interphase to cytokinesis (Pathway 1). Blue lines represent a cell-cycle progression that leads to a "correctly oriented" division. Red lines represent defects that may lead to an aberrantly positioned new cell wall (orange line). In Pathway 2, mispositioned PPBs result in misoriented spindles and phragmoplasts that lead to a final misoriented division. In Pathway 3, PPB formation does not occur which either results in wild-type division planes (blue line) or division-plane-orientation defects (red line). In Pathway 4, spindle rotation occurs both in mutant and non-mutant cells, but the tilt is corrected leading to normally positioned

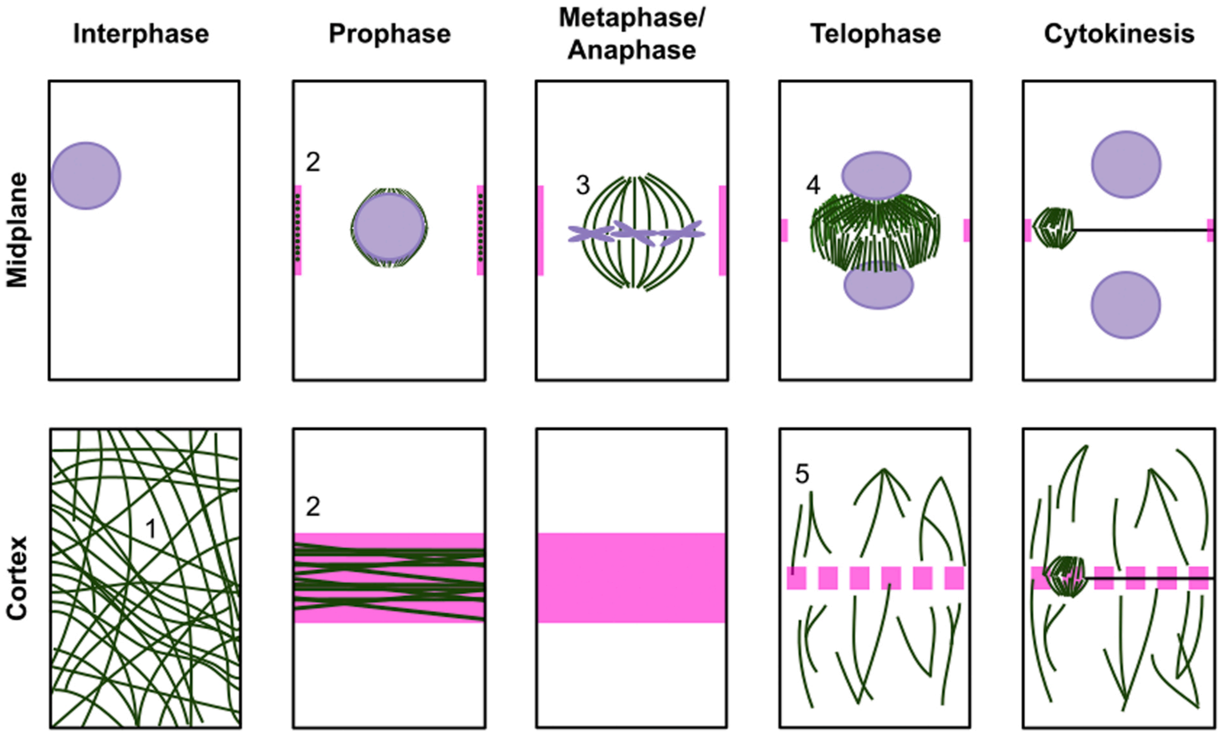

**Fig. 1. Overview of mitotic microtubule and DNA structures and locations important in typical land plant division plane orientation.** Typical land plant cells form five key microtubule arrays (green) during the cell cycle. The division site is marked in pink. Numbered microtubule arrays are described further in the text.

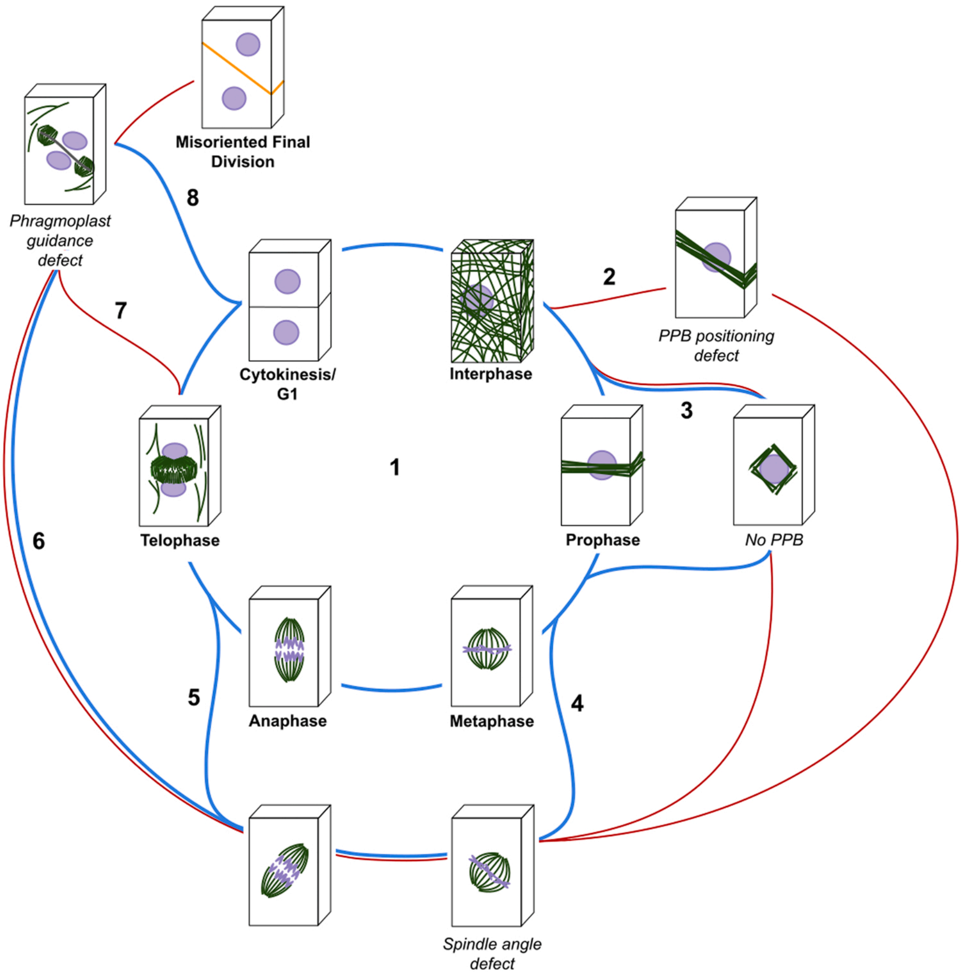

**Fig. 2. Temporal redundancy during division plane orientation showing schematic examples of correctly oriented divisions, and when mitotic structures deviate from the "correctly oriented" position.** Microtubule structures are green, DNA is purple, and black lines indicate the cell wall.

phragmoplasts (Pathway 5) or generating tilted phragmoplasts that are sometimes corrected later (Pathway 6). In Pathway 7, phragmoplast guidance defects result in misoriented divisions. Finally in Pathway 8, some misoriented phragmoplasts can be corrected as they near the cortical division site, but before cytokinesis is completed.

Plant cells are capable of robustly maintaining proper division plane orientation via dynamic re-positioning of mitotic structures (Fig. 2, Pathway 1). Analysis of divisions with and without PPBs provides insight into the stabilizing function of the PPB and its contribution to efficient coordination of mitotic progression. Although the PPB facilitates efficient spindle formation, cells lacking PPBs still assemble functionally and morphologically normal spindles (Fig. 2, Pathway 3). This includes both cells with defective/missing PPBs and those that always lack PPBs, such as the cells that will undergo meiosis (meiocytes) or some divisions in early diverging plants e.g. in ~~(~~Chan et al., 2005; Higgins et al., 2016; Otegui and Staehelin, 2000; Rensing et al., 2020; and Sakai et al., 2022~~)~~. Unlike cells that have PPBs, cells that lack PPBs may require additional time for spindle coalescence as exemplified in Arabidopsis cultured cells (Chan et al., 2005). In addition, naturally PPB-less meiotic spindles often form incorrectly, taking additional time to realign to form a bipolar spindle in maize (Weiss et al., 2022; Zhang and Dawe, 2011).

For cells that typically form PPBs, both spindle rotation and spindle morphology defects can be overcome to maintain proper division planes by corrective rotation of the phragmoplast (Fig. 2, Pathways 4 and 5, or Pathways 4 and 6). Phragmoplast correction has been observed in bean, maize, and onion cells where imaging experiments revealed tilted spindles (e.g. >50% in maize epidermal cells), but normal final division orientation~~s~~ (Cleary and Smith, 1998; Oud and Nanninga, 1992; Palevitz, 1986). In onion guard mother cells, live cell imaging demonstrated correction of oblique spindle and phragmoplast angles occurs as the cell plate expands along the location previously marked by the PPB (Palevitz, 1986). In addition, in tobacco, when cells with PPBs are treated with microtubule depolymerizing drugs followed by washout, spindles formed that are often tilted, but division positioning is typically corrected prior to cytokinesis (Marcus et al., 2005).

Corrections to spindle orientation are also observed in mutants with defects in spindle formation, morphology, and organization (Fig. 2, Pathway 4 and 5 or Pathway 4 and 6). Mutants of the gene encoding the microtubule severing protein KATANIN1 (KTN1) make defective PPBs and have spindles that exhibit random rotations in Arabidopsis (Komis et al., 2017). However, the phragmoplasts eventually return to the former location of the PPB (Komis et al., 2017). Other mutants that produce highly elongated, mispositioned, or multipolar spindles also typically divide in the correct location. Examples include Arabidopsis *endosperm defective 1* (*ede1*), which is a mutant in an *AUGMIN8* homolog (Lee et al., 2017), and mutants lacking minus end directed Kinesin 14 A motors *(atk1* and *atk5*) (Ambrose and Cyr, 2007; Chen et al., 2002; Hotta et al., 2022; Marcus et al., 2003).

Other redundant mechanisms that correct spindle mispositioning or multipolarity occur in cells lacking PPBs. In maize meiocytes, mutants in *Kinesin14A* have defects in spindle assembly and form multipolar spindles. However, multipolar spindles then coalesce to form bipolar spindles and division proceeds normally (Higgins et al., 2016; Weiss et al.,

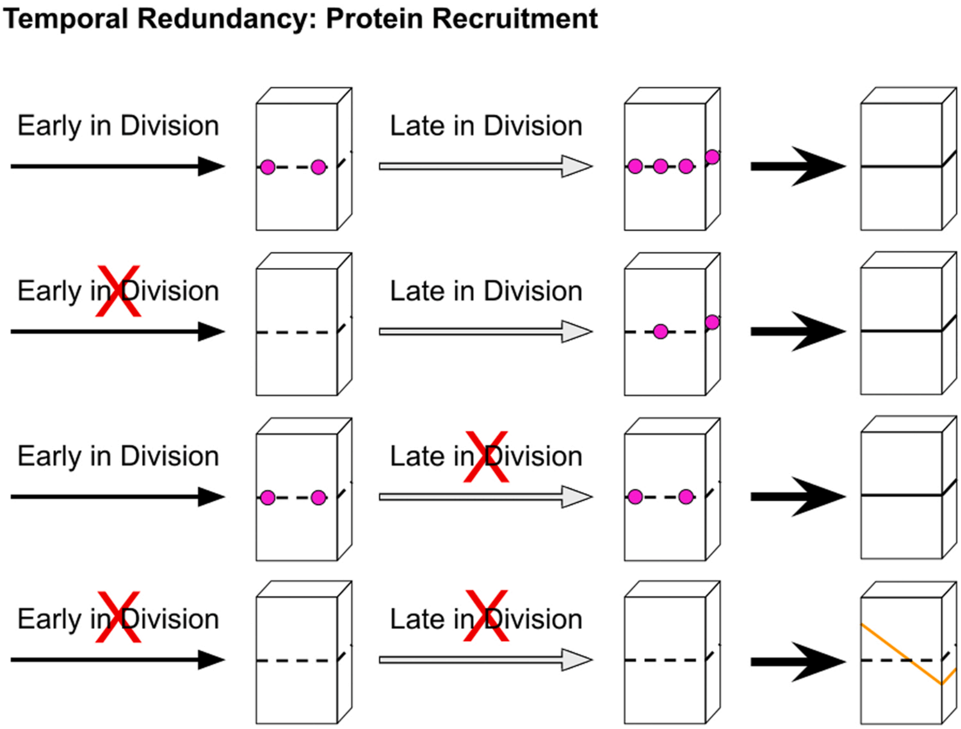

**Fig. 3. Temporal redundancy in protein recruitment.** In the wild-type example (top), early protein localization is reinforced by redundant, later recruitment to the same location. In the absence of either early or late recruitment (second and third from top), the protein is sufficient to maintain correct division plane orientation. Complete loss of recruitment results in a division plane orientation defect. Dotted lines represent the correct division site. Pink circles represent division site localized proteins. Solid orange line represents the final misoriented division.

2022). This suggests that spindle correction also occurs in a PPB-independent manner. A similar redundancy is observed in *M. polymorpha* suspension cells which have centrosome-like structures called polar organizers that define the poles of the cell and promote the formation of the PPB. In the absence of the PPB but presence of multiple polar organizers, *Marchantia* suspension cells form multipolar prometaphase spindles that resolve into a bipolar arrangement for normal division progression (Buschmann et al., 2016).

Alternatively, in some divisions without PPBs, such as those observed in *P. patens,* meiocytes, or mutants, spindle orientation may play a greater role in determining division plane orientation. Here, we propose that the PPB may provide one or more corrective mechanisms because it recruits division site localized proteins that later adjust phragmoplast positioning. Therefore in the absence of a PPB, defects in spindle positioning may not be corrected later in the cell cycle. For example, the PPB-less divisions of male meiocytes in the Arabidopsis *atk1* mutant (mentioned above) have a more severe phenotype consisting of chromosome segregation defects than in PPB-containing mitotic divisions (Chen et al., 2002; Marcus et al., 2003). In addition, *P. patens* gametophore initial cells lack PPBs but instead make a microtubule structure called the gametosome, which predicts spindle positioning (Kosetsu et al., 2017). Spindle mispositioning in the asymmetric divisions of gametophore initials in the *P. patens TPX2* mutant results in aberrant division positioning (Kozgunova et al., 2022). Finally, greater variation in spindle angle was also observed in an Arabidopsis triple mutant (discussed below in the genetic redundancy section) that rarely produced PPBs called *tonneau recruiting motif (trm678).* In the *trm678* mutant, spindle angle variation was correlated with variation in cell wall angle (Schaefer et al., 2017). However, confirming if spindle angle defects indeed lead to mispositioned final cell walls would require timelapse imaging. Together these examples suggest that in the absence of a PPB (e.g. in mutants such as *trm678,* some *P. patens* divisions, and, meiocytes), the spindle may play a greater role in division plane determination.

Spindle rotation and other defects are often compensated by phragmoplast guidance to the correct division plane (Pathway 8). In Arabidopsis, several proteins (discussed in more detail below) are hypothesized to guide the phragmoplast to the correct division site by interacting with microtubules emanating from the phragmoplast called peripheral phragmoplast microtubules (Livanos and Müller, 2019). In maize, another mechanism is proposed to coordinate phragmoplast positioning with division site localized proteins. Cortical telophase microtubules, a population of microtubules that nucleates at the cell cortex independent from phragmoplast microtubules, were observed to interact with the phragmoplast and likely influence phragmoplast positioning (Bellinger et al., 2023). Interaction of these cortical telophase microtubules with division site localized proteins (discussed below) pre-orients cortical telophase microtubules at the cell cortex ahead of phragmoplast expansion, thereby positioning the phragmoplast (Bellinger et al., 2023). These cortical telophase microtubules have been observed in both monocot and dicot species, suggesting that this type of phragmoplast positioning may be conserved through the plant lineage (Lucas, 2021; Panteris et al., 1995; Wick, 1985). Phragmoplast guidance is also mediated by both short and long range interactions between division site localized proteins, actin filaments, and microtubules. After centrifugation of dividing tobacco cells, long actin cables are observed connecting the displaced phragmoplast and the division site or former PPB location (Arima et al., 2018). Both classes of actin motor proteins, MYOSIN VIIIs and MYOSIN XIs, promote proper phragmoplast guidance (Abu-Abied et al., 2018; Huang et al., 2022; Nan et al., 2021; Wu and Bezanilla, 2014). MYOSIN VIII coordinates actin filaments and microtubules at the phragmoplast and the division site to move the phragmoplast towards the division site (Wu and Bezanilla, 2014).

A final example discusses temporal redundancy in terms of protein localization. TANGLED1 (TAN1) is a key division site localized protein recruited during both prophase and telophase by independent mechanisms (Rasmussen et al., 2011), although only a part of the protein is only required for full function (Mills et al., 2022). In Arabidopsis, this fragment accumulates at the division site during telophase, and interacts with another division site localized protein called PHRAGMOPLAST ORIENTING KINESIN1 (POK1) (Müller et al., 2006; Rasmussen et al., 2011), which is described in more detail in the genetic redundancy section. Why then is TAN recruited to the division site during prophase? Recent data shows that when TAN1 is recruited during prophase, both

TAN1-telophase recruitment and interaction with POK1 is less important for in vivo function. In other words, if TAN1 is already at the division site, there may be~~is~~ less need for it to be recruited again later and for interactions thought to mediate its telophase division site localization (Mills et al., 2022).

## 3. Genetic redundancy in division plane orientation

Genetic redundancy exists for some genes that are important for division plane orientation (Fig. 4). Genetic redundancy (on the scale of the individual rather than a population) is defined as the ability of closely related genes (homologs) to functionally compensate for the absence of the other (Ascencio and DeLuna, 2013; Láruson et al., 2020). Single mutants have no or subtle phenotypes, whereas two or more mutant combinations in related genes show phenotypes with varying severity. In contrast, mutants in non-redundant genes, genes without homologs in the genome, often have noticeable phenotypes. Below, we highlight some examples of genetic redundancy involved in division plane positioning.

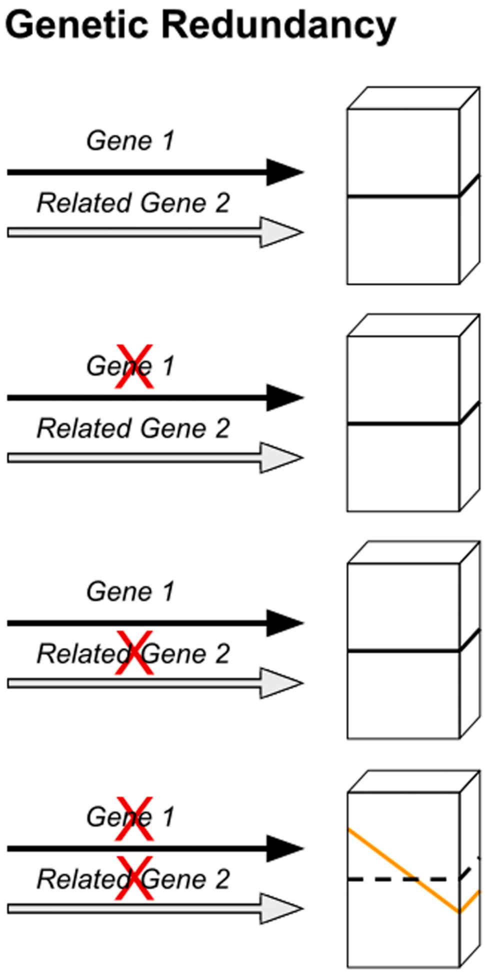

**Fig. 4. Genetic redundancy in division plane orientation.** In processes that involve two or more homologous genes within a family, some genes are able to functionally compensate for mutations within other related genes. For lower order mutants (e.g. single mutants shown here), this can result in a normally positioned division. Higher order mutants, such as the last example of the double mutant shown here, are required to observe division plane orientation defects (orange line).

### 3.1. Proteins important for PPB positioning

The first genes required for PPB positioning were discovered using forward genetic screens described below. Later, protein-protein interaction studies identified redundant partners that promote proper PPB positioning. As an example, we highlight the pathway that contributes to asymmetric divisions during stomatal formation in maize. The pathway required for PPB positioning and stomatal development in Arabidopsis has been beautifully and recently reviewed in Chen (2022); Guo and Dong (2022); Herrmann and Torii (2021).

The early components of the maize asymmetric subsidiary mother cell pathway were identified using forward genetics as many of the identified genes have non-redundant functions. Subsidiary mother cells divide into a subsidiary cell and pavement cell and begin with the polarized recruitment of BRICK to the subsidiary mother cell and guard mother cell interface. BRICK1 is a highly conserved component of the SCAR/WAVE (suppressor of cAR/WASP family/Verprolin-homologous protein) complex important for nucleating branched actin, first characterized in maize (Frank and Smith, 2002). Arabidopsis *brk1* mutants have aberrant actin organization and reduced trichome branching and pavement cell lobing (Le et al., 2006; Djakovic et al., 2006). Similarly maize *brick1* mutants with aberrant actin organization and form brick-shaped epidermal cells that lack lobes and have defects in subsidiary cell formation (Facette et al., 2015; Frank and Smith, 2002). BRICK1 is required for the recruitment of two catalytically dead leucine-rich-repeat receptor-like-kinases (LRR-RLK) PANGLOSS2 (PAN2) and PAN1 (Zhang et al., 2012; Cartwright et al., 2009).

Redundant players important for subsidiary mother cell divisions were identified through protein-protein interactions. PAN2 is required to recruit PAN1 to the subsidiary mother and guard cell interface, but they do not physically interact. Instead, PAN1 and PAN2 both interact with two members of the WEB1-PMI2-RELATED (WPR) protein family (Nan et al., 2022). Founding members of the WPR family, WEAK CHLOROPLAST MOVEMENT UNDER BLUE LIGHT 1 (WEB1) and PLASTED MOVEMENT IMPAIRED 2 (PMI2) promote actin nucleation during chloroplast movement (Kodama et al., 2010; Luesse et al., 2006; Suetsugu and Wada, 2017). WPRs are a large redundant family (16 in *A. thaliana* and 17 in maize) that share a coiled-coil domain which likely mediates protein-protein interactions (Nan et al., 2023. Four maize WPRs belonging to the WPRA and WPRB clades interact with each other, while WPRBs interact directly with PAN2 and PAN1. These WPRs polarly localize to the subsidiary mother cell face near the guard mother cell. PAN1 and PAN2 accumulation and interaction with these WPRs promote actin patch formation. Single *wpra* mutants have no phenotype, but double *wpra1 wpra2* mutants were not recovered and are therefore likely essential for viability (Nan et al., 2023). Similarly, the two *WPRB* genes are redundant: single mutants have no phenotype, while double mutants have subsidiary cell division defects. The WPRs may act redundantly to mediate PAN1 recruitment following polarization of BRIK1 and PAN2 (Nan et al., 2023). Finally, PAN1 is required for the recruitment of a class of small monomeric GTPase proteins found in plants called Rho-related GTPases of Plants (ROPs) (Facette et al., 2015), whose redundancy is discussed in more detail below.

#### 3.1.1. ROPs promote cell elongation required for division plane positioning

ROPs act as molecular switches critical for coordinating polar growth via cytoskeletal rearrangements and vesicle trafficking (Craddock et al., 2012; Li et al., 2023; Nielsen, 2020; Ou and Yi, 2022; Yang, 2008). Like other small GTPases, ROPs cycle between an activated GTP-bound state and an inactive GDP-bound state mediated by guanine nucleotide exchange factors (GEFs) and GTPase-activating proteins (GAPs) respectively. Activated ROP-GTP interacts with ROP effectors. A final class of ROP regulators called guanine dissociation inhibitors (GDIs) inhibit ROP activity by sequestering ROP-GDP away from the plasma membrane. ROPs and their related proteins are often highly redundant. For example, in moss (*P. patens)*, there are twelve GEFs, six ROPGAPs, and four GDIs. Silencing entire families of ROP regulators by RNAi results in loss of tip growth and highlights their role in cell expansion (Bascom et al., 2019). Arabidopsis has eleven highly similar ROPs, so overexpression or gain-of-function mutants have been used to overcome redundancy to reveal defects in directed cell expansion in root hairs, pollen tubes, during phloem development, and in epidermal cells (Fowler, 2009; Yang, 2002; Fu et al., 2005; Roszak et al., 2021). Interestingly, a few proteins within the ROP signaling module may also play roles in division plane orientation. These include ROPs, ROP-GAP proteins (also known as PLECKSTRIN HOMOLOGY GAPS, PHGAPs), ROP-GEFs, and ROP effectors called ROP INTERACTING PARTNERS (RIPs) (Hasi and Kakimoto, 2022; Rong et al., 2022; C. Zhang et al., 2022).

Two of the nine ROPs in maize play redundant roles in polarizing subsidiary mother cell divisions. Like Arabidopsis, maize ROPs can be classified based on post-translational modifications into two groups (Type-I or Type-II) which affect membrane targeting (Berken and Wittinghofer, 2008; Christensen et al., 2003). Maize Type-I *rop2/rop2 rop9/+* mutants have defective subsidiary mother cell divisions due to failure to accumulate actin patches during polarization (Humphries et al., 2011; Christensen et al., 2003). Maize ROPs are recruited by an initial BRICK/PAN polarizing signal (discussed above) to promote actin patch formation. After ROP recruitment, the guard mother cell and the subsidiary mother cell expand (Facette et al., 2015).

*P. patens* and *M. polymorpha*, have fewer ROP genes than Arabidopsis and maize. In *P. patens*, all four ROP genes act redundantly to regulate polarized tip growth and individually contribute to plant size (Burkart et al., 2015). Quadruple *rop1234* mutants lose polar growth completely, resulting in diffusely growing spherical cells that lack branches (Cheng et al., 2020). Less severe triple ROP mutants *rop134 (*Cheng et al., 2020*)* and *rop234* (Yi and Goshima, 2020) exhibit defective placement of asymmetric branch divisions (Cheng et al., 2020). Similar phenotypes can be seen in cells treated with Latrunculin A, a drug that disrupts actin filaments, suggesting that ROPs regulate actin accumulation to promote branch initiation and then cell elongation (Yi and Goshima, 2020). Division plane orientation defects in *rop234* mutants seem to be a consequence of failed branch expansion and failed nuclear migration (Yi and Goshima, 2020). The sole *ROP* gene in *M. polymorpha* is most similar to *AtROP2* (Rong et al., 2022). *rop* mutant thallus cells had aberrant shapes and defects in cortical microtubule organization that likely contributed to more random division positioning. While it is known that *M. polymorpha* cells forms PPBs following the formation of polar organizers (perinuclear microtubule accumulations), whether PPBs were misplaced in *rop* mutants is unknown because they were not observed in these cells (Buschmann et al., 2016; Rong et al., 2022).

Arabidopsis *PHGAPs/RENs* are another example of redundant genes that impact division plane positioning. Mutants in Arabidopsis *PHGAPs/RENs* have aberrant PPB localization, potentially due to defects in cell elongation. PHGAPS are a class of pleckstrin homology ROP GTPase-activating proteins (GAPs) that promote GTP hydrolysis and thus inactivation of ROP (Stöckle et al., 2016). The founding member, ROP ENHANCER1 (REN1), maintains pollen-tube tip growth through its regulation of ROP1 (Hwang et al., 2008). Two other closely related PHGAPs, PHGAP1/REN2 and PHGAP2/REN3, interact with ROP2 and are redundantly required for epidermal-cell lobing (Lauster et al., 2022). PHGAPs are stabilized by BRASSINOSTEROID INSENSITIVE 2 kinase-dependent phosphorylation, accumulating in pavement-cell indentations to deactivate ROP2 (C. Zhang et al., 2022). In addition to the role of PHGAPs in polar expansion, PHGAPs are recruited to the division site from metaphase to cytokinesis in the Arabidopsis root meristem (Stöckle et al., 2016). PHGAPs likely alter PPB positioning via their roles in cell elongation, although some other mechanism is possible. The role PHGAPs play at the division site remains unknown (Stöckle et al., 2016).

Other ROP-related proteins in Arabidopsis that influence the direction of cell division include a class of ROP effector proteins, interactor of constitutive active ROPs (ICRs)/ ROP interactive partners (RIPs) (Nagawa et al., 2010; Lavy et al., 2007), and the ROPGEFs (Roszak et al., 2021). Arabidopsis has five RIPs that all label cortical interphase microtubules (Hasi and Kakimoto, 2022). Several double or triple mutant combinations have no phenotype while the two quadruple mutants *rip1245* and *rip1235* as well as the quintuple *rip12345* mutant generate narrower leaves due to less longitudinally-oriented PPBs leading to fewer transversely-oriented cells (Hasi and Kakimoto, 2022). Thus far, mutants in another class of highly redundant ROP effectors, the ROP-interactive CRIB motif proteins (RICs), reveal functions in cell lobing in Arabidopsis (Wu et al., 2001) but no obvious function in *P. patens* (Bascom et al., 2019). Interestingly, individual overexpression of three Arabidopsis ROPGEFs (ROPGEF2, ROPGEF3, and ROPGEF5) activate ROPs to generate asymmetric periclinal divisions during phloem development (Roszak et al., 2021). These ROPGEFs localize ubiquitously on the plasma membrane but are depleted from the division site (Roszak et al., 2021), similar to the actin depleted zone (Panteris, 2008; Sano et al., 2005; Van Damme et al., 2007). This suggests that ROP activity may be reduced at the division site.

In summary, mutants of ROPs and ROP-related proteins demonstrate their roles in cell expansion and polar growth. Impacts on division plane placement may be indirect through alterations in cell shape mediated by cell expansion. However, the absence of ROPGEFs from the division site, and accumulation of PHGAPs at the division site may reflect more direct roles in division plane orientation.

### 3.1.2. IRK/PXC2

Preventing aberrant divisions is another critical role in division plane positioning played by two partially redundant leucine-rich-repeat receptor-like kinases (LRR-RLK) in Arabidopsis. One of them is INFLORESCENCE AND ROOT APICES RECEPTOR KINASE (IRK), a LRR-RLK that polarly localizes and is essential for preventing ectopic divisions in the endodermis and restricting stele width (Campos et al., 2020). A closely related LRR-RLK called PXY/TDR CORRELATED2 (PXC2) also restricts stele width. Double mutants have more frequent and aberrantly positioned divisions, wider steles and noticeable root growth defects: enhanced phenotypes are likely due to differences in gene expression domains (Goff and Van Norman, 2021).

### 3.1.3. GRAS Transcription Factors

The Arabidopsis GRAS family transcription factor SHORT-ROOT (SHR) together with another GRAS transcription factor, SCARECROW, promotes periclinal divisions in the root to generate cortex and endodermal cell layers (Benfey et al., 1993; Koizumi et al., 2012). Arabidopsis SHR is a mobile protein moves from the stele to the endodermis (Nakajima et al., 2001). Maize has three *SHR* homologs: *ZmSHR1, ZmSHR2,* and *ZmSHR2-h, while Setaria viridis* has two *SHR* homologs (Ortiz-Ramírez et al., 2021). In contrast to Arabidopsis, *ZmSHRs* are expressed in the endodermis and move to the cortex (Ortiz-Ramírez et al., 2021). While single mutants have no or slight phenotypes, maize and *S. viridis* double mutants have reduced cortical layer numbers, illustrating the redundant functions of two monocot *SHR* homologs in regulating root periclinal divisions (Ortiz-Ramírez et al., 2021). In *P. patens*, *SHR* homologs are also genetically redundant and play a role in division plane positioning of an asymmetric division that occurs in the phyllid (leaf) (Ishikawa et al., 2023). *P. patens* has two *SHR* homologs, *PpSHR1* and *PpSHR2* (Ishikawa et al., 2023; Moody et al., 2021). Double *ppshr1 ppshr2* mutants have defects in the orientation of a cell type called the most-medial lateral cell, resulting in narrower leaves and thicker midribs (Ishikawa et al., 2023). In most-medial lateral cells, PpSHR functions to promote longitudinal divisions instead of dividing along the path that minimizes surface area (Ishikawa et al., 2023).

## 3.2. Proteins important for PPB formation

One protein complex essential for PPB formation contains a core of five proteins called the TONNEAU1 (TON1)/TONNEAU1 RECRUITING

MOTIF (TRM)/ PROTEIN PHOSPHATASE TYPE 2 A (PP2A) (TTP) complex (Spinner et al., 2013). The complex contains a PP2A phosphatase holoenzyme composed of three subunits described below in more detail, a connector protein, TON1, and one or more proteins from the TRM family. Genes encoding proteins within the complexes are often redundant: double or triple mutants are required to see a phenotype, which is typically altered cell elongation due to misorganized microtubule arrays (except in the *trm678* mutant where arrays appear normal, although this was not quantitatively analyzed) and no PPB. When core TTP components are removed, lethality is sometimes observed, suggesting that the TTP complex plays multiple vital roles in both interphase and mitotic cells. The TTP complex is targeted to specific locations by TRMs and the B'' regulatory subunit of PP2A.

PP2A holoenzymes play important roles in plant defense, regulating transcription factor stability, and signaling e.g. (Bheri and Pandey, 2019; Bian et al., 2020; Máthé et al., 2019), but here we focus on its role in PPB formation. The PP2A heterotrimeric holoenzyme is composed of a scaffolding subunit (PP2AA), a regulatory B-type subunit that controls its localization, and a catalytic subunit (PP2AC). B-type subunits can be broken into B, B', and B'' families and function in substrate specificity or PP2A complex targeting. FASS/TON2 encodes a B'' type regulatory subunit (Camilleri et al., 2002). In Arabidopsis, *fass/ton2* mutants have defects in cortical-microtubule organization and lack PPBs (Camilleri et al., 2002; Kirik et al., 2012; McClinton and Sung, 1997; Torres-Ruiz and Jürgens, 1994). In maize, the B'' subunit is encoded by two homologs, *DISCORDIA1 (DCD1)* and *ALTERNATIVE DISCORDIA1* (*ADD1*). Similar to Arabidopsis *fass/ton2* loss-of-function mutants, maize *dcd1 add1* double mutants do not make PPBs and are seedling lethal. DCD1 and ADD1 localize to the division site from pre-prophase to metaphase (Wright et al., 2009) similar to FASS/TON2 (Kirik et al., 2012). Single *add1* mutants have no discernable phenotype (Wright et al., 2009). Single *dcd1* mutants have partially defective preprophase bands which disrupt subsidiary mother cell divisions but do not affect symmetric divisions (Wright et al., 2009). Perhaps symmetric divisions in maize have additional redundant mechanisms to ensure proper division plane orientation not found in asymmetric divisions.

There are five copies of the Arabidopsis PP2A phosphatase catalytic subunit. Single *pp2ac-3* or *pp2ac-4* mutants do not have significant root growth, microtubule organization, and division positioning defects until combined into a double mutant (Ballesteros et al., 2013; Spinner et al., 2013; Yoon et al., 2018; Yue et al., 2016). A receptor-like kinase called ARABIDOPSIS CRINKLY4 (ACR4) phosphorylates PP2A-C3, while PP2A-C3 dephosphorylates ACR4. This cross-regulation is implicated in formative cell divisions within the Arabidopsis root (Yue et al., 2016). Similarly, three PP2AA-scaffolding subunits facilitate PP2A assembly and double or triple mutants are required to observe cells lacking PPBs (Spinner et al., 2013; Zhou et al., 2004). Neither the scaffolding subunit double mutants (*pp2aa1-a3* or *pp2aa1-a2*) nor the catalytic subunit double mutant *pp2ac3-c4* make PPBs (Spinner et al., 2013). Enhanced phenotypes in higher order mutants reveal redundancies in the PP2A complex and its impact on PPB formation.

The original *ton1* mutant allele is actually a double mutant disrupting two tandemly-linked paralogs, *TON1a* and *TON1b* in Arabidopsis (Azimzadeh et al., 2008; Nacry et al., 1998; Traas et al., 1995). TON1a and TON1b are 86% identical at the amino acid level and both contain a serine-rich motif, a dimerization motif, and bind to the calcium-binding protein called centrin (Azimzadeh et al., 2008). TON1 also shares domains with human centrosome proteins and may be involved with microtubule nucleation (Azimzadeh et al., 2008). The double mutant produces a tiny plant with no PPBs and disordered microtubule arrays. In contrast, *ton1a-1* single mutants have a milder phenotype consisting of slightly slower root growth and misoriented symmetric divisions mostly in the root epidermis (Zhang et al., 2016). Disruption of the single gene *TON1* in *P. patens* leads to normally shaped but agravitropic vegetative cells and small, disorganized leafy gametophores with defects in PPB formation and cell elongation (Spinner et al., 2010).

A subset of highly redundant TON1 interactors, TRMs, were identified by yeast-two-hybrid screening that are required for both PPB positioning and formation. TRMs are a superfamily of 34 proteins that share a conserved C-terminal TON1 interacting motif. Some TRMs also contain microtubule-binding domains and FASS/TON2 interaction domains (Drevensek et al., 2012; Spinner et al., 2013). The founding *TRM* genes, called *LONGIFOLIA1 (LNG1)* and *LNG2,* were identified by a dominant mutant that overexpressed *LNG1/TRM2* in Arabidopsis, *lng1–1D* (Lee et al., 2006). The *lng1–1D* overexpression produces aberrantly elongated cells leading to long, narrow leaves. Neither *lng1* nor *lng2* loss-of-function mutants have a noticeable phenotype. However, *lng1 lng2* double mutants have short, round leaves (Lee et al., 2006). Progressively higher order mutant combinations generated cell elongation defects that led to shorter rounder leaves (Lee et al., 2018). Whether these mutants have PPB positioning defects is unknown. In maize, a naturally-occurring mutation within the *LNG1/TRM2* gene *ZmLNG1*, alters leaf shape and plant architecture in specific genetic backgrounds. The mutation generates a protein that disrupts ZmLNG1 and ZmTON1 interactions but does not alter ZmLNG1 localization. *ZmLNG1* overexpression generates long, narrow leaves and kernels. Yeast-three-hybrid assays suggest that ZmLNG1 may act as a bridge between TON1 and Ovate Family Proteins (OFPS, discussed below) (Wang et al., 2023).

While several *LNG/TRM* genes promote cell elongation, possibly due to modulation of interphase microtubule orientation or PPB location, other *TRM* genes are critical for PPB formation itself. A subset of three similar TRMs in Arabidopsis, *TRM6*, *TRM7* and *TRM8* (Drevensek et al., 2012), have partially redundant roles in PPB formation (Schaefer et al., 2017). Single and double mutants have minor phenotypes, but the triple *trm678* mutant has significantly impaired PPB formation (Schaefer et al., 2017). Triple *trm678* mutants do not have obvious growth defects but have increased spindle angle variance. Interestingly, division site localized proteins still accumulate, albeit less often than in wild-type cells (Huang et al., 2022; Schaefer et al., 2017). This suggests that a partial or defective PPB still accumulates in these mutants, and/or that division site protein localization is not strictly contingent on PPB formation.

Multiple TRMs interact with another class of plant-specific proteins called Ovate Family Proteins (OFPs) that likely alter PPB positioning or directional cell elongation, as mutants originally characterized in tomato produce elongated tomato fruits (Snouffer et al., 2019; van der Knaap et al., 2014; Wu et al., 2018). OFPs contain a conserved ~70 amino acid "ovate" motif in addition to protein-protein interaction domains (Liu et al., 2002). Multiple OFP family members are found across the land plants lineage: *P. patens* has 11, Arabidopsis has 19, and maize has 45 (Liu et al., 2014). Arabidopsis OFPs also interact with FASS/TON2 (Zhang et al., 2020). However, the founding OFP was a loss-of-function mutant in *OVATE* that produced elongated tomato fruits (Liu et al., 2002). Additional mutations in another *OFP* gene called *SlOFP20* led to highly elongated fruits in the *ovate* mutant background (Wu et al., 2018) indicating that redundant OFP functions can be revealed through higher order mutant combinations. Indeed, single loss-of-function *ofp* mutants often do not have any phenotype (Wang et al., 2011).

Although OFPs and TRMs interact, they often have antagonistic effects on fruit or organ shape in diverse plant species e.g. (Colle et al., 2017; Lazzaro et al., 2018; Snouffer et al., 2019; Wang et al., 2023; Yang et al., 2018; Zhao et al., 2018). TRM overexpression often generates elongated organs, while overexpression of OFPs often generates short, round organs (Snouffer et al., 2019). Transiently co-expressing OFPs with TRMs alters localization of one interacting partner or another (sometimes to microtubules or the cytosol), suggesting that both interactions and relative amounts are delicately balanced to generate proper localization eventually leading to correctly shaped organs (Wu et al., 2018).

### 3.2.1. IQ67 DOMAIN proteins

IQ67 DOMAIN proteins are a large family of plant-specific proteins (33 in Arabidopsis) that modulate cell shape, contain calmodulin binding motifs (IQ67) and often localize to microtubules (Liang et al., 2018; Bürstenbinder et al., 2013; Li et al., 2021, 2020, 2022; Yang et al., 2022; Lazzaro et al., 2018; van der Knaap et al., 2014). Similar to the TRMs, a subset of three IQD proteins (IQD6,7 and 8) are also redundantly required for PPB formation as triple *iqd678* mutants result in 50% of cells without PPBs (Kumari et al., 2021). IQD8 fused to GFP rescues the *iqd678* mutant and marks a broad zone that encompasses the division site until cytokinesis and colocalizes with phragmoplast microtubules (Kumari et al., 2021). IQD678 are also important for the asymmetric divisions in the Arabidopsis embryo and likely indirectly contribute to division plane positioning by influencing cell shape through auxin dependent cytoskeletal changes (Vaddepalli et al., 2021). Intriguingly, IQD8 interacts with PHGAP proteins, which are required for PPB placement (discussed above) and recruits them to microtubules when concurrently overexpressed in tobacco cells. IQD8 interacts with both PHRAGMOPLAST ORIENTING KINESIN1 (POK1) and POK2 discussed in more detail below (Kumari et al., 2021). In *iqd678* mutants, POK1 recruitment is delayed but eventually accumulates to wild-type levels (95%) by cytokinesis (Kumari et al., 2021).

## 3.3. Proteins important for phragmoplast guidance or the maintenance of division plane orientation

### 3.3.1. POK1/POK2

The homologs *POK1* and *POK2* encode two kinesin-12 class proteins in *A. thaliana* that localize to the division site from prophase to cytokinesis and together play critical roles in division plane orientation (Lipka et al., 2014; Herrmann et al., 2018; Müller et al., 2006). Both proteins have an N-terminal motor domain, coiled-coil domains, and a C-terminal cargo binding domain (Müller et al., 2006). Single mutants do not have division plane orientation defects. However, *pok1 pok2* double mutants have division plane orientation defects (Müller et al., 2006) due to defects in phragmoplast guidance, which often inserts the cell plate at a location different from the PPB (Lipka et al., 2014). POK1 also rescues the double mutant, suggesting functional redundancy (Lipka et al., 2014). However, phragmoplast expansion rates are significantly slower in *pok2* single mutants, indicating its distinct role (Herrmann et al., 2018). POK1 and POK2 have similar N-terminal motor domains but localize to the division site via C-terminal regions (Herrmann et al., 2018; Lipka et al., 2014). The C-terminus mediates interaction with another division site localized protein TANGLED1, described in the next section (Müller et al., 2006). POK1 is actively recruited to the division site during prophase but is statically maintained in metaphase (Lipka et al., 2014). POK2 motor activity is diffusive and weakly processive towards microtubule plus-ends (Chugh et al., 2018). POK2-YFP noticeably accumulates in the phragmoplast midline and the division site, in contrast to POK1, which is primarily at the division site in wild-type cells (Herrmann et al., 2018; Lipka et al., 2014; Mills et al., 2022). If POK1 is not recruited to the division site when interactions with other division site localized proteins are disrupted, it also accumulates in the phragmoplast midline and on the phragmoplast microtubules (Mills et al., 2022). Perhaps in the absence of division-site recruiters and stabilizers, plus-end directed kinesins preferentially localize to the phragmoplast midline and the phragmoplast where microtubule plus-ends accumulate. POK1 interacts with the RAN-GTPASE-ACTIVATING-PROTEIN1 (RAN-GAP1), a protein that localizes to the division site and is likely required for division positioning with its redundant partner RAN-GAP2 (Xu et al., 2008). POK1 is actively maintained at the division site after the PPB disassembles through direct or indirect interactions with two other proteins, TANGLED1 (TAN1) and AUXIN INDUCED IN ROOT CULTURES9 (AIR9) (Mills et al., 2022), which are discussed in more detail in the next section.

### 3.3.2. Myosin XI and Myosin VIII

POK1 and POK2 interact with other proteins including actin-binding motor proteins called myosins that transport cargo along actin filaments (Huang et al., 2022; Nan et al., 2021). Plants contain two myosin classes: MYOSIN XI, which contains a similar domain structure as Myosin class V proteins from animals and fungi, and MYOSIN VIII, which is plant specific (Nebenführ and Dixit, 2018). Interestingly, both MYOSIN XIs and MYOSIN VIIIs play critical but often highly redundant roles in division plane positioning in addition to their roles in cell elongation, nuclear and organelle movement, and cytoplasmic streaming (Bibeau et al., 2021; Haraguchi et al., 2018; Madison et al., 2015; Tominaga and Nakano, 2012). In Arabidopsis, there are 13 MYOSIN XIs: 3 of them, MYOSIN XI-K, MYOSIN XI-1 (also called MYA1) and MYOSIN XI-2, are redundantly required for division plane positioning, particularly within the stele (Abu-Abied et al., 2018). The *myosin xi-k xi-1 xi-2* triple mutant generates additional lateral and adventitious roots and shows both unpolarized auxin transport efflux protein localization and lower auxin response in roots. MYOSIN XI-K-YFP, rescues the triple myosin mutant and~~,~~ localizes to the division site during prophase, metaphase and telophase suggesting it may play a direct role in division plane positioning (Abu-Abied et al., 2018). The triple mutant was combined with a mutation in *MYOSIN XI-I* to generate a quadruple myosin mutant. Surprisingly, the quadruple mutant grew similarly to wild-type plants during the seedling stage. However, the quadruple mutant was hypersensitive to the microtubule-depolymerizing drug, oryzalin. Similar to MYOSIN XI-K-YFP, MYOSIN XI-1-YFP localized to the division site. MYOSIN XI-1 localization was dependent on a functional PPB, showing partially disrupted localization in the *trm678* triple mutant described above but no division site accumulation in the *fass/ton2* mutant. In addition, MYOSIN XI-K and XI-1 interact via co-immunoprecipitation and they are found together at the division site in puncta with other division site localized proteins including POK1, TAN1 and RAN-GAP1 (Huang et al., 2022).

In maize, a MYOSIN XI related to MYOSIN XI-I, called OPAQUE1 (O1) promotes phragmoplast guidance to the division site in asymmetric divisions and interacts with POK1 homologs and other myosins (Nan et al., 2021). The *o1* mutant has aberrant protein body accumulation in endosperm cells which produce the opaque kernel phenotype (Wang et al., 2012). Despite similarities in interactors, MYOSIN XIs also perform distinct, apparently non-conserved roles. For example, Arabidopsis MYOSIN XI-I is required for proper nuclear movement and nuclear shape (Muroyama et al., 2020; Tamura et al., 2013; Zhou et al., 2015), but the *o1* mutant does not have obvious defects in nuclear positioning or shape (Nan et al., 2021). Additionally, while several Arabidosis MYOSIN XIs fused to fluorescence proteins localize to the division site and the phragmoplast midline (Abu-Abied et al., 2018; Huang et al., 2022), immunolocalization shows that maize O1 localizes only to the phragmoplast midline (Nan et al., 2021). In *P. patens*, the two MYOSIN XIs are redundantly required for polarized growth via interaction with a RAB monomeric GTPAse and also play roles in vesicle clustering and trafficking (Vidali et al., 2010; Galotto et al., 2021; Orr et al., 2020). MYOSIN XI accumulates at the growing tip prior to actin filaments (Furt et al., 2013) and localizes to the spindle and phragmoplast midline but not at the division site (Sun et al., 2018). These recent exciting breakthroughs and differences among MYOSIN XIs illuminate the need to determine how MYOSIN XIs promote proper division plane positioning possibly through interaction with POKs or other proteins at the division site or the phragmoplast midline.

The plant-specific myosins, MYOSIN VIIIs, also play critical roles in division plane positioning, although their interaction with other division-site localized proteins is still unknown. *MYOSIN VIII* genes are found in large and sometimes partially redundant families. Deleting one, two, and up to five *MYOSIN VIIIs* in *P.* patens generates progressively smaller plants, with the quintuple mutant most severely affected (Wu et al., 2011). In addition, quintuple mutants have defects in division plane positioning that can be mostly rescued by overexpression of one

MYOSIN VIII. MYOSIN VIII localizes to the division site both in *P. patens* PPB-independent divisions, and in PPB-containing tobacco cells (Wu and Bezanilla, 2014). MYOSIN VIIIs also localize to plasmodesmata, plasma membrane, microtubule and actin filaments (Golomb et al., 2008; Kastner et al., 2022; Liu et al., 2001; Wu and Bezanilla, 2014). In *P. patens*, division site localization requires an intact actin cytoskeleton (Wu and Bezanilla, 2014). While mutants in a single MYOSIN VIII, *Arabidopsis thaliana myosin1 (atm1),* have slower growth and less dividing root cells, division plane orientation was not assessed (Olatunji et al., 2022). It will be interesting to determine whether MYOSIN VIIIs interact with division site localized proteins.

### 3.3.3. *MAP65s*

In addition to interacting with MYOSIN XIs, POK2 also interacts with several members of the MICROTUBULE ASSOCIATED PROTEIN65 (MAP65) family: MAP65–1, MAP65–3 and MAP65–5 (Herrmann et al., 2018). The founding MAP65 protein was identified through a robust interaction with microtubules, including in vitro bundling (Chang-Jie and Sonobe, 1993). MAP65s typically bundle parallel or antiparallel microtubules with shallow contact angles (Hashimoto, 2015; Smertenko et al., 2004; Tulin et al., 2012). MAP65 gene families tend to be large (9 in Arabidopsis), and have variable regions that provide specificity within subfamilies. In addition, expression, phosphoregulation, and localization of MAP65 proteins is variable (Hussey et al., 2002; Sasabe and Machida, 2012; Smertenko et al., 2008).

Unlike other MAP65s, MAP65–3 and MAP65–4 exhibit mitosis-specific expression and are together essential for cytokinesis (Li et al., 2017; Van Damme et al., 2004). MAP65–3 plays a critical and non-redundant role in antiparallel microtubule bundling within the phragmoplast (Ho et al., 2011). *map65–3/pleiade* mutants are small and have defects in cytokinesis (Müller et al., 2004) that cannot be rescued with *MAP65–1* driven by the *MAP65–3* promoter (Ho et al., 2012). MAP65–3 localizes to the phragmoplast midline (Müller et al., 2004) and interacts with many proteins including POK2 (Herrmann et al., 2018). Other MAP65s are also important in cytokinesis as demonstrated through exacerbated cytokinetic defects in MAP65–3 double mutants with MAP65–1, MAP65–2, or MAP65–4~~3~~ respectively (Li et al., 2017; Sasabe et al., 2011). Interestingly, *map65–1 map65–2* double mutants do not have defects in division positioning or cytokinesis and instead function redundantly in cell expansion (Lucas and Shaw, 2012; Sasabe et al., 2011). *map65–4* mutants have no noticeable phenotypes until combined with *map65–3* mutants but double mutants are not viable due to cytokinesis failures. MAP65–4 localizes to the division site and the phragmoplast midline, but its function at the division site is not yet known (Li et al., 2017).

## 4. Synthetic redundancy

In this section we discuss another type of redundancy that is mediated not by homologous genes, but by unrelated genes. The framework for understanding synthetic genetic interactions has been described (Zinovyev et al., 2013). Unrelated genes may contribute redundant functions through involvement in the same pathway (Fig. 5A-i, ii) or in different pathways (Fig. 5B). Within a singular genetic pathway, loss of an unrelated gene may represent a “partial loss of function” (Fig. 5A). Alternatively, unrelated genes may contribute to similar functions, likely in genetically parallel pathways that converge on a single phenotypic output (Fig. 5B). For both within or between pathway redundancies, when one gene or the other is disrupted there is no or little obvious phenotype, but the double mutant has a synthetic or synergistic phenotype, described as “synthetic sick” or “synthetic lethal”. The most comprehensive analysis of synthetic sick or synthetic lethal mutants comes from a systematic double mutant screen in budding yeast. This screen identified many unexpected genetic interactions between unrelated genes (Tong et al., 2001). Alternatively, synthetic lethality screens have led to treatments of human cancers: poly(ADP-ribose) polymerase (PARP) inhibitors are synthetically lethal with mutations in *Breast Cancer gene1* (*BRCA1*) or *BRCA2* (Turk and Wisinski, 2018).

One type of synthetic genetic interaction is observed when two genes from different parts of a single pathway are mutated (Fig. 5A-i). Several examples came from a screen that generated double mutants focused on the MITOGEN ACTIVATED PROTEIN KINASE (MAPK) pathway in Arabidopsis. Single mutants in different parts of the MAPK pathway have minor growth phenotypes, while the double mutants show synthetic short-root phenotypes (Su and Krysan, 2016). This conserved MAPK pathway is essential for cytokinesis, reviewed in Sasabe and

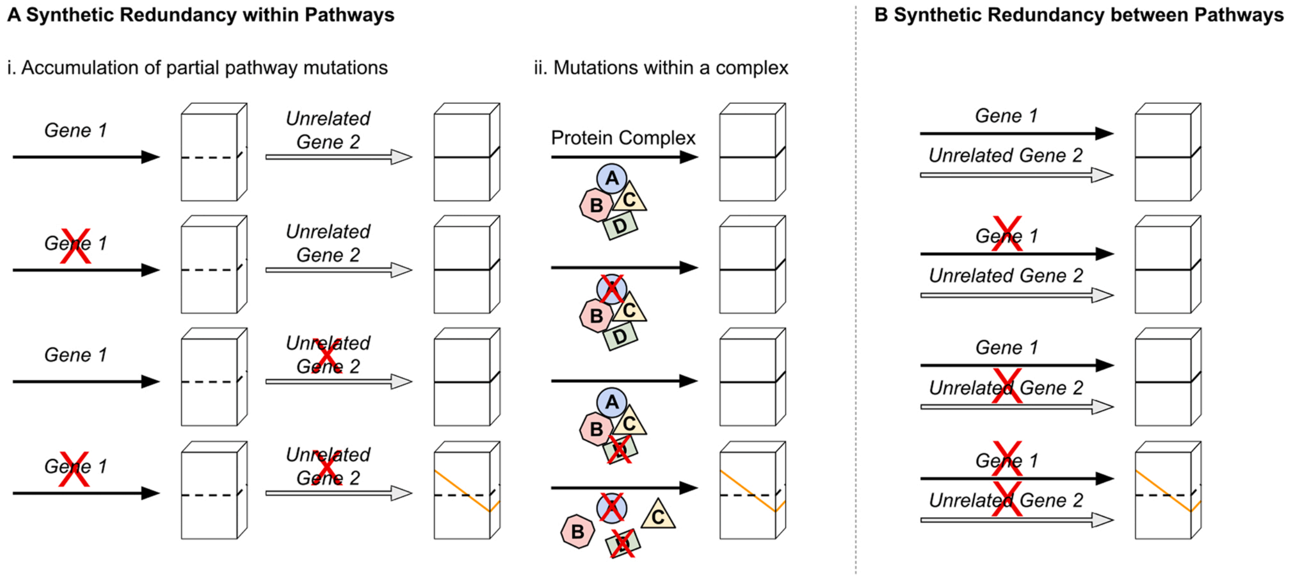

**Fig. 5. Modular redundancy in division plane orientation inspired by** (Zinovyev et al., 2013)**.** (A) Synthetic enhancement within pathways can occur (i) through accumulation of partial pathway mutations in genes (black and gray arrows) within the same pathway or (ii) through mutations within a complex that lead to complex disassembly. (B) Schematic of genes (black and gray arrows) that occur in two distinct but redundant pathways that contribute to correct division plane orientation. Loss of components in one pathway does not result in a phenotype. However, loss of both pathways results in a synthetically enhanced division plane orientation defect. Orange lines represent final misoriented divisions.

Machida (2012). An additional example of a synthetic genetic interaction occurs in *pan1 pan2* double mutants which have ~3X more asymmetric division defects than single mutants (Zhang et al., 2012). PAN1 and PAN2 are two different LRR-RLK proteins that accumulate during different times during the developmental sequence of subsidiary mother cell division (Facette et al., 2015).

When unrelated genes contribute to a singular pathway, partial-loss-of-function mutant alleles are enhanced by additional "within-complex" mutant alleles (Fig. 5A-ii). Two fascinating examples took advantage of weak alleles of *fass/ton2* to screen for enhancers. A new allele of *ton1a* was identified as a *ton2–15* enhancer (Kirik et al., 2012). TON1A protein directly interacts with FASS/TON2 (Spinner et al., 2013), suggesting that the "synthetic" phenotype may be caused by loss of multiple components within a complex. Another use of a different weak *fass/ton2* allele showed strong genetic enhancement when combined with *pp2aa1, pp2aa2* or *pp2aa3* mutants. The PP2AA proteins also interact directly with FASS/TON2 in the TTP complex (Spinner et al., 2013).

Another partial-loss-of-function mutant enhanced by additional "within complex" mutant alleles occurs during asymmetric divisions that produce the subsidiary cells in maize (BRICK/PAN/ROP pathway described earlier). Combining *rop2* homozygous mutants with *rop9* heterozygotes (*rop2/rop2 rop9/+)* generates a mild subsidiary cell division-positioning defect, likely representing a partial loss of ROP Type I function. Combining this with the *pan1* mutant (which by itself has ~20% defective subsidiary cells) generates plants with > 50% defective subsidiary cells. This synthetic enhanced phenotype is consistent with their physical interaction (Humphries et al., 2011).

A synthetic double mutant with defects in growth and division plane orientation was recently identified through the combination of a mutant in *TANGLED1 (TAN1),* which encodes a microtubule-binding protein that localizes to the division site, together with a mutant in *AUXIN INDUCED IN ROOT CULTURES9 (AIR9)*, which encodes an unrelated microtubule-binding protein that localizes to the division site in preprophase and late telophase in Arabidopsis (Buschmann et al., 2015, 2006; Walker et al., 2007). The current hypothesis is that TAN1 and AIR9 function in two separate but functionally redundant pathways (schematically outlined in Fig. 5B) that maintain division plane orientation in Arabidopsis because no interaction between them has been identified (Mir et al., 2018). *TAN1* was originally identified in maize, in which *tan1* mutants are short and have defects in phragmoplast guidance to the division site (Cleary and Smith, 1998; Martinez et al., 2017; Smith et al., 1996). *TAN1* is found in plants either as a single gene (e.g. Arabidopsis (Walker et al., 2007)) or is within a small family with a few paralogs (e.g. sorghum or maize). *TAN1* is plant-specific and in maize, it encodes a protein that binds, bundles and crosslinks microtubules in vitro (Martinez et al., 2020; Smith et al., 2001) and likely captures microtubules in vivo to position the expanding phragmoplast at the division site (Bellinger et al., 2023). In Arabidopsis, *tan1* and *air9* single mutants do not have significant division plane or growth defects. However, *tan1 air9* double mutants exhibit a synthetically enhanced phenotype, consisting of short, slow-growing plants with phragmoplast guidance defects. Unexpectedly, TAN1 and AIR9 functionally converge on their ability to maintain POK1 at the division site after metaphase. While POK1 localizes to the division site in either single mutant, POK1 is not maintained at the division site in *tan1 air9* double mutants after metaphase (Mills et al., 2022). It will be interesting to determine whether AIR9 directly interacts with POK1 similar to the direct interaction between TAN1 and POK1.

The synthetic *tan1 air9* double mutant phenotype in Arabidopsis is rescued by transforming it with TAN1 constructs, allowing identification of TAN1 domains that are critical for its function in growth and division plane positioning (Mills et al., 2022; Mills and Rasmussen, 2022; Mir et al., 2018). The first ~130 amino acids of TAN1 ($TAN1_{1–132}$) localize to the division site primarily during telophase, are necessary and sufficient for POK1 interaction, and fully rescued the *tan1 air9* double mutant (Rasmussen et al., 2011). Disrupting the interaction between TAN1 and POK1 in the *tan1 air9* double mutant causes phragmoplast guidance defects (Mills et al., 2022).

Another example of genes likely functioning in a parallel pathway was identified in the monocot *Brachypodium distachyon. BdPOLAR* was identified by its reduced RNA accumulation (D. Zhang et al., 2022) in a mutant which fails to form subsidiary cells (Raissig et al., 2017). POLAR is a plant-specific polarly-localized protein that accumulates during Arabidopsis stomatal development. Unlike the At*polar* mutants that have no phenotype (Pillitteri et al., 2011), *Bdpolar* mutants have misoriented subsidiary cell divisions, which are greatly enhanced by combination with *Bdpan1* mutants. Since BdPOLAR and BdPAN1 localize to opposite domains of the subsidiary mother cell, it is likely that they are in parallel pathways, although BpPOLAR requires BdPAN1 to localize correctly (D. Zhang et al., 2022).

## 5. Conclusions

Multiple types of redundancy make identifying the specific roles of proteins implicated in division plane positioning an exciting challenge. After protein-protein interactions identify additional components, high-throughput methods of gene editing such as CRISPR-Cas9 may be used to generate higher order mutants in genetically redundant pathways. Additional insight into synthetic redundancy may be provided by enhancer screens. Finally, detailed mechanistic studies will be required to unravel situations with temporal redundancy.

## CRediT authorship contribution statement

**Aimee N. Uyehara:** Conceptualization, Writing – original draft. preparation, Writing – review & editing, Funding acquisition, **Carolyn G. Rasmussen:** Conceptualization, Writing – original draft. preparation, Writing – review & editing, Funding acquisition.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data Availability

No data was used for the research described in the article.

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