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Cortical division zone establishment in plant cells

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Plant cell division is spatially organized to maintain a critical cell volume and to control growth directionality. The correct orientation of the separating cell wall is secured by means of specialized cytoskeletal structures that guide the newly formed cell plate toward a predefined cortical position. A ring of microtubules called preprophase band defines a cortical zone that corresponds to the future division plane. Coincident with the disappearance of the preprophase band microtubules, cortical actin is removed at the corresponding position, leaving an actin–depleted zone that persists throughout mitosis. Here, we review the spatial and structural organization of the cortical division zone and discuss evidence that implicate the plasma membrane in division plane establishment.

Cytokinesis and division plane determination

Cell division in higher plants involves the construction of new cell walls that are laid down with regular patterns as to ascertain a predefined tissue organization according to a conserved body plan emerging from the embryo [1]. Stem and root tissue, for example, are arranged in cell files that originate from repetitive anticlinal divisions at the apical or the basal meristem, respectively [2,3]. Because of the regularity of these cell patterns, it is assumed that correct division plane determination contributes to tissue organization and, consequently, to plant growth. The establishment of a division plane, which is usually perpendicular to the principal growth direction, is an intrinsic part of cytokinesis [4]. Although genetic analysis has shown that perfect control over the division planes is required for optimal growth performance, it is clearly not essential for cell patterning [5]. Other regulatory mechanisms, relaying on positional information and/or cell lineage, determine tissue organization [1]. These mechanisms are higher in the hierarchy of the cell patterning control and, supposedly, control the orientation of division. In suspension cultures, the tissue and organ context is absent, yet the division planes are still mostly parallel with the shortest cross section of the cell [4,6]. Division plane determination must therefore, next to tissue-organized control, depend on cell-autonomous mechanisms.

Thus far we have little clues on how division plane determination is controlled. Comparison of different eukaryote systems favors the idea that mechanisms involved in the establishment of the division plane have developed several times independently throughout evolution [7]. To accomplish oriented cell divisions, plants have developed unique cytoskeletal structures (Box 1). The PPB is a temporal structure formed before the start of mitosis (Figure 1). In most cells that are small and have few or small vacuoles, the cell plate emerges at the central part of the spindle midzone, and later expands toward the cell periphery, guided by the phragmoplast (Box 1). The phragmoplast MTs spread into the cytoplasm toward the cortical area previously occupied by the PPB (Figure 1). Based on these microscopic observations, it is believed that the PPB predefines the orientation and position of the division plane.

The latest findings with regard to microtubule dynamics, specific subcellular protein targeting during the different

Glossary

ADZ: actin-depleted zone
AIR9: auxin-induced in root cultures [Arabidopsis Genome Initiative (AGI) code At2g34680]
ATN: *Arabidopsis thaliana* TAN1 homolog
BFA: BrefeldinA
BY-2: *Nicotiana tabacum* Bright Yellow–2
cph: *cephalopod*
DMSO: dimethylsulfoxide
EB1: microtubule end-binding protein 1 (AGI codes: *AtEB1a*, At3g47690; *AtEB1b*, At5g62500; *AtEB1c*, At5g67270)
ER: endoplasmic reticulum
fk: *fackel*
FM4-64: *N*-(3-triethylamoniumpropyl)-4-(6-(4-(diethylamino)phenyl)-hexatrienyl)-pyridimium dibromide
GFP: green fluorescent protein
HRGP: Hyp-rich glycoprotein
hyd1: *hydra1*
KCA1: kinesin-like CDKA;1 associated protein 1 (AGI code At5g10470)
KDZ: KCA-depleted zone
MT: microtubule
NPA: 1-naphthylphthalamic acid
PM: plasma membrane
POK: phragmoplast orienting kinesin
PP2A: protein phosphatase 2A
PPB: preprophase band
RSH: root-shoot-hypocotyl-defective
smt1: *sterol methyltransferase1*
tan: *tangled*
+TIP: plus-end-tracking proteins
ton: *tonneau*
TPLATE: T-shaped cell plate (AGI code At3g01780)

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Box 1. Division plane establishment preceding plant somatic cytokinesis

When a somatic cell prepares for division, it produces a ring, the preprophase band (PPB), consisting of MTs and actin filaments. This ring circumvents the usually centered nucleus during prophase [72]. This PPB is thought to predict the future division plane (i.e. the axis along which the cell is going to divide) and is removed before chromosome segregation and cytokinesis [19].

A newly formed cell plate emerges at the spindle midzone and expands toward the cell periphery, guided by a bundle of two sets of MTs of opposite polarity. The cell plate sandwiched between the MT bundles is referred to as the phragmoplast [72]. The phragmoplast MTs spread into the cytoplasm, guided by a yet unknown mechanism, toward the cortical area previously occupied by the PPB. The position of the new cell wall after cytokinesis corresponds to the former position of the PPB, indicating that some factor should remain after PPB degradation to mark the division zone (i.e. the cortical area previously occupied by the PPB) throughout mitosis [19].

The actin cytoskeleton has a role in determining the division zone and cell plate guidance, although its role is not well understood, in part because actin drug treatments have different effects depending on the type of cells investigated [59–63]. Actin filaments are present in the PPB and phragmoplast structures and could in fact contribute to the formation and organization of the MTs that are the major components of both structures. When the PPB MTs degrade, cortical actin disappears at the position of the PPB, leaving behind an actin-depleted zone (ADZ) that lasts throughout mitosis [60]. The formation of the PPB and the ADZ provided the first molecular evidence for the establishment of a cortical division zone that acts as a signpost for the guidance of the expanding cell plate.

mitotic processes and novel cell division mutants have provided hints suggesting a role for the plasma membrane in the establishment of the cortical division plane. Here, we discuss newly discovered proteins and putative mechanisms in a context of already well-described ins and outs of division plane determination.

The cortical division zone

Several studies have shown that premitotic mobility and positioning of the nucleus already delineates the position of the future division plane. The intricate relationship between the premitotic nucleus and the subsequently formed PPB is evident from experiments showing that a displaced nucleus can trigger the initiation of a secondary PPB within close proximity of the new nuclear position [8]. Moreover, bi- and multinucleated cells generate two or more PPBs [9], supporting the idea that a nuclear signal drives PPB formation. The PPB emerges from the cortical MT network through a local change in the dynamic instability parameters of MT polymerization [10,11]. Cortical MTs gradually disappear while the MTs that contribute to PPB formation are crosslinked and stabilized [10,11]. The signaling pathway to induce PPB formation probably involves a dephosphorylation event, because the PP2A-type phosphatase mutants *fass* and *ton* no longer generate a PPB [12,13].

The *ton* mutants fall in two complementation groups: *ton2* (=*fass*) encodes a protein with similarity to the B' regulatory subunit of a heterotrimeric PP2A phosphatase complex, whereas *ton1* encodes a novel protein [13,14]. Given that *ton1* and *ton2* mutant phenotypes are similar, it is possible that both proteins interact and that TON1 is a target for dephosphorylation by TON2 [14].

The role of the nucleus in division zone establishment appears to be biphasic, as migration first occurs before, and thus independently from, the PPB and later becomes physically connected to the PPB MTs [15,16]. As the PPB emerges, the nucleus is suspended at the center of the cell by cytoplasmic strands that form the 'phragmosome' [17]. The phragmosome contains MTs and actin filaments that connect the nucleus with the PPB, and helps to position the premitotic nucleus relative to the PPB [16]. Prior to entry into prophase, the PPB develops into a narrow ring, coincident with the marking of the cortical division zone that is later used to guide the outgrowing cell plate along the required division plane [18]. The general consensus is that the PPB generates a signal to settle the division zone [19]. However, the evidence for this hypothesis is largely correlative, and the nature of the signal remains unknown. Moreover, the PPB might fulfill other functions, such as controlling the orientation and bipolarity of the spindle, which indirectly influences the positioning of the division plane (mechanisms that are analogous to those occurring in animal cells) [7].

In onion and guard mother cells of several Leguminosae, cell walls at the division zone are often differentially thickened, suggesting that this is the location of precursors of wall synthesis accumulation [20,21]. These cell wall thickenings are deposited at the position of the PPB, perhaps via the secretion of vesicles that are associated with the PPB MTs [22]. Cell wall modifications have been suggested to occur toward the end of cytokinesis [23]. For instance, the secretion of a HRGP-type cell wall protein RSH, which, in *Arabidopsis*, is crucial for the correct positioning of the cell plate and normal development of the *Arabidopsis* embryo, probably occurs at the site of cell plate insertion during the final steps of cytokinesis as part of the cell plate maturation process [22].

Other membrane-bound structures, including the endoplasmic reticulum (ER), Golgi and endocytic vesicles, accumulate in a belt-like formation close to the cortical division zone during mitosis [24–27]. The reason for such organelle redistribution is yet not clear, but might relate to targeting of a marker to the cortical division zone [24]. As the membrane transport inhibitor BFA does not have an irreversible effect on division zone establishment, other approaches to determine the role of this organelle organization must be explored [28].

Is the plasma membrane implicated in cortical division zone establishment?

The positional information laid down by the PPB resists mechanical stresses such as centrifugation, but is disturbed by wounding of the putative division zone using a microneedle [29,30]. Moreover, plasmolysis or treatment of dividing cells with DMSO or methanol lead to an increase in the percentage of cells carrying oblique-oriented cell plates [30,31]. These observations suggest that the integrity of the PM and/or the PM-to-cell wall connection is vital for the maintenance of the cortical positional information. The proper functioning of the PM depends on the renewal of its constituents via a continuous process of exo- and endocytosis [32]. Visible signs that

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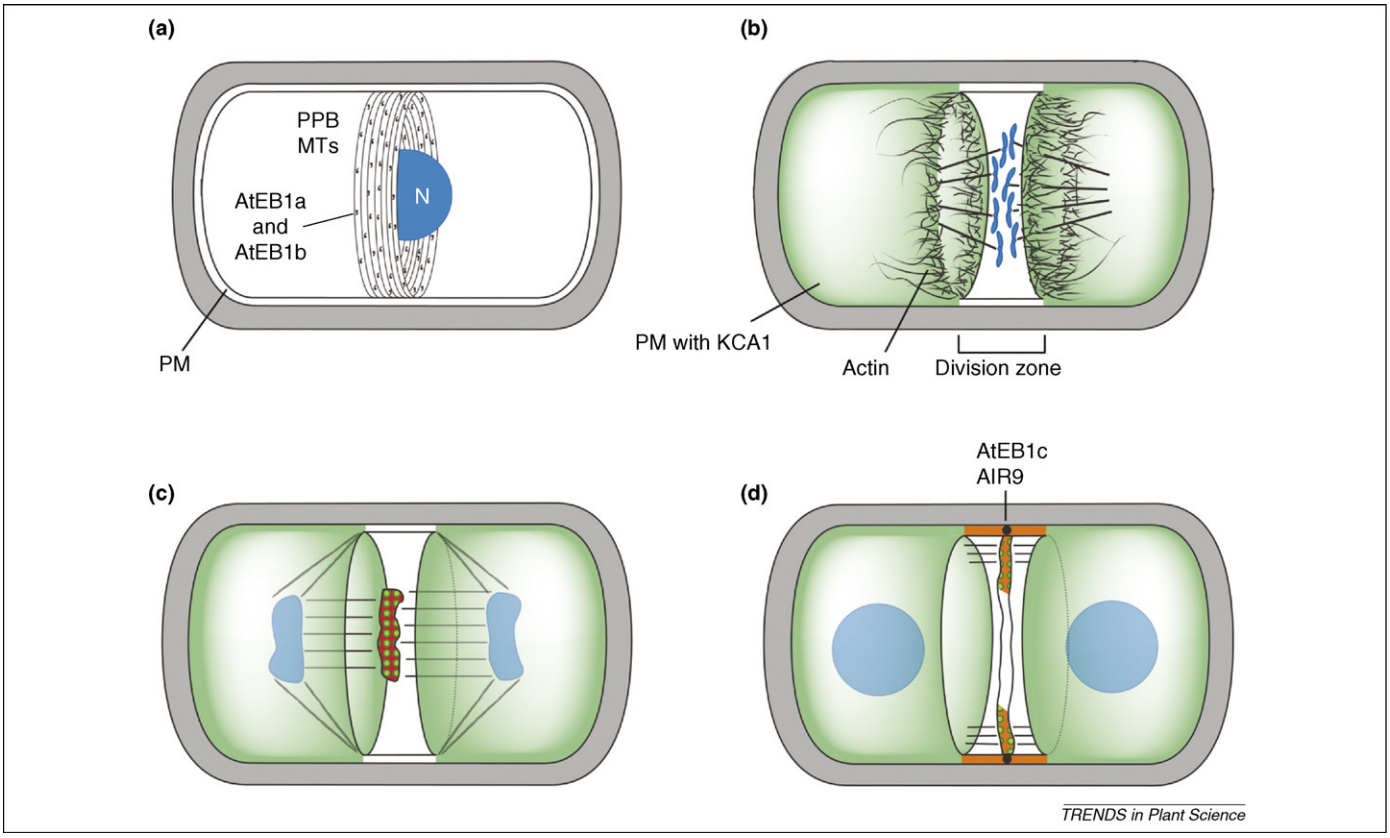

Figure 1. Formation of a distinct PM domain at the division zone. **(a)** Prophase cell during preprophase band (PPB) formation. The centrally located nucleus (N) is encircled by the PPB. At this stage, the cytoplasm becomes compacted between the nuclear zone and the PPB; this structure is termed the phragmosome (not shown) [18]. The PPB consists of highly dynamic microtubules (MT, shown) [10,11] and actin filaments (not shown) and is decorated with MT-binding proteins including AtEB1a and AtEB1b (shown) [67–69] and AIR9 [36] (not shown). **(b)** At metaphase, a plasma membrane (PM) band, termed the KCA1-depleted zone (KDZ), forms at the site of the former PPB. The KDZ is marked by the absence of the kinesin-like protein KCA1 (green) that accumulates in the PM outside the division zone [33]. The position of the KDZ corresponds to the actin-depleted zone (ADZ), which lies between two bands of actin filaments. The ADZ and the KDZ both mark the division zone and remain present throughout cytokinesis [33,59–61]. The AIR9 protein does not associate with the spindle microtubules [36], and both AIR9 and TPLATE are cytoplasmic at this stage (not shown). **(c)** During early plate formation (early cytokinesis), several proteins, including KCA1 (yellow) and TPLATE (red), accumulate in the cell plate between the two bundles of parallel phragmoplast microtubules [33,35]. The microtubule-binding capacity of AIR9 is restored and it decorates the phragmoplast microtubules [36] (not shown). Non-phragmoplast MTs connecting the nucleus to the division zone at this stage are shown. **(d)** TPLATE and KCA1 follow the leading edges of the cell plate during phragmoplast expansion (late cytokinesis). In addition to accumulating in the cell plate during insertion of the cell plate into the mother wall, TPLATE is also specifically targeted to the PM at the division zone, which it then occupies [33]. In contrast to the division zone labeling of TPLATE, AIR9 and AtEB1c accumulate only at the exact insertion site following plate insertion [36,38]. Later on, AIR9 spreads into the maturing cell plate [36] (not shown).

vesicles are trafficking at the cortical division zone are the presence of a Golgi belt circumscribing the nucleus at the division zone [24] and the coincidence of FM4-64-stained endocytic vesicles with MT plus-ends projecting to the division zone [26].

Our understanding of the process of division zone specification has recently been given a new twist through the finding that, next to the ADZ, a distinct band of PM appears at the division zone [33]. The idea that a band of PM with a unique composition exists at the division zone emerged from GFP-localization studies of a kinesin-like protein KCA1 [33]. The GFP–KCA1 protein localizes in the cytoplasm throughout interphase, and associates with the PM when the cells enter mitosis. The membrane association of KCA1 is probably caused by dephosphorylation of this protein at two putative CDKA;1 phosphorylation sites (S^{841} and S^{845}), which, presumably, changes the conformational status of the protein [34]. The PM-localized GFP–KCA1 is depleted in a narrow zone, the KDZ, which corresponds to the ADZ and persists throughout mitosis until the end of telophase [33]. Time-lapse studies and drug analysis showed that the KDZ was established during, and depended on, PPB formation. Cells that produced double PPBs, consequently also formed double KDZs. Once established, however, the persistence of the KDZ does not rely on MTs or actin filaments, because neither MT nor actin depolymerization removed the KDZ. This suggests that the PPB and the ADZ are involved in the modification of the PM at the division zone, and that this modification persists throughout cytokinesis [33].

Further evidence for a specific PM modulation at the division zone follows from the differential PM targeting of two proteins, TPLATE and AIR9 [35,36]. TPLATE contains domains with similarity to adaptin and coat proteins, suggesting that it is involved in membrane-trafficking events [35]. Detailed confocal analysis of TPLATE–GFP in dividing root cells revealed that it is targeted to the division zone during plate insertion, and that the fluorescence remained restricted to a region of ~5 μm surrounding the insertion site. Downregulation of TPLATE in tobacco BY-2 cells and *Arabidopsis* plants causes the formation of ectopic and incomplete cell walls, presumably because of a failure to anchor the expanding cell plate at the correct PM-docking site [35].

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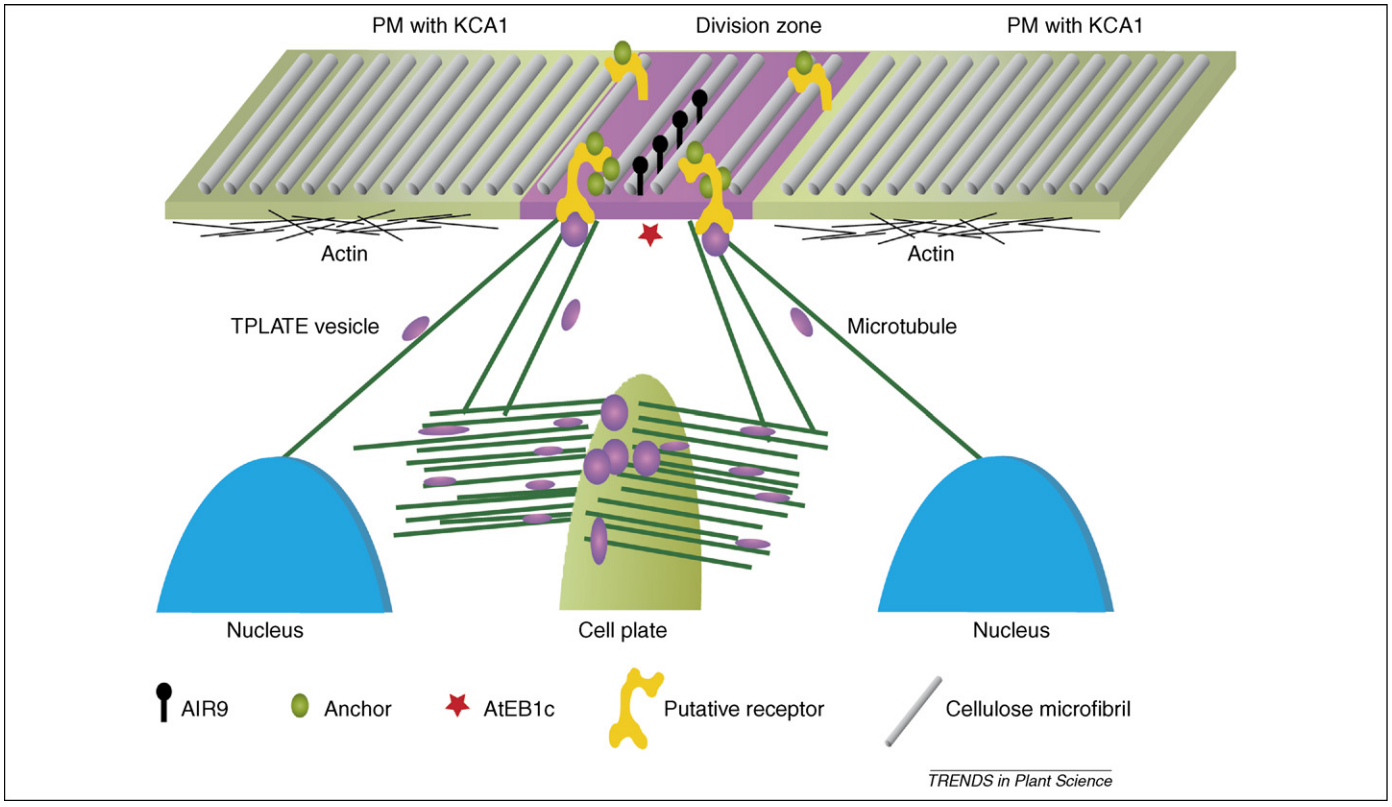

Figure 2. Model of the cortical division zone. The model shows a close-up of the plasma membrane located underneath the parallel organized cellulose microfibrils and the expanding cell plate in a late stage of cytokinesis. Following PPB breakdown, a cortical PM band (the division zone) forms, marked by the exclusion of the PM-associated kinesin KCA1 [33] and cortical actin [59–61]. The expanding cell plate is guided to the division zone and, besides accumulating in the cell plate, the membrane-associated TPLATE protein is targeted to this PM band during plate insertion (purple). Targeting of TPLATE-associated vesicles to the division zone most probably occurs via MTs that connect the phragmoplast and the nuclear surface to the division zone [26] through a putative membrane-anchored receptor. The restriction of the TPLATE localization inside and the KCA1 localization outside this PM band suggests that there is a diffusion barrier, created by anchor proteins that link the PM to the cell wall. Following plate insertion, both AIR9 and AtEB1c localize to the exact insertion site at the center of the division zone [36,38]. The specific and restricted localization patterns of TPLATE, KCA1 and AIR9 imply the formation of a PM band with a specific composition to restrict diffusion of these markers.

AIR9 was identified in a screen for distorted gametophytic transposon transmission and carries an N–terminal signal sequence suggesting that AIR9 is secreted or associated to membranes [37]. Constitutive expression of GFP–AIR9 shows a broad spectrum of MT association, in agreement with the presence of a microtubule-binding domain present at the N-terminal end of the AIR9 predicted polypeptide [36]. Furthermore, AIR9 contains a leucine-rich repeat domain that is not required for MT binding [36]. This domain might exert a separate function as GFP–AIR9 is temporally targeted to the developing cell plate and to the exact insertion site when the cell plate seals the two daughter cells [36]. The localization pattern is reminiscent to the accumulation of EB1c–GFP at the cell plate insertion site in BY-2 cells after disassembly of the phragmoplast MTs [38]. After completion of cytokinesis, AIR9 spreads centripetally into the cell plate, forming a torus. The gradual accumulation of AIR9 at the cell plate occurs earlier than the appearance of cortical microtubules, indicating that the function of AIR9 is to contribute to cell plate maturation and/or the initiation of a cortical microtubule network [36].

As TPLATE accumulation at the cell cortex occurs toward the end of cytokinesis, its activity might not be relevant to the establishment of the cortical division zone, but to anchoring the cell plate at the correct site. The KCA1 protein, by contrast, is excluded from the division zone and, therefore, cannot be directly responsible for establishing the division zone. In view of an important role for the PM, we might need to look for membrane-anchored proteins that are under mitotic control. In *Tradescantia* and BY-2 cells, an abundance of PM–cell wall connections have been visualized at the division zone [31,33]. PM–cell wall linker proteins could help to maintain the putative mark required for division zone specification at the correct position (Figure 2). However, the nature or identity of the mark itself is not yet clear.

Vesicle trafficking and the cortical division zone

The establishment of the KDZ during PPB narrowing, independent of the cytoskeleton, implies a mechanism that restricts KCA1 from the PM in the division zone around prophase. Conversely, the site-specific targeting of TPLATE and AIR9 at the PM must rely on a mechanism that has the resolving capacity to restrict localization to a distinct zone. The question that needs to be answered next is how these proteins are targeted and maintained outside of or inside the PM division zone. Several mechanisms can be envisaged that would result in the formation of an exclusive region. For instance, localized endocytosis could enable establishment of a KCA-depleted zone [33]. This mechanism only makes sense if a physical barrier is

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installed that can limit the entry of KCA and other proteins into the depleted zone or, alternatively, their mobility is reduced by means of anchor molecules providing connections with the cell wall or the cytoskeleton (Figure 2).

Cytokinesis in yeast involves the action of a septin ring that acts as a barrier to compartmentalize the cortex around the cleavage site and to prevent diffusion of cortical factors including sterol type lipids [39,40]. Septin homologs exist in *Arabidopsis* but their function remains to be determined [41]. Sterol-rich lipids are visualized using the glycolipid stain filipin, and accumulate at the division site where the septum is formed [40]. Filipin stains 3β-hydroxy-sterols in plants [42], but it does not accumulate at the cortical division zone [33]. Because biosynthesis of cholesterol is required for cytokinesis in human cells [43] and cholesterol-rich membrane domains accumulate at the future cleavage furrow in sea urchin eggs [44], it is tempting to speculate that sterol-type lipids are also implicated in plant cytokinesis. So far, however, direct evidence that sterols or sterol-containing lipid rafts play a role in cytokinesis in plant cells is still missing.

Sterol-deficient *Arabidopsis* mutants (*fk*, *smt1, cph* and *hyd1*) show embryonic cytokinesis defects and aberrant vascular differentiation [45–49]. A reduced level of brassinosteroids was found in the sterol C-14 reductase *fk* mutant, which could account for the pleiotropic cell growth defects reported. However, the random orientations of cell divisions are not typically associated with brassinosteroid hormone regulation [46]. External application of bioactive brassinolides did not rescue the *fk* phenotype, suggesting that other sterols or factors are involved [46]. In contrast to the *fk* and *hyd1* mutants, the polarity defects in the *stm1* mutant have been attributed to discrete alterations in the localization of auxin transporters, with major consequences for auxin distribution and cell patterning [50]. Raising the intracellular auxin concentrations by means of the auxin efflux inhibitor NPA increases the randomness of the position of the cell plates, suggesting that changes in auxin levels have a role in determining the division plane [51,52]. These findings support the possibility that specialized sterol molecules control cell polarity and the orientation of cell division via an auxin-dependent signaling mechanism.

During preprophase, endocytotic vesicles temporally accumulate at the PPB site, suggesting that site-specific targeting contributes to division plane establishment [26]. If localized clathrin-dependent endocytosis and exocytosis are connected with the presence of the PPB, dynamin molecules, which are the prime candidate proteins to mediate PM-recycling events, would also accumulate there. Thus far, there are no reports of the association of dynamin with the PPB [53]. Moreover, BFA treatment during an early phase of PPB formation did not appear to affect the positioning of the cell plates in BY-2 cells [28]. In conclusion, although it is appealing to hypothesize that sterols play a role in division zone determination in plant cytokinesis, the evidence is only circumstantial. One of the difficulties is that plant cells synthesize a complex mixture of sterol-type lipids that are not selectively recognized by standard sterol dyes, such as filipin [42].

Guidance of the phragmoplast

To communicate the position of the cortical division zone to the leading edge of an expanding cell plate, a chemical gradient or, alternatively, a physical connection has to be established that continuously monitors and guides plate growth. So far, there is no evidence for the existence of a cytoplasmic signal that is transported between the two sites. A polarized mode of cytokinesis is observed in vacuolate *Arabidopsis* cells, which was suggested to involve short-range interactions between the phragmoplast and the plasma membrane [54]. These 'interactions' are presumably mediated via strands of MTs and also, possibly, actin (Figure 2) [55–57]. Direct sightings of connective cytoskeletal strands are difficult because there might be only a few of them, which are likely to be highly mobile or might occur only at discrete areas of the cortical division zone as suggested by Cutler and Ehrhardt [54]. The contact between the growing cell plate and the cortical division zone is probably intense because the MT plus-end marker EB1a–GFP has been observed to move between the two sites, showing MT polymerization from the cell plate leading edge to the cortex [26]. Yet, a model whereby short-range interactions guide the phragmoplast along the predetermined division zone does not accommodate for cell plate expansion phenomena observed in BY-2 cells carrying two independent PPBs [58]. In some instances, both PPBs contribute to the guidance process; then, the final division plane cross-bridges the separate division zones predetermined by the two PPBs.

Unlike cortical MTs, actin filaments remain at the cell cortex outside the division zone after PPB breakdown, providing a negative template at the division zone [59,60]. Actin drugs do not have such dramatic effects on cell division as compared to MT drugs, indicating that the role of actin and actin dynamics is more subtle [33,59,61]. Actin drug treatments during ADZ formation cause misorientation of cell plates and abnormal cell plate insertion [62,63], although the guidance of the cell plate is relatively insensitive [61].

The maize mutant *tan* produces new cell walls that do not typically position at a 90° angle to the longest cell axis [64,65]. The phragmoplasts fail to be directed to the former PPB site because, although the mark left behind by the PPB is not there (or the detection mechanism is missing), it is malfunctioning. *tan* does produce PPBs and thus operates after *ton* or is dependent on *ton*. Because TAN is not conserved as strongly as TON, it might have a more specialized function that is crucial in some plant species but not in others [4,14]. Recently two homologous *Arabidopsis* kinesins (POK1 and POK2; see Glossary) were identified through a yeast two-hybrid screen using the maize TAN1 [66]. The double knockout mutant displays severe developmental defects similar to the phenotype of weak alleles of *ton2*. At the cellular level, multiple misoriented cell walls are observed in embryos and in root tips, suggesting that POK1 and POK2 cooperate with ATN, the TAN1 counterpart in *Arabidopsis*, to control phragmoplast guidance. POK1 and POK2 have conserved MT-binding domains and TAN1 associates with MTs in fixed cells [65,66]. These

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findings reinforce the idea that MTs are the prominent players when it comes down to guiding the cell plate to the cortical division zone.

In view of the importance of MT dynamics during guidance, recognition of the division zone could be achieved via a MT search-and-capture mechanism. The plus-ends are the most dynamic of a MT that is controlled by interacting +TIP proteins [67]. The +TIP protein EB1 is widely conserved and three homologs (EB1a–EB1c) are present in the *Arabidopsis* genome. GFP-tagging of the *Arabidopsis* EB1a, EB1b and EB1c proteins showed that all three bind to MT plus-ends [38,68,69]. Moreover, EB1a associates with the minus-end [69], EB1b with the endomembrane compartment [68] and EB1c accumulates in the nucleus [38]. Overexpression of GFP-tagged EB1b, but not EB1a, results in increased polymerization rate [70], suggesting that EB1 plus-end association regulates MT dynamics. In animal systems, a search-and-capture mechanism has been proposed to be responsible for the stabilization of microtubules that are attached to the cell cortex, mitotic kinetochores or different cellular organelles [71]. Although not unambiguously shown, if such a mechanism is also operative in plant cells, it could provide the structural requirements for phragmoplast guidance by stabilizing MTs that arrive at, or emanate from, the cortical division zone, and it could explain the increased occurrence of EB1–GFP fluorescence at the cortical division zone [26,70].

Concluding remarks and perspectives

Plant cells determine the orientation of cell division by means of a cortical division zone, marked by a PPB of MTs and a zone depleted of filamentous actin. The localization of the kinesin KCA1 revealed that the PM is also part of the mechanism that establishes the cortical division zone. The targeting of TPLATE and AIR9 to the cortical division zone favors the idea that, similarly to yeast and animal cells, the composition of the PM at the division zone is altered during cell division.

The questions that remain include how plant cells establish the resolving capacity at the PM to restrict the localization of PM-associated proteins, such as KCA1 and TPLATE, and whether this involves an alteration in membrane composition, anchor proteins or both. We also need to establish the timeframe in which the distinct PM band at the division zone forms with respect to the formation of the PPB and whether this PM zone is also established in cytokinesis events that are independent of PPB formation. Furthermore, it would be of interest to address how the establishment of a cortical division zone relates to the establishment of the exact insertion site of the cell plate, and how this is connected to the mechanism of phragmoplast guidance. As a starting point, it will be important to analyze the localization of proteins, such as TON, ATN and POK1/2, that are required for PPB-dependent division plane determination and phragmoplast guidance. The identification of a cortical division zone marker is highly desired, for it will facilitate the investigation of mechanisms by which tissue context, cellular position and cell lineage regulate division plane determination.

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