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Current Opinion in Plant Biology

Shifting foundations: the mechanical cell wall and development

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The cell wall has long been acknowledged as an important physical mediator of growth in plants. Recent experimental and modelling work has brought the importance of cell wall mechanics into the forefront again. These data have challenged existing dogmas that relate cell wall structure to cell/organ growth, that uncouple elasticity from extensibility, and those which treat the cell wall as a passive and non-stressed material. Within this review we describe experiments and models which have changed the ways in which we view the mechanical cell wall, leading to new hypotheses and research avenues. It has become increasingly apparent that while we often wish to simplify our systems, we now require more complex multi-scale experiments and models in order to gain further insight into growth mechanics. We are currently experiencing an exciting and challenging shift in the foundations of our understanding of cell wall mechanics in growth and development.

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Current Opinion in Plant Biology 2016, **29**:115–120

This review comes from a themed issue on **Growth and development**

Edited by **Doris Wagner** and **Dolf Weijers**

For a complete overview see the Issue and the Editorial

Available online 19th January 2016

http://dx.doi.org/10.1016/j.pbi.2015.09.008

Introduction

The cell wall is the final mediator of growth in plants, a gatekeeper of developmental processes. Complex genetic networks, intricate and interlaced hormonal signalling, dynamic sensing and responding to the environment: all regulate growth and form through this physical conduit. While several dogmas exist in textbooks that describe the mechanical role of the cell wall in growth, current research is revealing overlooked players, subtleties and complexities. In short, the foundation for our understanding of plant cell wall mechanics is shifting. Unifying new hypotheses with those of old, and developing ways to model the physical contribution of the cell wall to growth and development are stimulating challenges in plant biology today.

In an oversimplified sketch, the primary cell wall (that which undergoes growth during development) may be described as a network of cellulose microfibrils, connected by hemicellulose linkages, embedded in a pectin matrix. Along these lines, the commonly taught simple mechanical interpretation is as follows: the rigid cellulose microfibrils are ascribed the strongest mechanical role in the wall and provide growth direction, while hemicellulose provides extensibility and growth ability, and the pectin matrix holds everything together [1,2]. Within this review we will examine each of these major components and their traditionally ascribed roles in light of new research and computational modelling and identify some key outstanding questions and challenges.

Anisotropy, cellulose, and microtubules

In 1962, Paul Green referred to the orientation of cellulose fibres around a cell conducive to anisotropic elongation 'as hoops on a barrel' [3]. However, in Green's original work (in the giant internode cells of *Nitella*), he referenced exceptions [4]. Recent experimental work has recapitulated one of these old exceptions: when cellulose synthase tracks or microtubule orientation (used as a proxy for the most newly deposited cellulose orientation) is observed in elongating cells of the Arabidopsis hypocotyls, it is only the inner faces of epidermal cells that show alignment perpendicular to the growth direction, while the outer faces display more random alignments [5–7]. This highlights the complexity of the system and the need to investigate cell wall composition, heterogeneity and anisotropy at an increased level of detail. It is becoming increasingly evident that these exceptions stem, in part, from the fact that plant cells are usually part of tissues, themselves connected within an organ. This geometric structure and constraint will have a large influence on the ability of an individual cell to grow, and also on its growth direction [8]; a single cell in plants rarely has control over its own fate.

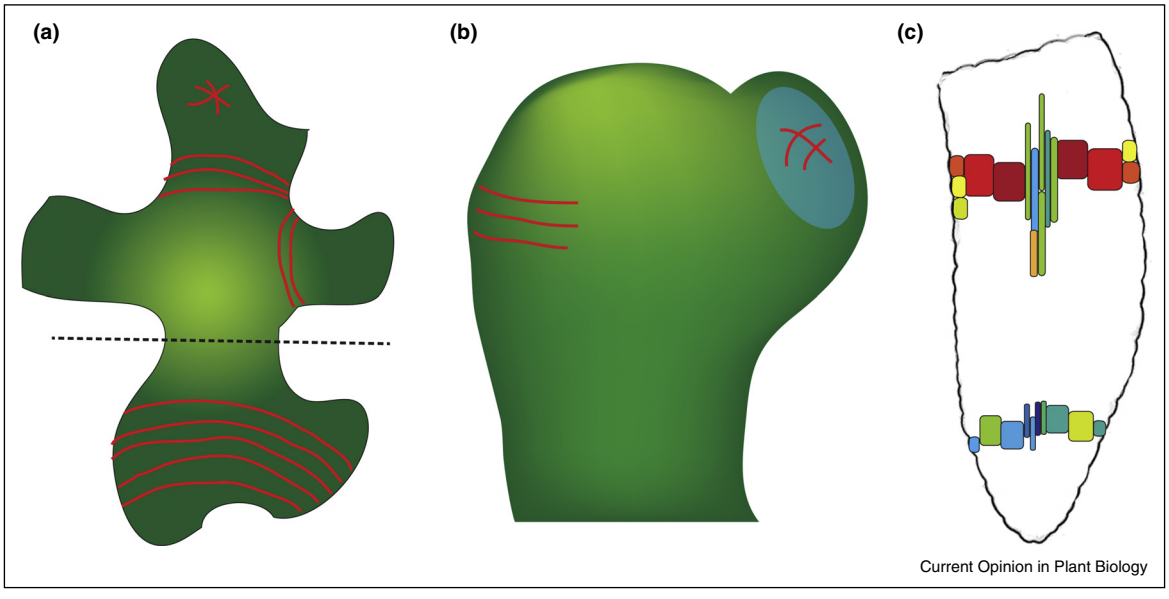
The key to unlocking anisotropy and its origin may lie in the responses of the cell wall synthesis machinery to predicted stress in the cell wall (See Box 1 for definition of terms). Microtubules direct the trajectories of cellulose synthase complexes in the cell membrane and thus affect the structure of newly deposited cellulose microfibrils within the cell wall [9–11]. Microtubules have been suggested to respond to stress and tend to reorient themselves

parallel to the maximum stress direction [12–14]. While the reorientation of microtubules with stress has long been postulated, it is only recently that this evidence has been revisited and reapplied in tissue contexts alongside geometry [12]. Computational efforts have also shown that stress-based feedback can robustly generate anisotropic growth while a strain-based feedback becomes unstable [15•]. These data suggest that growth and shape themselves do not inform upon anisotropy; but the stress they produce within the existing cell wall material does. While models strongly indicate a preference for stress-based anisotropy, it remains to be seen how cells might sense stress and translate this into cellular actions.

The interplay between a single cell and a cell within a tissue has recently been exemplified in studies of mature pavement cells in Arabidopsis [16••,17]. In both studies, cellular and supra-cellular microtubule patterns were assessed in pavement cells with and without external physical stresses. The general conclusions are that microtubules orient within a single cell based on cell-geometry-generated stress, but they also respond to tissue-level stresses based on tissue geometry or external load (Figure 1a). These data support the idea that while a single cell may act as a stress sensor and thus reorient its microtubules and cellulose fibres, the global tissue context and stresses also have an effect on these orientations. If we extrapolate these hypotheses back to stems, one might conclude that the outer face of epidermal walls is subject to different stresses from the inner wall, a hypothesis discussed in elegant detail by Baskin and Jensen; when the stem is considered as an assemblage of cells and not just a single giant cell, epidermal stress patterns become more complicated and can shift to the axial [8]. Moving from 2D or 3D cell descriptions to 3D descriptions of a tissue is a huge leap forward. However, the next challenge lies in extending models of cell wall mechanical anisotropy to encompass further layers and connections, and evaluating how stress and strain differ in a larger system, and how they influence growth.

Many early investigations simplified growing organ systems to one-dimensional descriptions. While this allowed for an initial interpretation of growth, a fully three-dimensional description of the tissue has led to constraints on possibilities for the generation of anisotropic growth. The need for a reinterpretation of mechanisms is becoming evident. Modelling efforts have been used to understand anisotropic growth in plant tissues and how tissue layers interact [18,19••,20,21•]. These efforts have revealed interesting insights, for example, small deviations in epidermal cell size from one side of an organ to

Figure 1



Examples of integrated experimental and computational work to elucidate morphodynamical events and mechanics in plant tissues, organs and cells. **(a)** Cell wall mechanics is influenced by cell shape, tissue geometry, and external forces. A representation of an Arabidopsis epidermal pavement cell with microtubules shown in red. Above the dashed line, microtubules align according to the stress pattern generated by the cell's own geometry, as predicted by models. Below the dashed line the microtubules have aligned to a hypothetic external force, either from the tissue geometry or an applied force. After [14]. **(b)** Organogenesis experiments and simulations demonstrate that a switch from anisotropy to isotropy (red lines) and a decrease in wall elasticity (blue) is required for organ emergence at the shoot apex. After [21•]. **(c)** Cell growth is influenced by a cell's context within an organ and tissue. Cell expansion derived from pseudo-growth tracking and modelling demonstrates that while all cells might have an equal capacity to grow, their tissue context alters their final expansion. Cell expansion in two regions of the hypocotyl from a germinating seedling is indicated by a colour scale from high to low (red to blue). After [17].

another may lead to bending [18]; and putative changes in wall structure will not necessarily drive growth unless in a geometrically favourable context [19••].

Tissue-based views of growing systems often include boundaries of isotropy and anisotropy. These can be generated by stress-based feedback models [15•], and similar boundaries in the single trichome cell are key to establishing their cell shape [22]. The boundaries might also have dynamics that are important for development: organ formation at the shoot apex results from an expansion of cells into a new plane from areas of highly oriented microtubules, necessitating a switch back to isotropy. A recent finite element model has demonstrated that a switch from anisotropic to isotropic material can promote organ outgrowth [23••]. Interestingly, emergence was most effective when an isotropy switch was combined with a general loosening of the wall (Figure 1b). In the model, these changes still lead to imperfect morphology, and to understand more complex morphogenesis, the relative contributions from surface and inner cell layers will be crucial (experimental example [24]). It is useful to point out that the majority of the data discussed above is from isolated cells or the epidermis alone. Further expansion of both observations and models beyond a single layer will literally add depth to our understanding of anisotropy and organ emergence. In particular, the discussed models provide evidence for a compelling feedback between molecular loosening (and 'isotropification') of wall mechanics and the resulting stress signal due to shape change. This feedback would robustly amplify morphogenesis, driven by changes at the surface. Experimentally, there is evidence for complex interactions between layers based on histology and more recently, on cell wall elasticity measurements in meristems (discussed and shown in [24]).

The role of hemicellulose in growth permission

Hemicelluloses (xyloglucan in particular) have been long implicated as agents of cell wall viscoplasticity or extensibility — the property relating irreversible cell wall deformation to applied stress [2,25,26]. Viscoplasticity is usually a term applied to wall material or single cell walls, whereas classical extensibility has referred to whole organ deformation or whole tissue deformation. The textbook model would describe xyloglucans as coating cellulose microfibrils and tethering them together. Severing of these tethers by modifying agents such as expansin would then lead to cell wall extension and growth, depending on the mircofibril orientation [2]. This model implies that whole-wall material viscoplasticity, underpinned by hemicellulose, has the most bearing on whole organ extensibility. Interestingly, recent enzymatic analysis of cell wall structure and mechanics indicates that such load-bearing xyloglucan might only exist in small areas, 'hot spots', of cellulose-cellulose contact [26,27]. These 'hot spots' seem less able to contribute to viscoplasticity [26] but perhaps more likely to yield of the wall. It is perhaps the most exciting and excruciating fact that the heterogeneity of the cell wall is its most important yet impenetrable mechanical characteristic.

Strikingly, mutants in Arabidopsis completely lacking xyloglucan were dwarfed but capable of growth and development [28]. Recent analysis by two teams has demonstrated that this growth ability is likely due to compensation within the cell wall by other components such as the pectin matrix [29,30]. It has also been posited that pectin might be an important linker between fibre elements important for achieving wall stiffness [31]. Lastly, tip-growth (e.g. pollen tubes) occurs where the wall is only pectin [32]. This block of research highlights two important points. First, while the cell wall is a heterogeneous and complex material, we often consider its composite mechanical behaviour in terms of continuous behaviour. However, if we wish to understand how the wall acts as a material, we require finer resolution of its structure and dynamics on these finer scales. Secondly, as the primary wall is a dynamic part of the cell, a compartment which is continually changing in response to external influences and internal cues, the nature of feedback regulation needs to be considered carefully when hypotheses are generated, since it can often generate results which differ largely from our intuition.

The integral role of xyloglucan in growth and development has been best analysed through ectopic-expression and overexpression of modifying agents. Overexpression of several xyloglucan endotransglucosylase/hydrolases (XET/XTH) in Arabidopsis leads to more pliant hypocotyl tissue with a lower yield threshold, although extensibility was unaffected [33]. Similar data were obtained in *Solanum lycopersicum* hypocotyls with overexpression of a tomato XET, and the converse was found in co-suppressed transgenics [34]. In germinating Arabidopsis seedlings, deviation in the expression of xyloglucan and expansin genes and the maximal growth rate was observed; a full 3-D finite element plate model of the same system led to hypotheses that growth rate was highly influenced by cell geometry, hence mechanics (Figure 1c, [19••]). An alternative view might be that there is a time delay between expression, action, and physical result. A further step in this modelling might involve changing parameters such as time, pressure, wall elasticity, thickness and anisotropy to assess the role of feedback within the system and the depth of influence of stress versus strain (an example in part [35•]). In the case of rapid cell elongation (in the hypocotyl), there is ample evidence for altered wall thickness during shape change, a property which likely has effects on wall strength and strain [36].

It is interesting that extensibility was not necessarily increased by XET/XTH activity. This indicates a more

complex relationship between the wall components and theoretical extensibility, and links back to xyloglucan 'hot-spots' which may not contribute significantly to extensibility or viscoplasticity. Recently, the pectin matrix has been proposed as an extensibility mediator (in postyield walls) in mathematical models [37]. Although perhaps intuitively obvious, recent data now support a complex feedback description of cell wall extension extending beyond hemicelluloses.

Pectin and growth permission

In earlier sections we have seen evidence and hypotheses indicating roles for pectin in cell wall mechanics (e.g. 'hot spots' and models mentioned above). NMR analyses of cell walls extracted from young Arabidopsis seedlings indicate that roughly 50% of the cellulose surfaces are associated with pectin and removal of pectin disrupted the mobility of cellulose within the material [38]. One cannot help but contrast this with the very low percentage of functional xyloglucan–cellulose associations described above. Recent work suggests that the chemical state of the pectin matrix may be vital for growth permission. In shoot apices of Arabidopsis, changes in homogalacturonan pectin esterification are essential for organ emergence, and these changes are triggered by auxin accumulation [24,39]. These changes in pectin chemistry are linked to changes in cell wall elasticity, measured at the cellular level by atomic force microscopy [24,39]. It is worth noting that there are contradictory reports in the literature regarding which chemical change in homogalacturonan leads to increased elasticity: in Arabidopsis meristems de-esterification leads to softening [24,39]; in pollen tubes the opposite is true [32]. Recent work in Arabidopsis hypocotyls seems to support the meristem case [40]. There are likely strong influences here based on the tissue being studied and the enzymes involved.

In order to gain a plausible idea of how growth might be effected, we must also recall the previously mentioned work in meristems with respect to isotropy appearing in an anisotropic domain at organ initiation [23••]. In combination these yield a hypothesis whereby auxin accumulation triggers an increase in wall elasticity via pectin, allowing more mobility in cellulose fibres, allowing for geometric change, increasing isotropic stress in the wall, thus triggering a break in microtubule anisotropy and allowing organ emergence. This hypothesis is strengthened further by models suggesting that the reorientation of cellulose fibres in growing cells could be a passive process [e.g. [37]]. Xyloglucans could mediate wall extensibility pre-wall-yielding, while pectin could do so post-wall-yielding as might be the case in a meristem flank cell. While this scenario is attractive, it requires extensive experimental and theoretical treatment to be tested.

In a more general case, it is tempting to propose that pectin might be a mediator of cell wall extensibility and thus a gate-keeper of growth permission. Although thus far pectin has only locally altered wall elasticity, it is possible that elasticity might link to changes in extensibility as follows: directly by lubricating cellulose interactions; indirectly by altering the hydration status of the cell wall and thus affecting other components; or again indirectly by changing the diffusion of modifying agents in the wall [41]. It is also possible that changes in pectin chemistry do alter viscoelasticity but this has not been tested yet, on a wall or cellular scale. These hypotheses all require experimental and theoretical investigation before we can hope to understand exactly how pectin might act mechanically within the growing cell wall.

Conclusion

The cell wall is a complex material whose structure is dictated by dynamic cellular processes and responsive both to external forces and to those generated by growth itself. The structure of the cell wall is currently understood only on a superficial level and recent advances in the literature demonstrate that our preconceptions were indeed naive and in some cases wrong. The dynamic changes in cell wall chemistry and underlying cellular components (i.e. microtubules) have only just begun to be characterised with respect to geometry, growth, and development. Furthermore, there are some serious hurdles in creating hypotheses and models that extend beyond single cells or single tissues to encapsulate the mechanics of an entire organ. Lastly, many models shy away from the geometric complexities of cell walls, which are themselves complex carbohydrate networks, or tissues which are structurally cellular solids. Given all of these unknowns — these shifting foundations — can we really attempt to model the mechanics of cell wall mediated growth and development?

Indeed, and now is the time to begin expanding our multi-scale understanding of wall mechanics, through new experiments and models. Increased sophistication in experimental methods and modelling have proven useful in starting to elucidate the interconnected roles of wall components within a wall, cells within a tissue, and tissues within an organ. As discussed in this review, we are on the verge of feeding models with subcellular measurements relating to individual cell wall components. Generating improved models at multiple scales will be essential in interpreting the experimental data. We are also just beginning to deepen our understanding of how the cell wall changes during development, both physically and chemically, as we uncover new roles for old players and new variations on old themes. Growth is not simply a result of loosened xyloglucan, direction not merely a result of 'hoops around barrels'; and growth itself is a composite property of components in walls in cells in tissues in organs.

Box 1 Glossary of mechanical terms

Stress: force per unit area, standardly in Newtons per square meter (N/m^2).

Strain: the deformation of a material, relative to its initial state (unitless).

Elasticity: the instantaneous and fully reversible deformation of a solid material under load. Maybe be measured in growing and non-growing plant material.

Viscoplasticity: the irreversible but rate-dependant deformation of a solid material under load. Rate-dependence here implies that the magnitude of the load will alter the rate of the deformation in time. Maybe be measured in growing and non-growing plant material.

Plasticity: the irreversible deformation of a solid material, usually occurring above a threshold. Maybe be measured in growing and non-growing plant material.

Extensibility: the ability of the cell wall material to deform irreversibly. This may include components of the material properties above, but also would include modification of the cell wall and addition of new material and is restricted to growing cell walls.

* Adapted from [42].

Acknowledgements

The authors thank FN Willson for editing and proofreading. Work in the authors' groups is funded by The Gatsby Charitable Foundation (GAT3396/PR4, SB; GAT3395/PR4, HJ), the Swedish Research Council (VR2013-4632, HJ), the Knut and Alice Wallenberg Foundation via ShapeSystems (HJ), and the BBSRC (BB.L002884.1, SB).

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