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Cellular basis of growth in plants: geometry matters

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The growth of individual cells underlies the development of biological forms. In plants, cells are interconnected by rigid walls, fixing their position with respect to one another and generating mechanical feedbacks between cells. Current research is shedding new light on how plant growth is controlled by physical inputs at the level of individual cells and growing tissues. In this review, we discuss recent progress in our understanding of the cellular basis of growth from a biomechanical perspective. We describe the role of the cell wall and turgor pressure in growth and highlight the often-overlooked role of cell geometry in this process. It is becoming apparent that a combination of experimental and theoretical approaches is required to answer new emerging questions in the biomechanics of plant morphogenesis. We summarise how this multidisciplinary approach brings us closer to a unified understanding of the generation of biological forms in plants.

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Introduction

A cell's geometry and its spatial relations to its neighbors (i.e. tissue topology) is an essential part of its biological functions [1]. Cell shape and size also reflect mechanical constraints imposed by the tissue and the external environment during development. The growth of a plant cell occurs when the rigid cell walls surrounding it yield under turgor pressure. As turgor acts equally in all directions, cell walls may be considered as the main determinant of growth [2]. Understanding cell wall mechanics is, however, not sufficient to draw a full picture of cell growth regulation. One also needs to consider cell geometry, as it determines the mechanical stresses ultimately driving growth. While 'morphodynamics' describes the process of patterning and expansion at the organ level [3], the term 'morphomechanics' would better fit the complex feedbacks regulating cell growth [4].

Progress in live-imaging and the development of quantitative image analysis allow a better characterization of cellular growth in 3D [5,6]. Moreover, new approaches permit more accurate measurements of the physical properties of cells and tissues [7,8•,9–11]. The development of computational modeling also continues to propose testable hypotheses for how cellular mechanics controls growth [12,13••,14,15]. In this review, we will discuss recent advances that bring us closer to the understanding of the cellular basis of plant growth, highlighting the role of cell geometry in this process.

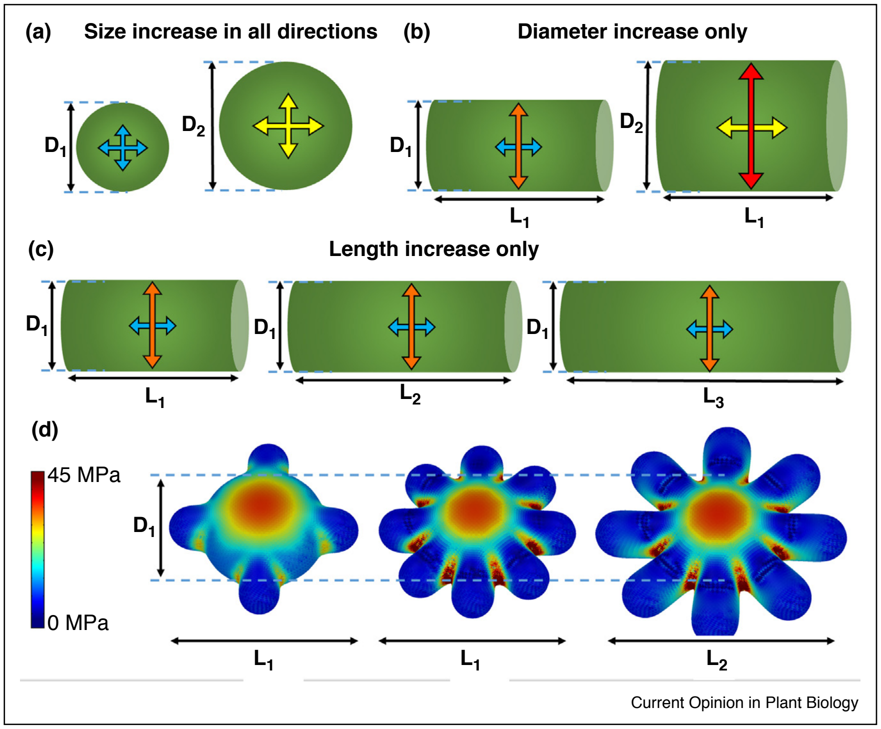
The growth of an isolated cell

An essential driver of growth in a plant cell is the internal turgor pressure, which typically compares to the pressure of bottles of champagne (~0.5 MPa) [9,10]. Turgor is uniform within all cell compartments. The cell membrane is however too soft to bear such pressure and would burst without support. Turgor is instead transmitted to the cell's surroundings, stretching the cell wall. The resulting elastic deformation of the cell wall can be translated into growth by the action of wall remodeling enzymes and the addition of new wall material [2].

Computer simulations can be used to predict the mechanical stresses generated by turgor pressure in individual cells, both in tissues [12,13••,16] and in isolation [7,13••,14,17]. Isolated cells — such as unicellular algae or trichomes — are free to grow without the mechanical constraints imposed by surrounding tissues, simplifying the mechanical picture. When the cell wall is assumed to be completely uniform, the predicted distribution of stresses of an isolated cell depends entirely on cell geometry (Figure 1). First, the average cell stress increases with cell diameter [13••,16]. Second, stress patterns depend on the cell shape. Spherical cells have the same stress in all directions. In elongated cells, the mechanical stress is anisotropic, with higher values around the circumference and lower along the main axis of the cell [7]. Importantly, the length of a wiry cell has no influence over its mechanical stress, only its diameter does (Figure 1).

How do the predicted stress patterns correlate with growth of a given cell? Surprisingly, the areas with a lower stress inferred from cell geometry often grow the fastest (Figure 2). Tobacco cells in culture or pollen tubes elongate against predicted stress patterns, keeping the diameter of the cell constant [7,18]. Growth in trichomes

Figure 1



Cell shape and size control mechanical stresses. Living plant cells are under a high hydrostatic pressure, resulting in mechanical stresses in their cell walls. These stress patterns can be entirely predicted based on the geometry of the cell, either analytically for simple shapes or by computational simulations for more complex ones. **(a)** Stresses in spherical cells are uniform and equal in all directions (isotropic). They are directly proportional to the cell size. **(b)** In a cylindrical cell, stresses are proportional to the cell's diameter, with the circumferential stress always two times larger than the longitudinal stress. **(c)** Increasing cell length has no effect on the stresses (cell diameter is the only dimension relevant to mechanical stress). **(d)** In an idealized lobed cell, the relevant dimension would be the diameter of the largest 'open space' within the cell, which bears the highest mechanical load. The number of lobes or their length as no impact on the maximal stresses in such a cell (colormap: the sum of local stresses in MPa, adapted from Ref. [13••]).

takes place principally at the tip of their branches, again where stress is lower [14] (Figure 2). Some plant cells can massively increase in size, but they must do it in a smart way to minimalize stresses and maintain mechanical integrity. Fiber-shaped cells can grow long without bursting, as the cell diameter and mechanical stress is kept constant (Figure 1c). In case of planar growth (e.g. leaf blade), cells usually develop complicated shapes. Adopting a puzzle shape enables leaf epidermal cells to grow in both directions, while keeping mechanical stresses relatively low. Using finite element method (FEM) simulations, Sapala *et al.* showed that the maximal stress acting on pavement cells is unrelated to the length or number of cell lobes [13••]. Instead, the highest stress is developed in the cell center, which is the largest region of the cell surface that is not 'anchored' by anticlinal walls (perpendicular to the organ surface). By growing lobes instead of the cell center [19], pavement cells can expand while limiting mechanical stress. It is worth noticing that elongating cells use similar rules to grow: they expand in length — which doesn't influence stress—while keeping a constant diameter — which dictates the stress (Figure 1d).

The clear difference between stress distribution and growth of the cell (Figure 2) suggests that cell wall mechanical properties can override the stress patterns created by cell geometry. Both cell wall structure and composition regulate cell wall mechanics and growth (Figure 2b). The plant cell wall is a network of cellulose microfibrils linked with each other by hemicellulose and embedded in a pectin matrix [2]. Cellulose microfibrils are rigid and their orientation defines the directionality of the wall extensibility that allows anisotropic growth. The deposition of cellulose microfibrils is controlled by the cortical microtubules as they guide the cellulose synthases complexes [20]. Many studies show that microtubules can respond to mechanical stresses and align with the direction of maximal stress [21–23]. In the 60s, Paul Green already proposed that this microtubule response to stress could guide the orientation of cellulose deposition along the direction of maximal tension [24]. This