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A novel plant cell division algorithm based on ellipse/ellipsoid fitting

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Highlights: A novel plant cell division algorithm is presented for both 2D and 3D representation of cells. The position and orientation of the dividing cell wall were determined by fitting ellipse/ellipsoid to the cell vertices. The new wall is then inserted along the minor diameter of the fitted ellipse/ellipsoid perpendicular to the major diameter of the fitted ellipse/ellipsoid.

Keywords: cell division, biomechanics, turgor pressure, thin-walled structure, Hooke's law, Newton's law, ellipse fitting, ellipsoid fitting

INTRODUCTION

Cellular pattern studies and simulation of higher level processes such as phyllotaxis and vascular patterning calls for models of the division and arrangement of cells into tissues (Smith *et al*., 2006). Many biophysiological processes in plant organs, such as gas transport, are strong functions of the microstructural geometry of the tissue (Ho et al., 2011) which is in turn dependent on the cell division and arrangement of cells.

In contrast to animal cells, plant cell walls are relatively rigid. The walls of the neighbouring cells are joined by the middle lamellas, which are composed mainly of pectins. Moreover, the walls are traversed by plasmodesmata (thin, intercellular, plasmic channels) (Romberger *et al.*, 1993). Unless the cell is in the division phase, or pores are generated by separation of cells or death of cells, the contiguous walls of the neighbouring cells do not slide or slip with respect to each other, thus the cell topology is maintained. These aspects should be taken into account when considering cell division and expansive growth. Cell division rules that were proposed by Hofmeister (1863), Sachs (1878) and Errera (1886) are still the most prominent works which are the basis for modern thoughts. According to Hofmeister, the dividing wall is inserted at right angle to the longitudinal axis of the mother cell; while Sachs suggested that the new wall intersects the side walls at right angles. Errera's rule states that the dividing wall should be the shortest wall that partitions the mother cell into two equal daughter cells (reviewed by Prusinkiewicz & Runions, 2012).

Besson and Dumais (2011) have developed a rule for symmetric division of plant cells based on probabilistic selection of division planes. According to their work, the Errera's rule of cell division failed to account for the variability observed in symmetric cell divisions, in particular, the fact that cells of identical shape do not necessarily adopt the same division plane. The variability in symmetric cell division is accounted for by introducing the concept of local minima rather than global minima. The division planes are then selected based on a probability which scales inversely to the difference between a candidate plane and a plane which is the global minima. In our model we have achieved this using the random selection of the minor diameter when the fitted ellipse/ellipsoid is a circle/sphere which will result in infinitely many possible candidates for the dividing wall. Robinson *et al*. (2011) introduced an asymmetric cell division algorithm in which the division wall is chosen as the shortest wall which passes through the nucleus of the mother cell. In their model, the asymmetric cell division is achieved by displacing the nucleus of the mother cell from the centroid of the cell in a random direction. In our model we have achieved this by randomly moving the position of dividing wall along the major diameter of the fitted ellipse/ellipsoid. The dynamic pattern of cell arrangement is a function of not only the position and orientation of division walls but also the timing of cell division and growth of the tissue. The early work of Korn (1969) reintroduced by Merks and Glazier (2005) represents cells as a set of points, and growth is achieved by the addition of new points to a cell. Cell division is carried out according to Errera's rule. Cell mechanics based models for 2D cell growth were developed by different researchers (Dupuy *et al*., 2010; Sahilin and Jönson, 2010 & Abera *et al*., 2012a 'in press'). The 2D cell growth model developed by Abera et al. (2012) has recently been extended to a 3D cell growth model (Abera et al. 2012b).

Based on the literatures detailed above, there is no single generic model. Some models are intended either for symmetric or asymmetric cell division. Some of them are focused merely on the division rules, without paying attention to the timing of cell division and the actual expansive growth and others are not accounting for cell mechanics when modeling cell growth. To our knowledge, 3D plant cell division models are scarce. Knowledge on the 3D arrangement of plant cells and their growth in tissues is however of high importance to our understanding of biophysiological processes. The objective of this paper is to develop both 2D and 3D plant cell division algorithms that are generic and based on cell growth mechanics.

METHODOLOGY

In our model, the cell is considered as a closed thin walled structure, maintained in tension by turgor pressure. The cell walls of adjacent cells are modeled as parallel, linear elastic elements which obey Hooke's law. Cell expansion then results from turgor pressure acting on the yielding cell wall material. To find the sequence of positions of each vertex and thus the shape of the tissue with time, a system of differential equations for the positions and velocities of each vertex is established and solved using a Matlab ordinary differential equation solver (For details, see Abera et al., 2012a ‘in press’). The cell division algorithm calculates the area/volume of the cells and checks if there are cells which exceed a predefined cell area/volume. The readiness of the cell to divide was determined based on cell size which is a function of time. A dividing wall is inserted whenever a cell exceeds its predefined size. In order to determine the position and orientation of the new wall that divides the cell, an ellipse/ellipsoid fitting algorithm is implemented, based on the cell vertices. The new wall is then inserted along the shortest diameter of the fitted ellipse/ellipsoid perpendicular to the longest diameter of the fitted ellipse/ellipsoid (see Fig. 1). The cell vertices, walls and edges are then updated and the cell expansion resumes. By moving the position of the dividing wall in either direction along the major axis based on a random factor chosen between -1 and 1 a switch between symmetric and asymmetric division is possible.

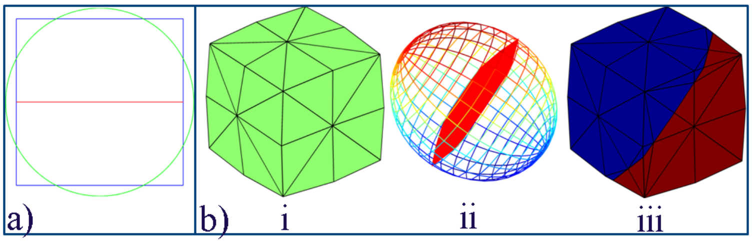

Fig. 1. Demonstration of the cell division algorithm: a) 2D cell division where blue lines are boundaries of the mother cell; green line is the fitted ellipse and red line is the new wall dividing the cell; b) 3D cell division where i) is the mother cell; ii) is the fitted ellipsoid (the red plane shows the orientation and position of the new wall); iii) shows the two daughter cells with distinct colors.

RESULTS AND DISCUSSION

We have developed a generic algorithm, based on cell wall mechanics, that is capable of producing variety of cell and tissue types. The algorithm can produce the variability observed in symmetric cell division without introducing the concept of local minima but sticking to the Errera’s rule of global minima (Besson and Dumais, 2011). In our model, an ellipse/ellipsoid is fitted to the vertices of the mother cell. The position and orientation of the minor diameter of the ellipse/ellipsoid is used as the position and orientation of the dividing wall. If the fitted ellipse/ellipsoid is a circle/sphere, we have infinitely many possible orientations for the candidate dividing wall. The random selection of one of them made it possible to produce the variability observed in symmetric cell division (see Fig. 2).

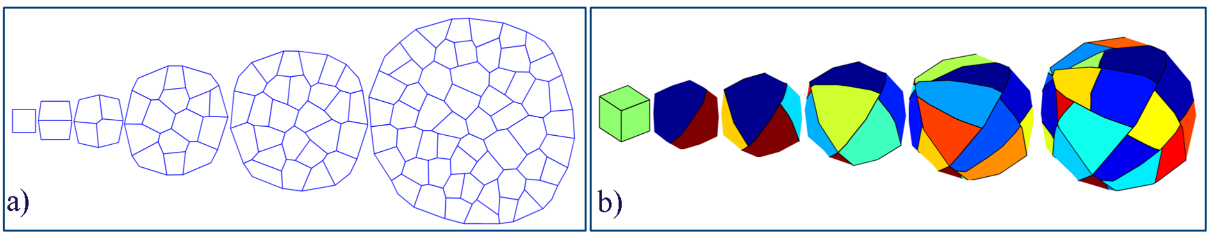

Fig. 2. Symmetric 2D cell division (a) and symmetric 3D cell division (b).

The asymmetric cell division (Robinson *et al*., 2011) is achieved by random displacement of the dividing wall along the major diameter of the fitted ellipse/ellipsoid. By making the mechanical properties and the maximum resting length of the walls/edges global direction dependent, the model allows both isotropic and anisotropic cell growth which leads to different tissue types. The cell division algorithms can be coupled to the 2D expansive plant cell growth model (Abera et al., 2012a, 'in press') and the 3D expansive plant cell growth model (Abera et al., 2012b) which were initiated from a 2D and 3D Voronoi tessellations respectively.

In conclusion, the main merits of the algorithm are: 1) both cell shape and topology are taken care of; 2) it is based on physics; 3) the equations for the actual growth of the cell walls (change in resting length of the walls) and cell division are solved continuously; 4) it is generic in that a switch between isotropic growth and anisotropic growth as well as between symmetric cell division and asymmetric cell division is automatic and easy; 5) there is no need for an iterative procedure to find the shortest wall for cell division. In our algorithm, the division wall is inserted along the minor diameter of the ellipse/ellipsoid. To our knowledge, the 3D cell division and cell growth algorithm presented here is the first one based on cell wall mechanics introduced to the literature.

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