

COMMENTARY

Forces behind plant cell division

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The cell theory developed in the early 19th century teaches us that only cells beget cells (1). As a consequence, the evolution of life on Earth is but a long sequence of cell divisions; wherever this sequence is broken, life ends. Cell division is not only how organisms perpetuate themselves, it is also one way in which complexity is built during development. The contribution of cell division to development is particularly striking in plants because plant cells are surrounded by stiff walls, making them clearly distinguishable from each other and fixing their spatial relation by preventing cell migration. As a result, many of the first microscopic observations ever published are of regularly organized cells within plant tissues. Based on these observations, many theories were put forward to explain how plant cells select their axis of division. The most perennial cell-division theory emerged from the work of Sachs (2), Berthold (3), and Errera (4), who posited implicitly that cells “sense” their shape and are therefore able to divide into two daughter cells of equal size separated by a cell wall of the least possible area. Although many exceptions are known to this division rule, it is probably fair to say that a majority of biologists, then and now, have been inclined to accept geometry as a basic element of how plant cells select their division plane. During the same period that various geometrical division rules were debated, a competing theory emerged: cells could be responding to large-scale tensional fields when selecting their plane of division (5). Evidence of this has come mostly in the form of experimental treatments, whereby the application of global physical constraints on a growing tissue can align new cell-division planes (5–8). Despite a century of coexistence, the two theories—least-area division plane vs. tensional fields—have never been reconciled. A contribution by Louveaux et al. in PNAS may have just tipped the balance in favor of wall tension as the most fundamental determinant of plant cell division (9).

Louveaux et al. (9) present two new experimental results indicating that wall tension is important in determining the position of the division plane. Their first result emerges from a careful analysis of cell division within distinct regions of the *Arabidopsis* inflorescence meristem. Whereas the great majority of cells

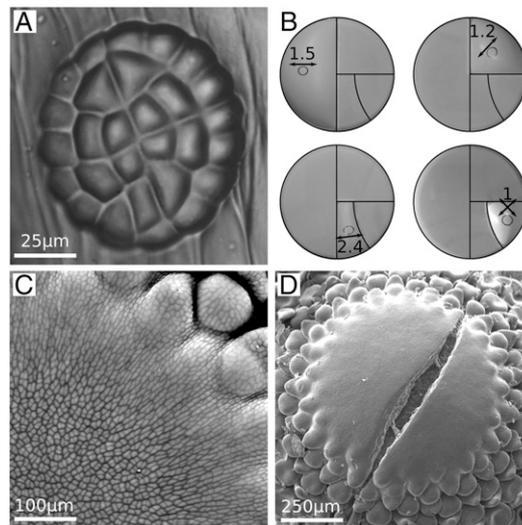


Fig. 1. Plant cell division under local and global tension. (A) The glandular trichome of *Dionaea muscipula*, a classic example of a division pattern compatible with a least-area division rule. (B) Simple membrane models indicating that the direction of maximal tension shown by the deformation of circles coincides with the division planes observed in the gland cells. (C) Electron micrograph of the inflorescence meristem of *Zinnia elegans*, where an isotropically growing central region (lower left corner) gives way to a zone of pronounced radial growth (arc spanning the upper left to the lower right). (D) The gapping pattern of a transverse cut indicates the presence of a large radial tension (leading to ~10% strain) and circumferential compression in the zone of organogenesis.

follows closely a least-area division rule, some cells deviate markedly from such as a rule and, more importantly, these cells are located principally in the highly curved creases separating the meristem proper from emerging primordia. Previous investigation from the same group had inferred the presence of strong tensional stresses along the axis of the crease (10). The alignment of the division planes with the direction of maximal tension and not with the shorter axis of the cell has led Louveaux et al. (9) to conclude that stress is a better predictor of the orientation of the division plane in this region.

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Author contributions: A.G., S.G., and J.D. designed research; A.G. and S.G. performed research; and J.D. wrote the paper.

The authors declare no conflict of interest.

See companion article 10.1073/pnas.1600677113.

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To test more specifically the role of stresses in directing cell division, Louveaux et al. (9) proceeded to produce lesions within the central region of the meristem, where the least-area division rule is normally a robust predictor of division plane orientation. To their surprise, the authors found that divisions were now redirected to be mostly parallel to the free edges created by the lesion, irrespective of cell geometry. The mechanical interpretation of this experiment is based on a classic result in mechanical engineering that edges of a plate or shell cannot support loads perpendicular to their free surface. Thus, the ablation must have released all of the tensions leading to its free edges but left the tensions parallel to the edge unaffected. The latter tensions would have directed the cells to divide parallel to the free edge.

Based on their results, Louveaux et al. (9) put forward the following general division rule: plant cells align their division plane in the direction of the greatest tension present in their wall. The wall stresses experienced by a cell are the superposition of two distinct sources of stresses: the cell's own turgor pressure and what have been called tissue stresses. In the shoot apical meristem, tissue stresses reflect the collective turgor pressure of the cells located within the inner tissue layers of the meristem. It is thought that a substantial fraction of this "inner pressure" is transferred to the cells of the tunica (11, 12). Because there is no way for the cell to distinguish between the two sources of stresses—both are experienced as tensions within the wall—Louveaux et al. (9) suggest that the cell will align its division plane with the direction of greatest tension as a whole. This hypothesis immediately raises two questions that will have to be answered fully before we can safely say that tensional forces within the cell wall are what align the division planes of plant cells.

First, the direction of greatest turgor-induced tension in the cell wall must coincide with the prediction inferred from the least-area division rule for a broad range of cell geometries. This step is essential because many papers have shown a clear relation between cell geometry and the alignment of the plane of division (13); hence, tensional fields must coalign with the shorter axis of the cell in those systems. To convince ourselves of the potential validity of this statement, we performed a simple experiment to test the predictive power of the maximal tension division rule for the regular cell patterns observed in glandular trichomes (Fig. 1A). This cellular arrangement was one of the first to be presented as supporting evidence for a least-area division rule (3, 14, 15), and therefore holds a special place in the heart of would-be cell-division geometers. Using an inflated elastic membrane to reproduce the force equilibrium in complex cell geometries, we found, to our surprise, that the direction of maximal tension in the elastic membrane is also the observed direction of cell division. Moreover, the magnitude of the stretch asymmetry correlates well with how reliably a given division plane is adopted by the cell (Fig. 1B) (13). Although these observations are

promising, more work will be needed to prove without doubt that turgor-induced stresses are compatible with a least-area division rule, and therefore may be the true determinant of the plane of division.

Second, where there is evidence for strong and directed tissue stresses, the division plane must comply with the direction of maximal tissue tension irrespective of cell geometry. In other words, the results for the primordium crease presented by Louveaux et al. (9) must be repeated elsewhere. Unfortunately, quantitative analyses of stresses in growing plant tissues are challenging; therefore, it is

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not trivial to point to systems where tissue stresses are known to be of such magnitude that cell-bound turgor stresses are irrelevant. One promising system is the sunflower hypocotyl, where tissue stresses in the epidermis reach 2.4 MPa, which is approximately five times the turgor pressure of these cells (16). An analysis of cell division in this structure would be interesting. Our own observation of large and anisotropic elastic strains in inflorescence meristems would suggest important tissue stresses in those organs as well (17). The inflorescence meristem of *Zinnia elegans* is particularly interesting because the cells populating its central region are known to follow a least-area division rule (Fig. 1C) (13), whereas the cells of the peripheral zone show evidence of strong radial anisotropy in their growth (Fig. 1C), suggesting that tissue stresses may have a strong radial component in this region. This conclusion is confirmed by incisions whose gaping pattern suggests the presence of radial tension and perhaps circumferential compression in the peripheral zone (Fig. 1D) (17). Here, however, division planes are preferentially aligned with the circumferential direction and thus orthogonal to the inferred alignment of maximal tension. Obviously, this type of system must be studied carefully to ascertain whether large tissue tensions can reliably overrule the division plane dictated by cell geometry.

Although the two cell-division theories may seem completely orthogonal, they both have been ascribed to cytoskeletal dynamics, although in one case the cytoskeleton is purported to sense cell shape (13, 18), whereas in the other case the cytoskeleton would respond to wall stresses (10, 19, 20). Thus, the two theories may have more in common mechanistically than might be expected at first sight. With their work, Louveaux et al. (9) have managed to bring wall stresses to the forefront of cell biology. Even though many details remain to be ironed out, future studies of plant cell division cannot neglect stresses as a possible contributor to the cell-division process.

Acknowledgments

Research in the J.D. laboratory is supported by Fondecyt (grant #1130129) and Fondef IDeA (ID15110387), Chile.

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