The role of mechanics in morphogenesis

Jérôme Chopard, Christophe Godin

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Chopard Jérôme and Godin Christophe
INRIA, Virtual Plants INRIA team, UMR DAP, TA A-96/02,
34398 Montpellier Cedex 5, France

jerome.chopard@sophia.inria.fr

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Introduction

In recent years our knowledge on the molecular basis of plant and animal development has made spectacular advances. For instance, the stereotypic positioning of the organs in plants starts to be well understood. Barbier [1], Jonsson [2], Smith [3] and Stoma [4] proposed similar models showing how local cell biochemistry (fluxes, creation and decay of substances) in the meristem could lead to emergent cell differentiation patterning at the scale of the organ. However, while these models provide a plausible explanation of how particular cells initiate organs in a non-random location, they do not provide any clue as to how the spatial patterns of gene expression are translated into a geometrical development of the organism into space.

More generally, very little is known on the link between the regulatory gene networks active in every cell and the specific changes in shape during morphogenesis. To address this issue, new adapted tools and approaches must be developed, in particular in the field of informatics and mathematics. In a pioneering work, Coen [5] proposed to decompose the complex problem of describing globally the change of tissue shape into a set of elementary geometrical transformations defined locally for each region, where regions divide the tissue into smaller entities that grow in the same way. This approach, however, does not address the question of how to maintain tissue coherence when two neighbor regions intend to grow at a different speed.

In the first part of this paper, we demonstrate that mechanics is a plausible choice to ensure that neighbor regions remain contiguous throughout time even if not growing at the same pace. Moreover, the mechanical state of the cell must be included as a state variable in the local decision process mediated by genes that defines the local growth of each cell [6]. Since measurements of the mechanical state of a tissue are lacking, in a second part, we will emphasize the use of virtual tissues to simulate the mechanical behavior of cells based on their real geometry.

Growth modeling

In the last decades, new optical tools have given us a good insight on the shape of cells and the precise definition of genetic expression patterns. However, measurements of cell growth are sparse and mainly limited to cells in the surface of organs. Still, a simple look at the images presented figure 1 shows a strong correspondence between the local descriptors of cell growth and the expression patterns of some genes.

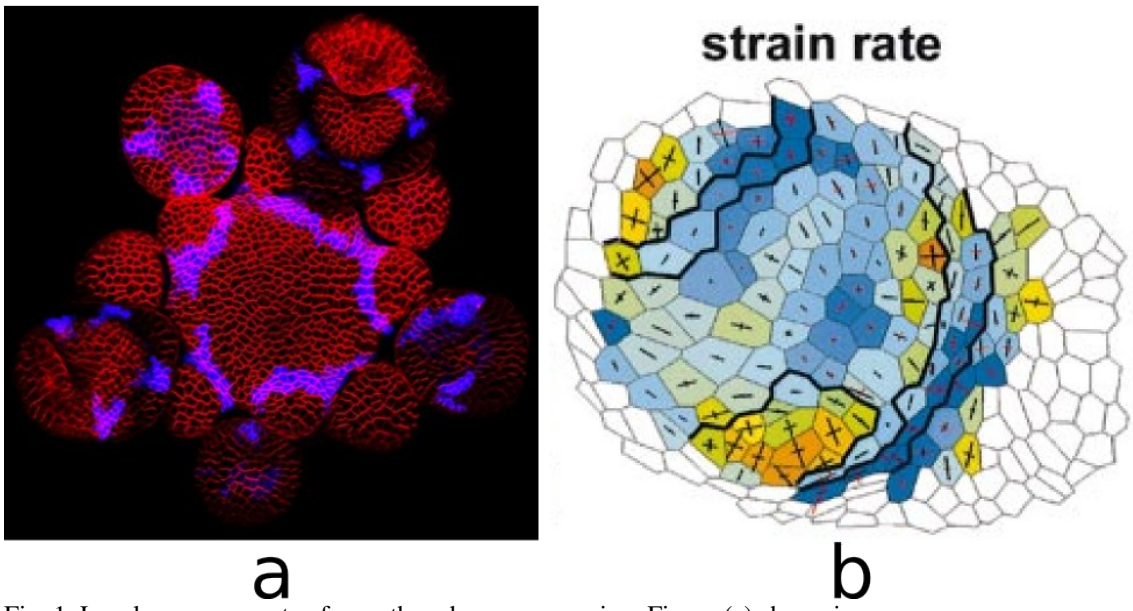

Fig. 1. Local measurements of growth and gene expression. Figure (a) shows in purple the expression pattern of the CUC gene (data Pradeep Das, unpublished). Figure (b) describes the growth measurements obtained on the surface of a meristem in [7]. Colors range from blue, small growth, to red that represent a bigger growth. The black cross represents the main directions of growth.

Hence, based on this correlation, a first idea would be, for a given cell i, to establish a direct link between gene activity (φi) and cell growth (Gi).

$$Gi = f(\varphi i) \qquad (1)$$

Since this approach does not take into account cell neighborhood, the coherence of the tissue would be extremely difficult to maintain between two physically connected cells that do not grow at the same pace. One way to account for these discrepancies is to introduce the elasticity of cell walls and allow a small deformation of each cell in order to maintain the continuity of the tissue and accommodate for local differential growth. In this new approach, the resulting growth is obtained as a balance between the potential growth ($Gp\ i$) defined by genes (φi) and the mechanical deformation (εi) necessary to maintain tissue coherence.

$$Gi = Gpi(\varphi i) + \varepsilon i \qquad (2)$$

A simple reasoning shows that this approach is not sustainable either. The accumulation of stress leads the tissue to break. To prevent this accumulation, mechanics must be introduced as a state variable in order for genes to take into account the current level of stress in the definition of cell growth. In this new model, the tissue is put under tension by turgor pressure. Then locally, genes decide or not to release a part of this tension through wall remodeling and synthesis. Leading to the growth of cells.

$$Gi = H(\varepsilon(\varphi i, P\pi)) \qquad (3)$$

With this approach, stress in a given cell wall is limited to a fraction of turgor pressure and the continuity of the tissue is ensured. Compared to equation 1, now genes do not appear directly in the expression of growth. Rather, they modify the mechanical state of the cell and this mechanical state is used as the main determinant of growth.

The importance of mechanical signaling has been demonstrated as a signal to orient the direction of microtubules [6]. In this paper, the authors measured a strong correlation between the local orientation of microtubuls and the principal direction of the stress encountered by a cell. This demonstration is indirect however, since, if the orientation of microtubules might be directly visualy measured, the amount of stress sensed by a given cell must be estimated. Classical measurements of stress that involve the measure of the deformation of small gauges are unavailable at this scale.

Virtual tissues

Recently, new methods of image analysis, provided access to the real geometry of cells. In the Virtual Plants team, we used these representations to develop a virtual tissue. Many measurements and simulation may be performed on this tissue including computation of the mechanical state of the tissue. This virtual tissue allowed us to test hypothesis on morphogenesis. Especially, two aspects have been studied:

- the role of the external layer of cells (L1) in the mechanical state of the tissue. A classical assumption considers that the L1 account for most of the resistance, the tissue is represented by a surface in 3D and the stress axis is oriented perpendicularly to the stem. If the tissue were a full solid, the stress would be isotropic. Real tissues are in between with a kind of hollow structure created by internal walls.

- the importance of frontier genes like CUC to establish sharp geometrical transitions between organs.

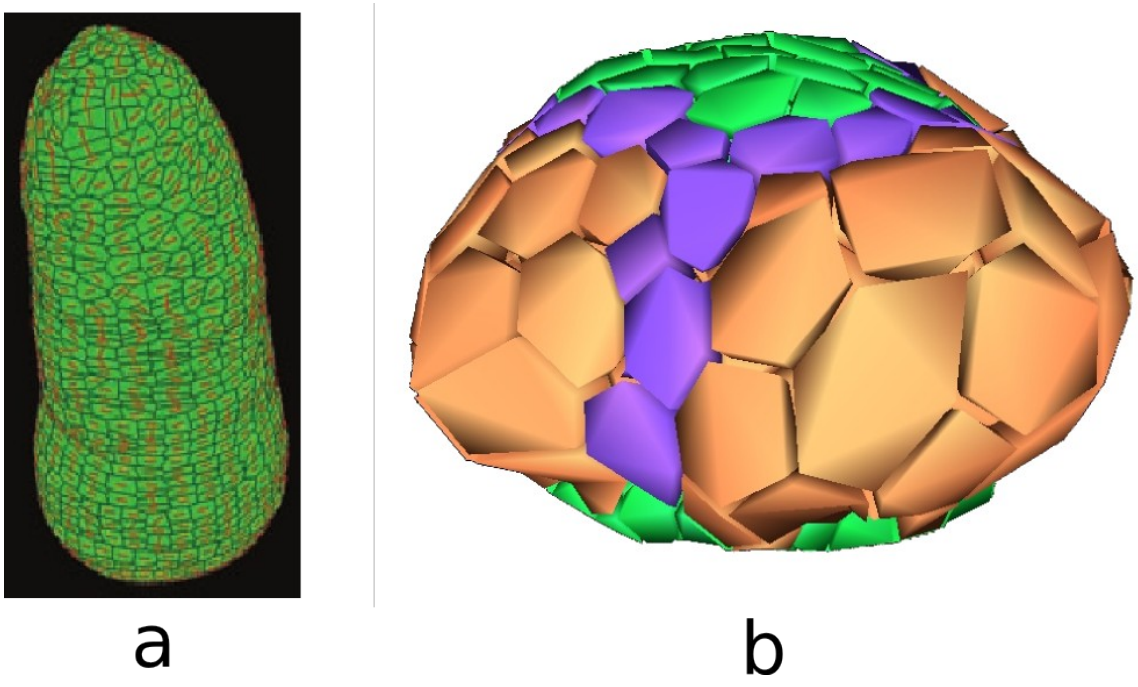

Fig. 2. simulation of mechanics and growth of a tissue. Figure (a) shows the mechanical state of a surfacic tissue taken from [6]. Red segments in each cell show the main orientation of the stress in the cell. This computation is to be compared with the mechanical state of a full tissue with inner cells as used in figure (b). Figure (b) show the result of a growth simulation performed on a reconstructed tissue where all cells

are represented. Orange cells are more elastic than their neighbors, therefore grow faster, purple ones are frontier cells where growth is genetically blocked.

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