

*Tansley insight*

Mechanobiology of cell division in plant growth

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Summary

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Cell division in plants is particularly important as cells cannot rearrange. It therefore determines the arrangement of cells (topology) and their size and shape (geometry). Cell division reduces mechanical stress locally by producing smaller cells and alters mechanical properties by reinforcing the mechanical wall network, both of which can alter overall tissue morphology. Division orientation is often regarded as following geometric rules, however recent work has suggested that divisions align with the direction of maximal tensile stress. Mechanical stress has already been shown to feed into many processes of development including those that alter mechanical properties. Such an alignment may enable cell division to selectively reinforce the cell wall network in the direction of maximal tensile stress. Therefore there exists potential feedback between cell division, mechanical stress and growth. Improving our understanding of this topic will help to shed light on the debated role of cell division in organ scale growth.

I. Introduction

The quantification of mechanical properties in model organisms has improved our understanding of their relationship with growth. Cell walls have been seen to soften before growth (Milani *et al.*, 2011; Peaucelle *et al.*, 2011) and to stiffen as growth slows or arrests (Yarahmadov *et al.*, 2020). Differences in mechanical properties can yield elaborate 3D structures or flat leaves (Rebocho *et al.*, 2017; Whitewoods *et al.*, 2020) due to the resultant differential growth. However, tissues are made of pressurised cells that divide and differentiate, adding new material to the system and constraints on the growth (Hervieux *et al.*, 2017), respectively. Cell division orientation is

of particular importance in plants where the cells cannot rearrange. The position of the new cell wall simultaneously determines cellular topology (number of neighbours), cell geometry (size and shape) and the overall structure of the mechanical wall network. The geometry of pressurised cells is a key determinant of the direction of maximal tension within the cell, but it can be overcome by tissue-level stresses that result from the shape or growth of the tissue (Sampathkumar *et al.*, 2014; Whitewoods *et al.*, 2020). Many key regulators of development align with the maximal direction of tensile stress (Hamant *et al.*, 2008; Nakayama *et al.*, 2012; Robinson & Kuhlemeier, 2018; Zhao *et al.*, 2020). In this review, we examine recent advancements in our understanding of the regulation of cell division by mechanical stress.

We also examine what is known about the impact of cell division on the mechanical stress and mechanical properties of the tissue, and its overall impact on morphology. We will not discuss how mechanical stress is perceived as this is the topic of other reviews (Hamant & Haswell, 2017; Fruleux *et al.*, 2019; Hamant *et al.*, 2019).

II. Do new cell walls align with geometric or mechanical signals?

The most accepted default cell division rules are geometry based such that the new cell wall follows the shortest path or is a surface of

minimum area across the cell (Fig. 1a), and passes through the centre of mass. These rules are based on early observations that cells behave like soap bubbles (Errera, 1886), with the new wall adopting the same position as a soap film would under the same conditions. Investigating cell division in cells with simple geometries from a range of species including the glandular trichomes of *Dionaea muscipula* and *Coleochaete* validated this result and demonstrated that the division plane selects the minimum surface in a probabilistic manner (Fig. 1b; Besson & Dumais, 2011).

Alternative rules have been proposed including alignment with the direction of maximal tension (Kny, 1896; Lintilhac & Vesecy,

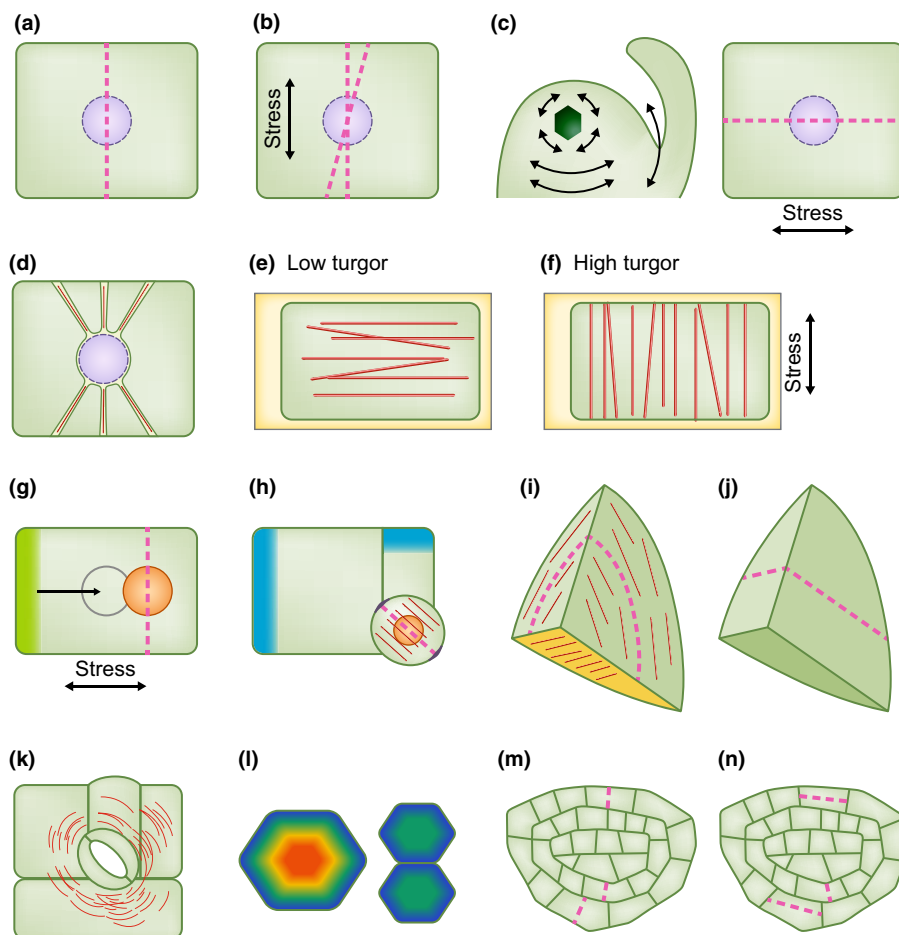


Fig. 1 Feedbacks between mechanics and cell division. (a) Cell divisions (dashed magenta) are traditionally thought to follow the shortest path through the centre of mass (purple circles; Besson & Dumais, 2011). (b) An updated model predicts one of the shortest paths through the centre of mass is selected stochastically. The shortest path often aligns with the direction of maximal tensile stress. (c) Where tissue scale stress dominates, cell divisions align with the direction of maximal tensile stress for example in the boundary region and around an ablation in the *Arabidopsis* shoot apical meristem (Louveau *et al.*, 2016a). (d) Before division the nucleus is positioned in the centre of the cell by microtubule-containing cytoplasmic strands that are under tension. (e, f) Protoplasts were put into wells (yellow) to determine the effect on microtubule orientation (red). (e) At low turgor the microtubules align along the long axis of the cell (Durand-Smet *et al.*, 2020). (f) At high turgor the microtubules align with the direction of maximal tensile stress (Colin *et al.*, 2020). (g) The polarised protein BASL (green) may align with mechanical stress or global polarity factors, BASL displaces the nucleus away from the centre of mass to produce an asymmetrical division (Bringmann & Bergmann, 2017; Mansfield *et al.*, 2018; Muroyama *et al.*, 2020). (h) BASL localisation in successive divisions follows intrinsic polarity cues (blue: previous BASL locations; Robinson *et al.*, 2011). (g, h) Auxin is high in the meristemoids (g) (orange) then reduces in the guard mother cell (GMC) (h) that swells and divides symmetrically (Le *et al.*, 2014). Microtubules (red) align with the division and the cell wall thickens at the pole before cell division (purple). (i) Cell division of the 8-cell embryo is very robust. It aligns with the orientation of microtubules (red). The pattern of microtubules can be predicted by a model based on geometry with edge catastrophe and stabilisation on the newest faces (yellow). Removal of face stabilisation results in cell division following the shortest path (minimum area) as in the *bodenlos* mutant (j) (Chakraborty *et al.*, 2018). (k) Stomata alter the pattern of mechanical stress around them. They also influence the position of the first lobe of the stomata lineage ground cell (Grones *et al.*, 2020). (l) Cell division reduces cell size and stress on the top wall (red: high stress; blue: low stress; Sapala *et al.*, 2018). (m) Cell division plays a role in stress feedback on growth and helps leaves to grow flat. In wild-type most divisions align with abaxial–adaxial polarity. (n) In oryzalin-treated leaves parallel divisions can be observed (Zhao *et al.*, 2020).

1984). Louveaux *et al.* (2016a) compared the success of models in which the cell division follows the geometric shortest wall vs the direction of maximal tensile stress to predict cell division in the shoot apical meristem of *Arabidopsis*. In the central region where growth and mechanical stress are isotropic, both models had similar success (Fig. 1b). However, in the boundary region of the meristem, there are more longitudinal divisions than would be expected from the Besson–Dumais model. This region has anisotropic stress due to its shape and growth rates. The mechanical-based model of cell division is better at predicting the division orientation here. Similarly when a stress direction was imposed by ablating a cell in the central region the division plane aligned with the predicted direction of maximal tensile stress (Fig. 1c).

For many cells, a tension-based model would produce the same results as the Dumais–Besson stochastic shortest wall (Guérin *et al.*, 2016; Louveaux *et al.*, 2016a) due to the dominant role of cellular geometry in determining the direction of mechanical stress. However, in cases in which there is a discrepancy between the geometric prediction and the mechanical prediction due to dominating tissue-level stress, the mechanical model is a better predictor of cell division orientation.

III. Are microtubules sensing mechanics or geometry?

Before cell division, the nucleus is positioned at the centre of the cell by microtubule-containing cytoplasmic strands. As the strands are under tension, they more frequently span shorter distances between the nucleus and cell cortex (Fig. 1d; Flanders *et al.*, 1990; Lloyd, 1991). It is thought that these strands could stabilise the recruitment of cortical microtubules to the preprophase band, which marks the future division site and therefore enables the cell to find the minimal surface area (Besson & Dumais, 2011). The preprophase band contains cortical microtubules and cell division orientation usually aligns with the orientation of the microtubules before division. A result that has been confirmed in the early *Arabidopsis* embryo (Chakraborty *et al.*, 2018) and guard mother cells (Lucas *et al.*, 2006).

By putting *Arabidopsis* protoplasts into wells of different shapes it was shown that when turgor pressure is low (Mirabet *et al.*, 2018; Durand-Smet *et al.*, 2020) cortical microtubules align with the axis of lowest curvature (the long axis of elongated cells) due to their high bending stiffness (Fig. 1e). However, when turgor pressure is high enough to induce surface tension the microtubules align with the direction of maximal tensile stress, which is transverse to the long axis in elongated cells (Colin *et al.*, 2020; Fig. 1f). Microtubules have also been shown to align with the direction of maximal tension in some organs and to act as integrators of cellular geometry-derived mechanical stress and supracellular stress (Sampathkumar *et al.*, 2014; Louveaux *et al.*, 2016b). The alignment of microtubules with tension is not perfect and the identification of NEK6 suggests that it is being actively regulated (Takatani *et al.*, 2020). The orientation of microtubules therefore mirrors the observed probabilistic nature of cell division orientation (Besson & Dumais, 2011) and is likely to determine the division plane.

IV. Does turgor pressure alter division orientation?

Changing the turgor status of a cell has been shown to alter cell division orientation. When the root is wounded, a restorative asymmetrical division occurs orthogonal to the normal division plane and parallel to the wound (Hoermayer *et al.*, 2020). The division is associated with a spike in auxin, turgor driven swelling of the cell adjacent to the wound and expression of the wound responsive transcription factor ERF115. If the swelling is inhibited by treatment with mannitol then the restorative divisions do not occur, although normal divisions still occur, suggesting that it is important in orienting the division. Additionally, plasmolysing tobacco cells results in more cells dividing longitudinally (Asada, 2013). These examples demonstrate that changing turgor pressure may be a method of altering division orientation. It is most likely that this occurs by altering microtubule alignment, either by changing the direction of maximal tension or by removing turgor, such that the microtubules align with cellular geometry.

V. Exceptions to the default rules

Asymmetrical cell divisions often break the default cell division rules by not passing through the centre of mass of the cell or not following the shortest path across the cell. The asymmetrical divisions of the stomatal lineage are controlled by polarly localised proteins (Dong *et al.*, 2009; Pillitteri *et al.*, 2011; Houbaert *et al.*, 2018). One of the proteins, BASL, was shown to displace the nucleus from the centre of the cell in a microtubule-dependent manner (Muroyama *et al.*, 2020; Fig. 1g). After division, the nucleus is moved towards the BASL crescent in an actin-dependent manner. The division follows the shortest path across the cell through the displaced nucleus (Robinson *et al.*, 2011; Moukhtar *et al.*, 2019) and, as such, may not deviate from the direction of maximal tension, but this remains to be determined. BASL localisation in successive rounds of division can be predicted by cell-autonomous polarity switching (Robinson *et al.*, 2011; Fig. 1h). However, ectopically expressed BASL or the binding partner BRXL shows alignment with global tissue polarity (Bringmann & Bergmann, 2017; Mansfield *et al.*, 2018) and with tissue scale mechanical stress (Bringmann & Bergmann, 2017). BASL polarity can also form spontaneously in tobacco BY2 cells and aligns with the axis of growth (Chan *et al.*, 2020). These results suggest that asymmetrical divisions could be sensitive to mechanical stress, however further work is needed to determine the mechanism and distinguish between the competing theories.

Inhibiting BASL-directed nuclear movements removed the directed asymmetry of the division in stomatal lineage cells, however the random nuclear movement still occurred and resulted in daughter cells with unequal cell volumes (Muroyama *et al.*, 2020). Daughter cells of unequal volumes have also been frequently observed in *Arabidopsis* shoot apical meristems, representing *c.* 20% of divisions (Louveaux *et al.*, 2016b). This raises the question of whether passing through the centre of mass of the cell should be considered a default state. The final division of the stomatal pathway that produces two guard cell precursors of equal volume is preceded by swelling of the guard mother cell (Zhao & Sack, 1999;

Fig. 1h), and microtubules aligning longitudinally (Lucas *et al.*, 2006). The swelling is associated with a reduction in auxin (Le *et al.*, 2014). If auxin transport is inhibited with NPA, auxin levels remain high in the guard mother cell (GMC) and the final division is unequal (Le *et al.*, 2014). This argues in favour of an active mechanism being required to ensure symmetric division.

In the embryo, the division to form the protoderm is precisely controlled. Although some models predict the division to be one of the minimum surface areas (Moukhtar *et al.*, 2019), others do not (Yoshida *et al.*, 2014). The robustness of the division makes it likely that there is additional control to orient it correctly (Fig. 1i). Recently a microtubule model was developed to provide a plausible model for the division plane orientation (Chakraborty *et al.*, 2018). The authors proposed a model of microtubule dynamics that resulted in them aligning with the cell geometry, consistent with previous models (Mirabet *et al.*, 2018). However, there was poor agreement between the model and the observed microtubule alignment until they added an enhanced catastrophe at cell edges with high curvature. This basic model was able to predict microtubule alignment and cell division orientation similar to that observed in the *bodenlos* mutant (Fig. 1j). To model the wild-type behaviour the authors further modified the relative stability of the microtubules on the different faces to decrease with the age of the face in an auxin-dependent manner. Using this model was possible to find parameters that correctly predicted the orientation of the divisions (Fig. 1i). The authors argued that their model did not require microtubules to align with mechanical stress, however they did not test whether a mechanical stress-based model would also be plausible.

There is a prominent role for auxin in many of the divisions that do not follow the shortest wall. Further investigation is needed into whether the direction of stress is altered or whether these divisions override the mechanical-based rules and under which circumstances.

VI. What are the consequences of cell division on tissue mechanics, stress and morphology?

Cell divisions themselves are associated with the addition of new material to the tissue that will change its mechanical properties. Using probes that are sensitive to microviscosity Michels *et al.* (2020) showed that there were differences in the cell wall tension between newly formed cell walls and older ones. The implications for this on overall mechanical properties remains to be seen, but differences in cell wall and membrane tension can alter the recruitment of polarity proteins and potentially alter tissue polarity (Nakayama *et al.*, 2012; Yoshida *et al.*, 2019). The membranes of new divisions have a different identity compared with the other membranes, particularly having a higher abundance of phosphatidylinositol-4-phosphate (Simon *et al.*, 2016). Differences between new and old walls/membranes play an important role in several models of asymmetrical division (Robinson *et al.*, 2011; Chakraborty *et al.*, 2018), although the mechanisms have not been determined. For stomata, the new walls are different in composition and there is additional thickening of the existing walls before cell division (Zhao & Sack, 1999; Fig. 1h). The resultant structures

also alter the surrounding stress pattern and influence the position of lobe formation of pavement cells (Grones *et al.*, 2020; Fig. 1k). Differences in cell wall and membrane composition and the ability to recruit polarity properties are likely to have at least indirect effects on the mechanical properties of the tissue.

Cell division reduces the stress on the outer epidermal wall by creating cells with smaller surface areas (Sapala *et al.*, 2018; Fig. 1l). Creating a larger pool of cells before organ growth may allow the organ to achieve a larger final size by reducing mechanical stress. The orientation of the cell division determines the extent to which in-plane stresses are reduced. Where cell division aligns with either the shortest wall or the direction of maximal tension there is a reduction in the variability of stress and growth in the tissue compared with random placement of the cell division walls or no division (Alim *et al.*, 2012; Fruleux & Boudaoud, 2019). Cell divisions in the leaf tend to be oriented parallel to the abaxial–adaxial plane and have been shown to help leaves grow flat by enhancing the strength of the feedback from mechanical stress above that resulting from microtubule reorientation alone (Zhao *et al.*, 2020; Fig. 1m). Disruption of microtubule orientation with oryzalin resulted in cell divisions occurring perpendicular to the abaxial–adaxial axis and further exacerbated the loss of the flat-leaf phenotype caused by the microtubule disruption (Fig. 1n).

More indirectly, cell division alters the neighbourhood of the cell. It has been proposed that the new cell wall may be placed to preserve topological relationships, although the results are usually indistinguishable from the shortest path (Gibson *et al.*, 2011; Carter *et al.*, 2017; Jackson *et al.*, 2019). Changes in the immediate topology of a cell alter the tension in the walls and lead to heterogeneity in the turgor pressure values (Long *et al.*, 2020). Cells with fewer neighbours have higher turgor pressure. In wild-type meristems the higher pressure in the small cells correlated with them having a higher growth rate that could potentially lead to cell size homeostasis and also cell division increasing growth. The vacuole can also be asymmetrically distributed between daughter cells in asymmetrical divisions potentially leading to turgor pressure differences (Kimata *et al.*, 2019).

VII. Conclusion


The direction of mechanical stress is a better predictor of cell division orientation compared with cellular geometry (Louveau *et al.*, 2016a). This is likely to be due to the prominent role of microtubules in guiding cell division orientation (Besson & Dumais, 2011; Chakraborty *et al.*, 2018) and their role as integrators of local and global mechanical stress (Sampathkumar *et al.*, 2014). However, further investigation is needed to understand the apparent exceptions. The consequences of cell division aligning with mechanics stress are not yet fully understood, but it may make the divisions more sensitive to tissue scale features, such as tissue curvature or differential growth that can change the directions of mechanical stress. This possibility of tissue-level coordination of cell division orientation is exciting and could help our understanding of how cells and tissues coordinate their behaviour during development. There is also some evidence that cell division can change mechanical properties (Michels *et al.*,

2020) and stress locally (Sapala *et al.*, 2018; Long *et al.*, 2020) that may affect growth directly or by changes in the orientation of mechanosensitive proteins (Hamant *et al.*, 2008; Nakayama *et al.*, 2012). While there are still many unknowns this could suggest a tighter feedback between cell division and overall growth. Further advances in this field will improve our understanding of the relationship between cells and tissues.

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