Using mechanics in the modelling of meristem morphogenesis

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Introduction

Shoot apical meristems are small groups of rapidly dividing, undifferentiated cells, which generate all aerial parts of the plants. Recently, spectacul ar advances in molecular biology and genetics have provided a wealth of information on meristem functioning. However, the amount of available information is now such, that an integrated view is no longer possible. As a result, researchers have been led to develop computational models in the form of *virtual meristems* to analyse this complexity *in silico* and to test different hypotheses. Only very recently three such models have been described [10, 1, 5]. All three are able to integrate various cell-based processes and show different emerging behaviours (e.g. meristem maintenance, phyllotaxis). This pioneering work has demonstrated that the *in silico* analysis of plant development can be an extremely useful complement to classical experimentation.

Previous models have focused their interrogations on physiological processes in the meristem for a given, predefined, tissue shape. However, in nature, the shape itself is the result of a continuous feedback loop between physiological information and growth. As suggested by [4, 2], the mechanical components of the cells could provide such a link. In this work, we consider the problem of integrating such a feedback loop in meristem development.

The role of mechanics

As physical objects, cells obey mechanical laws. In plants, a major factor controlling cell shape is the cell wall, which resists to the internal turgor pressure and guarantees the final shape of the cell [9]. Turgor (Π_0) induces mechanical constraints ($\underline{\underline{\sigma}}$) into the walls :

$$\mathrm{div}\underline{\underline{\sigma}} = \Pi_0 \tag{1}$$

Being elastic, walls deform and elongate to adjust to this stress. This deformation ($\underline{\underline{\varepsilon}}$) depends on mechanical properties of each wall which is caracterized by set of parameters (called tensor of elasticity, $\underline{\underline{\underline{\underline{K}}}}$):

$$\underline{\underline{\sigma}} = \underline{\underline{\underline{\underline{K}}}}(\underline{\underline{\varepsilon}} - \underline{\underline{\varepsilon^0}}) \tag{2}$$

The equations of mechanics (1 and 2) allow us to compute the elongation ($\underline{\underline{\varepsilon}} - \underline{\underline{\varepsilon^0}}$) of each wall (and thus each cell) for a given state (turgor pressure). However, to obtain a given shape, elastic deformations are not sufficient and plants must add material into the walls to achieve some plastic deformation. One biochemical hypothesis [3] is that cells add material to fill the void between cellulose microfibrils in the wall. The more the wall is stretched, the more gaps are being created between fibrils, the more material must be added to the wall. This modifies the reference state ($\underline{\underline{\varepsilon^0}}$) of the wall and thus growth is increased in the direction for which ($\underline{\underline{\varepsilon}} - \underline{\underline{\varepsilon^0}}$) reaches maximum. By synthesising expansins (e.g. auxin) that change cell walls' elasticity ($\underline{\underline{\underline{\underline{K}}}}$ and then $\underline{\underline{\varepsilon}}$) or wall *repair* rate (parameter G in equation 3), meristem shape can emerge fom cell physiological properties.

Mechanical model of meristem surface

In *Arabidopsis*, the external cell layer (called L1) plays a crucial role in meristem functioning [6]. To build up a mechanical model of this surface, we projected the L1 cells on the external surface of the meristem to obtain a polygonal mesh. Each polygonal cell is surrounded by the edges that stand for the projection of

its anticlinal walls, assuming an infinitely small thickness of the walls. A junction between edges is called a vertex. The behaviour of all inner cells of the meristem is summarized by an overall turgor pressure that perpendiculary pushes the surface and prevents the L1 layer from collapsing (as expressed in (d) on figure 1).

To describe the mechanical properties of a meristem the representation described above is expressed (as in [7]) in terms of a mass-spring system (MSS). Each edge e_i has an associated spring while masses are attached to the vertices. The mechanical behaviour of each spring is characterised by two parameters: a stiffness K_i and a rest length l_i^0. Growth is expressed as a change of spring rest length l^0 depending on the current spring tension :

$$\frac{\partial l_i^0}{\partial t} = \begin{cases} 0 & \text{if} \quad [l_i(t) - l_i^0] < \text{threshold} \\ G[l_i(t) - l_i^0] & \text{else} \end{cases} \tag{3}$$

where G is a growth rate. This change, in turn, induces a new mechanical state. A solver for particle systems [11] was designed to trace the shape evolution of the mesh.

This model was used to reproduce *in silico* the change of shape of the *Arabidopsis pin1* mutant depicted by Reinhardt [8]. This paper describes the emergence of a young primordium near the position of an applied patch of auxin. Cells with high auxin concentration grow faster, possibly due to the change in the mechanical properties of their walls. We simulate this behaviour by changing the mechanical parameters K of the springs associated with edges of the cells with high auxin concentration. In our model this resulted in faster, local growth in the *auxin-positive* region (in red on figure 1 (a)). The *bump* shaped structure, that appears, reproduces the appearance of a young primordium (simulation output presented in figure 1 (a)).

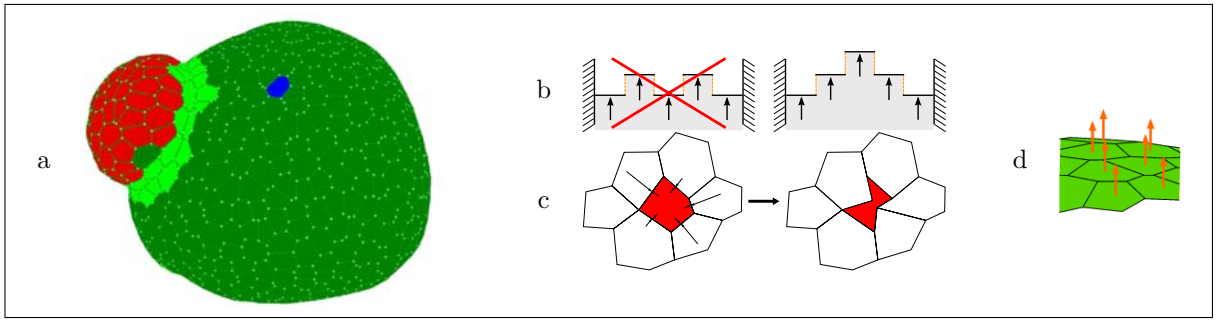

Figure 1: Model of meristem surface

This figure shows in (a) the modelling of *primordium* induction by an auxin patch applied in the red region. On (b), solid bars (horizontal segments, in black) are linked by elastic springs (vertical segments, in yellow). Extremities of the system are fixed. A pressure applied from bottom on the system will push all the bars to top. Crest formation is thus impossible. The red cell in (c) collapses due to the load of its neighbors. The explicit L1 layer representation (green poligons) with implicit inner cells (represented as pressure force – orange arrows) in (d).

Modelling only surface cells with 1D walls as springs is an efficient way to address meristem shape modelling. It allows fast computation of meristem shapes when testing different parameters of this complex system. In addition, the use of springs seems to be compatible with what is known on the biological system. In particular the concept of growing springs yielding to an inner force is clearly coherent with the idea of cell wall synthesis permitting the cells to yield to inner pressure. However, the implicit representation of the inner cells as a generalised pressure makes it impossible to generate more complex shapes (see figure 1 (b)). To model a crest instead of a bump, for instance, we need to explicitely represent the interior of the meristem. In addition, the use of MSS is suitable for small shape deformations but becomes less straight forward when dealing with more complex deformations. Because the link between two springs has no rotational constraint, cells under external load tend to collapse (see figure 1 (c)).

Mechanical model of meristem volume

To address complex shape changes, we need to model explicitly the interior of the meristem. The simplest conceptual way to do it consists of implementing a full 3D model of a tissue. In this model, all cells are

represented as polyhedra as shown on figure 2 (a). We assume that the wall between two cells remains planar and can thus be represented as a polygon in space. Wall mechanical properties are summarized by the two principal directions of the elasticity tensor in this plane. This assumption allows us to use the shell theory to compute strains and constraints in the meristem with a finite elements method. As in the previous model, growth is computed as a function of the amount of strain of the mesh standing for the meristem, parameterized by the physiological state of each individual cell.

The young carpels formed by the young Arabidopsis flower, arise together as a cylindrical shape on the top of the floral meristem. They provide a typical example of complex structure (see figure 2 (b)) previously described on figure 1 (b). The model makes it possible to simulate the result of a differentiation of a ringlike domain cells around the meristem center. These cells grow out more quickly than their neighbours, which is caracterized by a more rapid extension of the cell walls in the model. A 3D representation of this meristem shows the formation of the cylindrical *style tube* (see figure 2 (c))

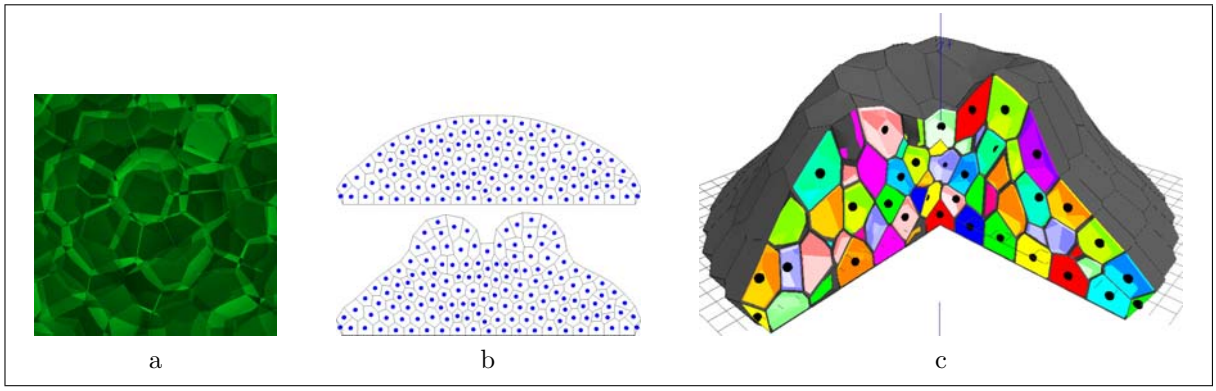

Figure 2: Carpel formation

(a) 3D meristem representation where cells appear as polyhedra. (b) Simulation of carpel development. From an initial state (on top) with a bump shaped meristem, the simulation runs to a crest shaped tissue (on bottom). (c) 3D representation of the final state of the simulation depicted in (b) that shows the formation of the *style tube*.

Conclusion

In the talk, we shall present the application of mechanical models to the integrated simulation of primordia generation and carpel development. We shall discuss how these models relate physiological information to meristem morphogenesis. By closing the feedback loop, they provide, a useful complement to previous models that mainly concentrated on physiological processes.

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