

Review Article

Plant cell divisions: variations from the shortest symmetric path

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In plants, the spatial arrangement of cells within tissues and organs is a direct consequence of the positioning of the new cell walls during cell division. Since the nineteenth century, scientists have proposed rules to explain the orientation of plant cell divisions. Most of these rules predict the new wall will follow the shortest path passing through the cell centroid halving the cell into two equal volumes. However, in some developmental contexts, divisions deviate significantly from this rule. In these situations, mechanical stress, hormonal signalling, or cell polarity have been described to influence the division path. Here we discuss the mechanism and subcellular structure required to define the cell division placement then we provide an overview of the situations where division deviates from the shortest symmetric path.

Introduction

In plants, the presence of cell walls implies that tissue forms a mechanical continuum where cells are attached to their neighbours. The position of new cell walls is thus of importance since it will influence cell shape, tissue topology, patterning, and to some extent the overall organ morphology. The positioning of new cell walls in plants has retained the attention of scientists for more than a century, as their non-random orientation has been noticed quite early, several rules explaining their positions have been proposed. In 1863 Hofmeister proposed that new cell walls formed perpendicular to the main direction of growth of the mother cell [1]. In relation to Hofmeister's rule, Sachs proposed that new cell walls were inserted at a 90° angle from the mother cell wall [2]. Then in 1886, Errera proposed that most planes of plant cell divisions followed the shortest possible path (i.e. minimal surface area), halving the cell into two daughter cells of equal volume in a way similar to soap film formation that tends to optimize the energy by minimising their surface area [3]. More than 100 years later Flanders et al. added another rule on top of these: the new cell wall inserts in the pre-existing one to avoid the formation of four-way junctions [4]. More recently, Besson and Dumais revised Errera's rule by including a probabilistic component: the path followed by the new wall is selected from several alternative paths with an increased probability toward the shortest one [5]. These rules are based on cell geometry or growth but some authors have recently proposed that the positioning of new cell walls maintains the topological properties of the tissue such as each cell having an average of six neighbours [6,7] or homogeneity of the cells network [8]. However, since topology is an emergent property of the division pattern, both geometry-based and topology-based rules predict new cell walls to be (or very close to) the shortest possible one going through the mother cell centroid, halving the cell in two equal volumes. But there are some cases where the selected path deviates significantly from this rule by following a path longer than the shortest one, creating an asymmetry in the volume of the two daughter cells or not passing through the mother cell centroid. Here we present the essential subcellular structures required for the positioning of the new cell wall then we provide an overview of situations where the division path deviates from the shortest one going through the cell centroid.

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New cell wall and division orientation establishment

The definition of the division path and the formation of the new cell wall is a multistep process initiated by the end of interphase, here we will briefly present these steps before discussing the potential keystones for the definition of division orientation. The first events relating to the definition of the new cell wall position occur at the end of interphase when the cell nucleus often moves to a new position; central for divisions that pass through the centroid and away from the cell centroid for those that do not [9,10]. The movement of the nucleus is associated with the formation of cytoplasmic strands containing actin and microtubules (MTs) radiating from the nucleus [4,9,11], the nuclear membrane having the ability to nucleate MTs [12] (Figure 1A,B). The Pre Prophase Band (PPB) of microtubules is formed soon after nuclear displacement and consists of highly ordered microtubules [13] (Figure 1C). The cortical division zone (CDZ) that marks the future site of cell plate insertion is formed concomitantly to the PPB and is characterised by a local change in plasma membrane composition and enrichment in a specific type of kinase and microtubule-associated proteins. Changes in plasma membrane composition and associated proteins during cell division are reviewed in detail in [14]. The PPB narrows then coalesce during prophase [15], the mitotic spindle forms during prophase, and metaphase segregate chromosomes in anaphase (Figure 1D). In telophase, vesicles from golgi and trans-golgi networks fuse at the cell equator to form the cell plate. These vesicles are transported by a dense network of microtubules and actin: the phragmoplast, they carry both plasma membrane material, cell wall material, and proteins responsible for cell wall material biosynthesis [16]. The new cell plate is formed centrifugally following the movement of the phragmoplast [17,18], it then fuses with the existing cell wall and the plasma membrane at the division site [19,20] (Figure 1E,F). We will now discuss how some of these events are instrumental in division plane orientation determination.

All division rules imply a mechanism to identify the shortest path, measure the potential angle of cell plate insertion, or evaluate the direction of tensile stress. This mechanism could rely on the physical properties of the structures involved in cell division or on the modulation of these properties by additional molecular actors. One important property of plant structures is the level of tension or compression they support. Tension and compression are forces bearing directional information. The main direction of tensile stress within single cells can align with the shortest path across the cell. For instance, the shortest path predictions made by Besson and Dumais can be recapitulated by a simple inflated elastic membrane model predicting the direction of tensile stress [5,21]. At the subcellular level, MTs have been shown to align with the maximal direction of tensile stress [22] and could be tension sensors *per se* [23]. During interphase, a dense network of intertwined MT is present at the cell cortex often referenced as Cortical Microtubules array (CMT), its principal direction is influenced by the tensile and compressive force [22,24,25]. Several structures involved in cell division are made of MTs and as we will now discuss, some of them are under tension or align with the principal direction of tensile stress. For instance, cytoplasmic strands associated with nuclear displacement are under tension [26,27], and like a soap film in a rigid frame, they tend to reach the cell edge at 90° following the shortest path [4]. Another structure aligning with tension is the PPB whose orientation often follows the main orientation of cortical microtubules in interphase. PPB position is accurately predicted by the soap-film area minimization model run on real 3D segmented cell templates, in turn, the PPB position predicts the position of the future division plane [13,28]. However, PPB is not present in all plant species [29] and its function has recently been re-evaluated. PPB formation is regulated by the TONNEAU1 (TON1)-TON1 RECRUITING MOTIF (TRM)-PROTEIN PHOSPHATASE 2A (PP2A) (TTP) protein complex. Several mutants affected in this complex do not form a PPB and have cell division orientation defects. Defective expression of the regulatory subunit of PP2A (*fass* mutant) severely disrupts division plane placement in *Arabidopsis* embryo [30]. TON1 defectives alleles also exhibit strong cell division orientation defects [31]. However, both *fass* and *ton1* have defects in other microtubules structures such as the interphasic cortical microtubules array, and have strong developmental defects (*ton1* mutant is named after ‘tonneau’ the French word for a barrel, as the plantlet looks like a tiny barrel), making the relationships between lack of PPB and cell division defects complex to interpret. Recently, a *trm678* triple mutant has been isolated, this line does not form PPB and does not seem to have other microtubules defects [32]. On the contrary of other PPB defectives lines, the mean orientation of division in *trm678* roots is similar to wild type although more variable, indicating that, at least in roots, the PPB would ensure the robustness of cell division orientation rather than determining the orientation [32]. Another main MT-based structure involved in cell division is the spindle. It is formed perpendicular to the axis of the PPB during prophase [33,34] but its position does not seem to be the determining factor of division plane position

gally following the movement of the phragmoplast [17,18], it then fuses with the existing cell wall and the plasma membrane at the division site [19,20] (Figure 1E,F). We will now discuss how some of these events are instrumental in division plane orientation determination. **Figure 1. Schematic view of plant cell division.**

(A) Nuclear migration at the end of interphase. (B) Cytoplasmic strands containing actin and microtubules radiates from the nucleus and participate in anchoring it to its new position. (C) Cortical microtubules accumulate in a dense band, the PPB that will mark the future site of cell plate insertion (the divisi

since centrifugation experiments have shown that displaced spindles can track back to the initial position of the PPB [35–37]. In addition, rotations ending in the alignment of the spindle or even developing cell plates with the PPB position are frequent during guard mother cell division in *Allium* [38]. All these studies indicate that the division orientation and thus the location of cell plate insertion are defined prior to spindle formation by structures under tension or aligned with the principal direction of tension.

After its specification, the division site has to be maintained to ensure the proper guidance of the phragmoplast, here we provide a brief description of the few known actors involved in this process, a more detailed review of these actors is provided in [39]. Most of the actors identified to have a role in phragmoplast guidance are located at the CDZ underlying the PPB and remain there after PPB disassembly. For instance, the presence of PHRAGMOPLAST ORIENTING KINESIN (POK)1 and POK2 at the CDZ are essential for phragmoplast guidance, their absence in a *pok1pok2* mutant causes a mismatch between phragmoplast and PPB orientation leading to severe division orientation defects [40] as the cell plate fuses outside of the CDZ. The positioning of POK1 at the CDZ partially depends on PLECKSTRIN HOMOLOGY GAPS (PHGAPS) proteins, mispositioning of POK1 in *phgaps1phgaps2* double mutant also give rise to division orientation defects [41]. The presence of POK1 at the CDZ is required to maintain other important actors at the CDZ after the PPB disassembly. This is the case for TANGLED1 (TAN1) whose location at the CDZ is not maintained after PPB disassembly in *pok1pok2* [42]. TAN1 is a microtubule-associated protein whose loss of function in the maize line *tan1* results in strong division orientation defects due to a mismatch between phragmoplast and PPB orientation [43]. It has been proposed that the interaction between TAN1 at the division site and microtubules at the

leading edge of the phragmoplast would maintain its trajectory [43]. In addition to the CDZ, POK2 is also present in the midzone of the expanding phragmoplast and interacts with microtubule cross-linker MAP65-3/PLEIADE, this interaction would stabilize the phragmoplast and favour its rapid expansion toward the division site [44]. The microtubule severing activity of KATANIN is essential for proper orientation of the spindle and guidance of the phragmoplast to the division site. Strong katanin mutant alleles show defects in these processes resulting in cell division plane defects [45,46]. In addition, a line with a mutation in *CORD4*, a protein recruiting katanin to the phragmoplast, shows a delayed progression of the phragmoplast to the division site [47]. After the initial definition of the future division plane by the PPB orientation, the spatial information is retained by some of the above-mentioned proteins, but the precise mechanism by which the leading edge of the phragmoplast grows in the precise direction of the division site remains unclear. Although the guidance of the phragmoplast to the division site is an important part of the division orientation process, the actors modulating the division path are likely to act on the early steps of the cell division process prior to spindle formation. Indeed, in a wild type context, no new division has been reported not to match the position of the division site. In the next section, we will describe the situations where the selected division path is not the shortest one going through the cell centre halving the cell in two equal volumes as well as the factors associated with the definition of these alternative division paths.

Variations from the shortest symmetric path

Although most divisions seem to follow the shortest path, there are a number of examples where this is not the case (Figure 2A). Divisions parallel to the longest axis of the cell, referred to as longitudinal divisions hereafter, are frequent during leaf development in maize [48]. However, they tend to occur in nearly isotropic cells, making the selected path not so distant from the shortest path [28]. Besides this situation that can be interpreted as an extreme case of the Besson and Dumais rule, some deviations from the shortest path cannot be explained by cell geometry-based rules alone. For instance in Shoot Apical Meristems (SAM), cells in the boundary region that separates organ primordia from the rest of the meristem almost systematically divide longitudinally [49–53]. These divisions occur perpendicular to the main direction of compression generated by the differential growth between organ primordia and SAM (Figure 2B–D). This is in accordance with the classical experiments using compression or wounding on dividing plant tissues that have repeatedly reported divisions to occur perpendicular to the direction of compression or parallel to the main direction of tensile stress [54–56]. More recently, cell laser ablation experiments further confirmed the influence of mechanical stress on the orientation of cell division. In Arabidopsis SAM, cell ablation leads to the formation of a circumferential pattern of mechanical stress as visualized by the alignment of cortical microtubules [22] and cell division occurring parallel to the main direction of tensile stress [49]. The local or global mechanical stress pattern influences the orientation of cell division but they are not the only factor affecting cell divisions.

Beside longitudinal divisions, asymmetric divisions represent another type of deviation from the shortest symmetric path. Asymmetric cell divisions are found in distinct contexts during plant development, for instance within the early steps of the stomatal lineage in Arabidopsis [57–59], during the formation of subsidiary cells in monocotyledons [60] or the first steps of lateral roots development [61–63]. In Arabidopsis, the very first division giving rise to the suspensor and embryo lineages or divisions leading to the formation of protodermal layers between the 8 and 16 cells stage of the embryo are asymmetric [64,65]. In the case of the division to form the protoderm the division plane still passes through the centroid of the cell [66] but does not produce daughter cells of equal volume. The division plane is a possible surface area minimisation [66], however, there is evidence that other factors influence its placement, perhaps to ensure its selection over other minimal surfaces [30,65,67]. Polarly distributed proteins and auxin signalling are the two main factors commonly associated with asymmetric divisions in various developmental contexts.

In the amplifying divisions of the stomata lineage, the nucleus and division plane are displaced from the centroid of the cell. The polar distribution of BREAKING OF ASYMMETRY IN THE STOMATAL LINEAGE (BASL) and its interacting members BREVIX RADIX (BRX) or BRX-LIKE (BRXL) is essential to ensure the asymmetry of divisions in the stomatal lineage. BASL is present in a crescent in meristemoids, and its polarity switches following division to generate the characteristic spiral pattern seen in stomatal lineages. BASL triggers nucleus migration away from its location prior to cell division and then towards its location following division with the new cell wall forming away from the cell edge where BASL is enriched [68,69] (Figure 2E–G). Defective expression of BASL or BRX and BRXL family members leads to symmetric divisions in the stomatal lineage [70,71]. In Maize, the polar distribution of PANGLOSS receptors like kinase (PAN1 and PAN2) in the

e orientation of cell division. In *Arabidopsis* SAM, cell ablation leads to the formation of a circumferential pattern of mechanical stress as visualized by the alignment of cortical microtubules [22] and cell division occurring parallel to the main direction of tensile stress [49]. The local or global mechanical stress pattern influences the orientation of cell division but they are not the only factor affecting cell divisions. **Figure 2.**

Deviations from the shortest symmetric path.

Part 1 of 2

(A) Schematic representations of different cell divisions: shortest path symmetric, longitudinal symmetric, and shortest path asymmetric. (B) Drawing of *Arabidopsis thaliana* with highlights of some locations where deviations from the shortest path are found. (C) Illustration of the Shoot Apical Meristem (SAM) where differential growth associated with organogenesis generate compressive forces (red arrows) (based on results from [22,86]). (D) Confocal image of the region of the SAM under compression exhibiting longitudinal divisions (as in (c), red arrows represents compressive forces). (E) Confocal image of a cotyledon. (F) Close up of the cotyledon in (E) showing asymmetric divisions in the stomatal lineage (highlighted in red). (G) BASL polar distribution (in green) is required to make the divisions asymmetric. In a *bas1* mutant divisions of the stomatal lineage are symmetric and lead to the formation of stomatal clusters (Based on results from [68,71,87]). (H) *Arabidopsis thaliana* seed. (I) In wild type embryos the presence of an auxin response is associated with asymmetric divisions. In transgenic lines expressing a negative regulator of auxin signaling (*pRPS5A::bd1*), these embryonic divisions become symmetric and are reminiscent of the conformation adopted by soap film in quadrant (based on result from [

subsidiary mother cell is essential for setting the asymmetry of the division which produces the subsidiary cells [72,73]. The importance of protein polarity for asymmetric cell division could be wider than these specific contexts, indeed recently identified polar proteins of the SOSEKI family are widely expressed in plants and ectopic expression of their members leads to the formation of asymmetric divisions in various organs [74,75]. In addition to polar proteins, auxin signalling has been shown to be associated with the formation of asymmetric divisions.

Auxin is involved in many aspects of plant development from early embryogenesis to the late developmental stages of lateral organs. In many of these developmental processes, divisions associated with auxin signalling are asymmetric. For instance, while high auxin signalling is associated with the asymmetric divisions of the stomatal lineage leading to the guard mother cell formation, the last symmetric division giving rise to the guard cells is preceded by a decrease in auxin responses [76]. Another developmental process where auxin is associated with asymmetric division is the formation of lateral roots (LR). LR are initiated from the pericycle by a pair of anticlinal asymmetric divisions taking place after a local auxin response maxima [77–79]. Pericycle divisions can be triggered by laser ablation of endodermal cells, but only concomitant auxin application can recapitulate the anticlinal asymmetric division [80]. This relationship between auxin and asymmetric divisions is further illustrated by genetic approaches in the embryo. Defective alleles of AUXIN RESPONSE FACTOR 5 are widely affected in auxin responses and presents a shift from asymmetric to symmetric division during embryonic ground tissue initiation [81]. Consistently, ectopic expression of the stabilized negative regulator of auxin responses *bodenlos/iaa12* directs symmetric divisions instead of asymmetric at the 8 to 16 cell transition [30] (Figure 2H–I). These symmetric divisions are reminiscent of the conformation adopted by soap films in quadrant (Figure 2J) and the resulting pattern is frequently observed in other globular structures such as glandular trichomes (Figure 2K) [5]. This similar pattern between constrained soap film, glandular trichomes, and auxin response deficient embryos suggests that auxin is able to shift divisions from symmetric to asymmetric. Interestingly auxin triggered asymmetric divisions seem to require local tuning of microtubule stability both in embryonic and lateral root development. Indeed the auxin triggered asymmetric division of pericycle cells requires functional microtubule severing protein KATANIN [80] and pericycle divisions are misplaced in *katanin* mutants [82]. In addition, a study combining modelling and imaging demonstrated that cell divisions in the embryo could be predicted from the observed CMT orientation. In turn, the CMT orientation prior to division could be predicted by cell geometry with the addition of a cell-edge triggered catastrophe and microtubule stabilization at a selected cell-face. The authors proposed that auxin is the factor responsible for tuning the stability of microtubules at the faces of the cells [67]. Auxin, like mechanical stress and polarity, is a factor that can impact the division plane orientation, but the processes involving these factors are highly intertwined as illustrated by the influence of mechanical stress on both polarly distributed BRXL [83] or auxin transporter PIN FORMED 1 (PIN1) [22,84,85] and microtubules dynamics [85]. While microtubule dynamics are not required for mediating mechanical-stress triggered changes in BRXL or PIN1 polarity [83,85], BASL and BRX effects on pre-division nuclear migration and division asymmetry do require functional microtubule dynamics [69]. Microtubules appear to be central in the integration of multiple signals in the process of division path selection.

Conclusion

Studies spanning several decades have highlighted the fundamental role of microtubules and associated structures in defining cell division orientation. Distinct factors like mechanical stress, polar proteins, and auxin signalling have been described in deviating the division path from the shortest symmetric one. One challenge for the future will be to elucidate the mechanism by which these factors act on the main structures involved in cell division orientation. Another challenge for the future is to unify the proposed rules for cell division into a common conceptual framework and to understand their biological significance.

Perspectives

Importance to the field: Ultimately all cells result from cell division. As plant cell movements are restricted by cell walls, the orientation of cell divisions determines the organisation of tissues, however, after more than a century of research, the precise mechanism of cell division orientation and the factors acting on it remains an open question.

Current thinking: Improvements in live-imaging, image analyses, computational modelling as well as the establishment of new model species continuously increase our understanding of cell division orientation, however, none of the existing rules can explain all of the observed divisions. Auxin signalling, mechanical stress, and polarly distributed proteins are commonly associated with divisions not following the shortest path.

Future directions: An important challenge for the future would be to determine if there is a universal rule for determining cell division orientation and if not, to identify the mechanism by which cell division orientation is changed. Another important step would be to clarify the function of the PPB.

[UNDEFINED TAG] Competing Interests

The authors declare that there are no competing interests associated with the manuscript.

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L.S. and S.R. conceived the review, L.S. wrote the manuscript and made the figure with input and editing from S.R.

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Abbreviations

BASL,
BREAKING OF ASYMMETRY IN THE STOMATAL LINEAGE; BRX,
BREVIX RADIX; BRXL,
BRX-LIKE;
CDZ,
Cortical Division Zone; LR,
Lateral Roots; MTs,
Microtubules; PAN1,
PANGLOSS1; PAN2,
PANGLOSS2; PHGAPS,

PLECKSTRIN HOMOLOGY GAPs; PIN1,
 PIN FORMED 1; POK1/2,
 PHRAGMOPLAST ORIENTING KINESIN1/2; PP2A,
 PROTEIN PHOSPHATASE 2A; PPB,
 Pre-Prophase Band of microtubules; SAM,
 Shoot Apical Meristem; TAN1,
 TANGLED1; TON1,
 TONNEAU1; TRM,
 TON1 RECRUITING MOTIF; TTP,
 TON1-TRM-PP2A.

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