Micromechanics Governing the Undulation Patterns of Inter-Cellular Boundaries of Plant Epidermis Cells

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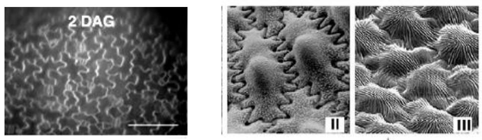
Summary Analytical and finite element models are developed for exploring underlying mechanisms of the formation of the undulation pattern of the inter-cellular boundaries of plant epidermis cells during growth. The wave-length and the critical compressive stress of the undulation patterns are derived as functions of the geometry (thickness of the cell wall) and material properties (Young's moduli and Poisson's ratios) of the cell wall and internal gel-like pectin core. The undulation pattern governs the mechanical integrity of the interface as well as the mechanical performance of assemblies of these cells while also increasing the surface area of the intercellular interfaces and hence influences intercellular processes such as transport or signalling. The analytical and numerical models can be used to derive biomimetic principles for bio-inspired active hybrid materials or actuating devices.

Introduction

Plant epidermis is an intermediate layer of cells between the outmost cuticle layer and the ground tissue. It is an important architectural control element that regulates the growth properties of underlying tissues and therefore the size and shape of the plant organ[1]. The inter-cellular boundaries of many plant epidermis cells exhibit a wavy undulating pattern[2] (sometimes even zigzag, as shown in Fig.1), such as the epidermis cells of *Arabidopsis thaliana*, *Panicum javanicum*, and the seed coat of *Viscaria vulgaris*. It is widely taken as an axiom in botany that, during growth, the plant cell wall constrains the rate of cell expansion and limits the final cell size, and the mechanical properties determine the volume and shape changes of plant cells, although experimental data to directly support this axiom is absent [3]. In this investigation, we developed analytical and numerical mechanical models to explore the underlying mechanisms and the role of cell walls in the formation of the undulating patterns of the inter-cellular boundaries of plant epidermis cells during growth.



(a) (b)

Fig. 1 Patterns of plant epidermis cells in nature, (a) visualization of epidermis cells of *Arabidopsis thaliana* at different time points after germination [1] (bar: 100μm, DAG: days after germination, (b) SEM micrographs showing undulation pattern of cell boundaries [2].

Mechanical Modeling

Each plant cell consists of stiff semicrystalline cellulose fibrils, cross-linked by hemicellulose polymers, embedded in a gel-like matrix of pectins. We postulate that the undulation pattern of the intercellular boundaries of the epidermis cells is caused by the local instability of cell walls due to the compressive stress arising in the walls due to the constrained growth of the cells. Since plant epidermis cells are constrained by the cuticle layer and the ground tissue underneath, cell growth occurs preferentially within the plane of the epidermis. Therefore, the cellular structure of plant epidermis is approximated at a planar structure where the cells are modelled as a soft gel encapsulated within a very thin but relatively higher modulus cell wall (captured mechanically as a "shell" or "beam"). To explore the underlying mechanisms of the local buckling instability of cell walls during cell growth, both analytical model and finite element models are developed to quantify the relationship between the characteristics of the undulation pattern and material properties and the geometry of the cell walls and the cell core.

An analytical model

A schematic of a mechanical model of the cell wall is shown in Fig.2, in which an infinite long beam is perfectly bonded to an elastic medium on both sides. The Young's modulus and the Poisson ratio of the beam are E_1, v_1 and those of the matrix are E_0, v_0. This structure is assumed to have a unit width, and a rectangular cross-section, with thickness t, and is subjected to in-plane compression.

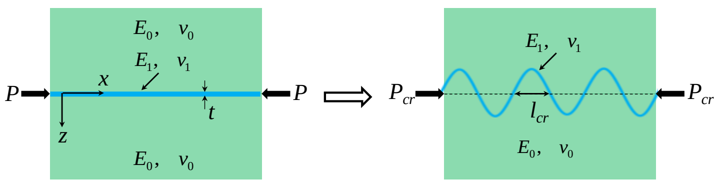


Fig.2 Schematic of the mechanical model for cell wall wrinkling (beam embedded in elastic matrix).

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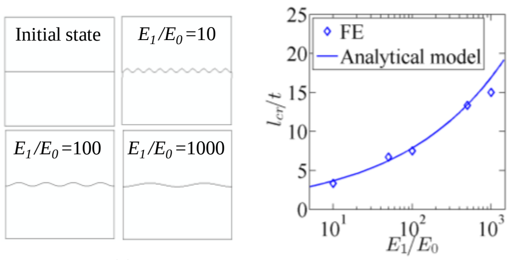
An analytical model is derived which builds on earlier models which had determined the instability of a beam supported on one side by an elastic medium [4,5]. Here, we derive the instability conditions, including the critical stress σ_{cr} and the resulting non-dimensional wavelength $\frac{l_{cr}}{t}$, for the buckling of a beam supported embedded within an elastic medium (i.e., top and bottom surfaces of the beam are adhered to the elastic medium). The instability patterns are obtained as functions of the stiffness ratio $\frac{E_1}{E_0}$ between the beam and the matrix materials and the Poisson ratio of the matrix υ_0.

The analytical derivation is verified by finite element simulations. In the simulations, the loading conditions are generated by the constrained thermal expansion of the beam, emulating a growth of the core. Periodic boundary conditions are used at the boundaries. Finite element simulation results of the wavy patterns of the beam are shown in Fig. 3. Figs. 3(a) and 3(b) show that the new analytical model is quite accurate for a large range of stiffness ratio.



(a) (b)

Fig.3 Comparison of the results of analytical derivation and the finite element simulations, (a) finite element simulation results of the undulation patterns for various stiffness ratios. (b) nondimensional wavelength vs. stiffness ratio.

Finite element simulations of the undulation pattern of hexagonal epidermis cells

To mimic the growth of an array of plant epidermis cells, finite element models of a periodic hexagonal array of epidermis cells with edge length 35μm and wall thickness *t*=1μm are constructed as shown in Fig. 4. For simplicity, the cell core and wall materials are each taken to be homogeneous, although the cell walls are usually a composite like material reinforced by cellulose fibrils [3]. The wall and core materials are modelled as hyperelastic and mechanically incompressible using a Neo-Hookean model, where the core material shear modulus is G_0=0.18 MPa and the cell wall shear modulus is G_1 = 10, 100 and 200 MPa as shown in Fig. 4. Both matrix and walls are subjected to constrained thermal expansion to mimic cell growth.

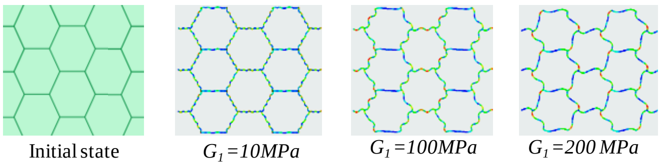


Fig.4. Simulation results of the undulation pattern of the finite element hexagonal epidermis cell model (*t*=1μm) for various cell wall stiffness.

CONCLUSIONS

As quantitatively predicted by the present analytical mechanical model of cell undulation, when the stiffness ratio between the wall and matrix increases, the non-dimensional critical compressive stress decreases and the non-dimensional wavelength increases, as shown in Fig.3. Furthermore, finite element simulations of the hexagonal cell model qualitatively capture the undulation pattern observed during the diffuse growth of plant epidermis cells. By tailoring the stiffness ratio, a similar pattern to Fig. 1(a) can be obtained, as shown in Fig.4. The hexagonal cell model has a more complicated geometry than the analytical model. Nevertheless, when the stiffness ratio increases, the numerical results of the characteristics of the undulation pattern of the hexagonal cell model show the same trend predicted by the analytical model. The analytical model together with the numerical approaches have a great potential to be used to derive biomimetic principles for bio-inspired active hybrid materials or actuating devices. In particular, the change in the mechanical performance of the interfaces with changes in wavelength and its impact on the overall mechanical performance of the multi-cellular structure together with the increased inter-cellular surface area on other properties (e.g., inter-cellular transport) are direct outcomes of this growth-induced inter-cellular boundary. In addition, the modelling results can provide deeper insights into the morphogenesis and phenotype diversity of plant epidermis cells.

References

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