GEOMETRICAL DYNAMICS FOR MORPHOGENESIS

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ABSTRACT

Models for the growth of unicellular algae have been developed which involve various components such as strain and stress of visco-elastic shells coupled to ionic concentrations. These models are relatively difficult to study and we propose here another class of models, much simpler to study, involving a few coefficients, which characterize the growth from a macroscopic point of view. These models are called "geometric" since they determine the dynamics of a boundary, the cell wall, in terms of elongation rate versus local curvature. Similar approach was performed in crystal growth, where the full dynamics of the liquid-solid interface, involving non locality of diffusion fields, is simplified to the dynamics of a curve whose normal velocity is function of the local curvature. The geometrical models that we develop here allow us to recover shapes well known from botanists such as Micrasterias (radiata or rotata) and rhizoids.

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Since D'Arcy Thompson [1] and Turing [2], the hope to understand biological shapes by using physical laws and mathematical tools is continuously increasing. However, no clear application of these ideas has been performed up to now essentially because of the lack of precise experiments on a sufficiently simple system. But progress in this field is important and biological diagnostics are more and more precise. For instance, many studies on algae, like the pattern formation in turgor reduced cells of the desmid Micrasterias by Kiermayer [3], or the discovery of ionic currents associated with the morphogenesis of Fucus or Pelvetia zygotes by Jaffe et al. [4], are essential, before a physical or mathematical description of these systems can be performed. Encouraged by this progress, we focus our study on the morphogenesis of unicellular algae.

There exists a great variety of algae [5]: unicellular, motile, nonmotile, colonial, filamentous, membranous or foliar, tubular. In contrast, all plant cells expand under the effect of the large turgor pressure generated inside them. The plant cell wall, an elastic or viscoelastic structure composed mainly of cellulose microfibrils, supports the growth by elongation and will determine the future shape of the cell. Cell wall elongation can proceed by two essential mechanisms [6]: tip growth and diffuse growth.

The first concerns unicellular entities like root hairs, rhizoids, pollen tubes. Cell expansion is confined to an apical dome leaving behind a long cylindrical cell. Associated with the growth are physicochemical phenomena like the appearance of ionic currents leading to an inhomogeneous concentration of calcium in the cytoplasm. The origin of these currents is not clear. They could arise through a redistribution of ion channels or pumps in the plasma membrane induced by the electric field generated by the ionic currents themselves [7],[8]. Furthermore, a wide variety of external gradients, including light intensity, pH, ions and electric potential gradients, can orientate the axis of growth of these cells. Despite a lack of a complete understanding of these phenomena, tip growth mechanism seems mainly under cytoplasmic control.

In contrast, growth of cells within multicellular organisms typically involves the second mechanism, i.e. a uniform expansion of the primary cell wall. Morphogenesis in that case is simply due to an anisotropy of the mechanical properties of the cell wall. Microtubules, aligned along the inner side of the plasma membrane orientate the newly deposited cellulose microfibrils and induce an anisotropy in the mechanical properties of the wall. When plant cells are treated with drugs that cause microtubule disassembly, such as colchicine, orientation is lost and cells expand equally in all directions. As the same microtubules are involved in cell division, it seems that diffuse growth mechanism is under nuclear control.

Thus, for our purpose, we will consider the first mechanism, tip growth, for which physicochemical phenomena take an important part in the morphogenesis. Then, the cell wall appears as a deformable boundary in interaction with physicochemical fields like electric potential, stress pattern, ion concentration. The modelisation of all these phenomena is extremely complex and even simpler models which involve only stress and strain of visco-elastic shells coupled to ionic concentrations are relatively difficult to work with [9]. The situation is similar in the case of the propagation of interfaces like crystals or flames [10] (even if the full dynamics is much simpler than for a living system) and the understanding of these physical shapes increased much when geometrical models were introduced [11]. These models simply consider a free moving boundary whose normal velocity is given as a function of the local geometric quantities of the curve like the curvature and its derivatives with respect to the curvilinear coordinate.

In the case of algae such a geometrical model for two-dimensional growth was recently developed by Pelce and Pocheau [12]. The difference with the propagating interfaces is that, because of physical origin, the relative elongation rate and not the normal velocity is given as a function of the local geometrical quantities of the curve. A primordial linear instability of this model has been found which could be responsible for the morphogenesis of the cell. We now analyse the wide variety of shapes that can be obtained from this model. Of course algal outgrowths are in general three-dimensional and comparison of shapes obtained from a two-dimensional model with real shapes can only be qualitative. In principle, a three-dimensional model can be worked out in

similar lines but it's necessary mathematical complexity could hide the basic features of tip growth.

GEOMETRICAL MODELS.

Considering algae growing by the tip growth mechanism, it is clear that the observed non-circular shapes are non-equilibrium shapes. In that case, microfibrils are incorporated inside the cell wall with random orientations. Thus, the primary cell wall has isotropic mechanical properties and, because a turgor pressure larger than outside is maintained inside the cell, an equilibrium shape will be necessarily a circle or a sphere. At the end of the growth, the dynamical effects which maintained noncircular shapes during the growth disappear and nonspherical shapes will relax to spherical shapes. This is not the case since, in general, a secondary cell wall is synthesized by the organism, much more rigid than the first, which completely stiffens the elongated or circumvoluted shape generated by the growth.

From this observation, algal shapes must be determined from equations for dynamical variables characterizing the cell wall. The simplest equation of this kind was introduced by Green [13] and relates the relative elongation rate of the boundary to the turgor pressure P as

$$\frac{1}{\delta l}\frac{d(\delta l)}{dt} = m(P - Y) \qquad (1)$$

where m is the extensibility of the cell wall and Y the yield threshold. If one assumes that turgor pressure acts on the cell wall by means of the tangential stress $\sigma = P / h\kappa$ applied to the microfibrils, where κ and h are curvature and thickness of the wall respectively, the relative elongation rate (1) can be generalized to a function $H(\kappa)$ of the curvature of the boundary. This assumption is supported by the experimental observation that the relative elongation rate is much larger at the cell tips than at the other parts. Moreover, membrane-bound calcium is observed close

to the cell tips [14]. Since calcium is known to affect biochemical reactions, this may explain why tip growth is enhanced. When curvature is not uniform, it is natural to introduce derivatives of the curvature with respect to arclength in the equation for the relative elongation rate:

$$\frac{1}{\delta l}\frac{d(\delta l)}{dt} = H(\kappa) + \gamma\frac{\partial^2 \kappa}{\partial l^2} \qquad (2)$$

Here δl is the distance between two neighbouring microfibrils present in the cell wall at the beginning of the growth, l the curvilinear coordinate and γ an arbitrary coefficient.

The kinematic relation [12]

$$\frac{1}{\delta l}\frac{d(\delta l)}{dt} = U\kappa + \frac{\partial V}{\partial l} \qquad (3)$$

relates the relative elongation of the wall to the normal and tangential components of the velocity of the microfibrils. As the motion of a curve is only determined by the normal velocity of its points, eqn.(2) is not sufficient to determine the evolution of the cell boundary. The necessity to introduce a second law for the deformation of the cell wall was missed in previous approaches [15]. Pelce and Pocheau [12] propose, in addition to eqn.(2), a relation between the rotation velocity of the slope of the boundary $d\theta / dt$ and the curvature of the cell boundary and its first derivatives with respect to the curvilinear coordinate. Such a relation can be written as:

$$\frac{d}{dl}\left(\frac{d\theta}{dt}\right) = -\alpha\frac{d^2\kappa}{dl^2} + \beta\frac{d^4\kappa}{dl^4} \qquad (4)$$

where α and β are arbitrary coefficients. In ref. [12], $\beta = 0$, but, when a numerical integration of eqns. (2) and (4) is performed, non zero negative values of β are necessary to ensure stabilisation of the shape at small scale. In this kind of model, all the genetic information is

contained in the coefficients α, β and γ and the characteristics of the function $H(\kappa)$.

Since another independent kinematic relation

$$\frac{d\theta}{dt} = -\frac{\partial U}{\partial l} + V\kappa \qquad (5)$$

relates the normal and tangential components of the point velocity U and V, eqns. (2) and (4) form a complete set of equations determining the evolution of the cell boundary. These equations are clearly compatible with two particular simple cell wall configurations: the flat expanding wall ($U = 0, \kappa = 0$) and the expanding circle ($V = 0$, κ uniform).

We investigate now the shape evolution obtained when the parameters α, β and γ are varied. For this, one can derive from eqns. (3) and (5) an evolution equation for the curvature as [12]:

$$\frac{d\kappa}{dt} = -\left(\kappa^2 + \frac{\partial^2}{\partial l^2}\right) U + V\frac{\partial \kappa}{\partial l} \qquad (7)$$

where U and V are determined as a function of the curvature by using the kinematic relations (3) and (5) and the equations for the cell wall dynamics (2) and (4). When $\kappa(l, t)$ is known we reconstruct the curve by using the geometrical relations $\kappa = d\theta / dl$, $\cos\theta = dx / dl$, $\sin\theta = dy / dl$.

We consider two functions $H(\kappa)$: $H_1(\kappa) = .1 \exp(5\kappa(1 - .2\kappa))$, $H_2(\kappa) = .1 \exp(15(\kappa - .1)(1 - .2\kappa)(\kappa + .5)^2)$. In both cases, the relative elongation rate vanishes exponentially for negative values of the curvature. It follows that the concave part of the cell walls, the notches, appear completely inactive in the cell wall elongation process. They move

passively, pulled by the active tips. As required for tip growth, elongation only occurs for positive curvature. The relative elongation rate decreases above a positive critical value of the curvature. This last property of the elongation rate mimics the existence of a yield threshold reached by turgor reduced cells. As mentioned above, if one assumes that the turgor pressure acts on the cell wall only via the tangential stress $P / h \kappa$, small turgor pressure is equivalent to large curvature.

As observed by Lacalli [17], three mechanisms interact in shape formation: tip growth, lobe branching and lobe broadening. We illustrate these mechanisms by the evolution of three typical shapes observed in the algal world: a Chara rhizoid (Fig.1b) [16], an apical dome leaving behind a long cylindrical cell, growing steadily from the tip; a semicell of the two species of the desmid Micrasterias, radiata (Fig.2b) and rotata (Fig.3b). Shape evolution of M.radiata mixes, in an elegant fashion, tip growth and lobe branching. Shape evolution of M. rotata mixes tip growth, lobe branching and lobe broadening. Desmids are good candidates for tip growth mechanism since Kiermayer [3] showed that application of colchicine on these algae had little influence on their shape formation.

The evolution of these three shapes can be qualitatively reproduced by the geometrical model. In all cases, the initial condition is a disturbance of hexagonal symmetry ($j = 6$). In the case of (Fig.2a) and (Fig.3a) the shape evolution is stopped just before two lobes begin to overlap. After this event a local geometrical model has no meaning and nonlocal effects need to be introduced in the model to prevent the overlap. It is noteworthy that the two first shapes (rhizoid (Fig.1a) and M. radiata (Fig.2a)) can be obtained by using the same model (elongation rate H_1) with very close coefficients. In both cases $\alpha = 1.5$, $\beta = -1$; $\gamma = 10$ for the rhizoid, $\gamma = 8$ for M. radiata. (Fig.1a) is one of the six rhizoids generated by the initial disturbance. After some transient time the tip almost grows with constant velocity and stationnary shape. At the base of the rhizoid, secondary lobes are generated. (Fig.2a) is one half of the shape generated by the initial disturbance. The resemblance with a semicell of M.radiata is amazing. In both cases thin lobes are formed and branch periodically, without broadening. Shape evolution of M. rotata (Fig.3a) is

obtained with the second model (elongation rate H_2) $\alpha = 1.5$, $\beta = -1$ and $\gamma = 1$. Contrary to the previous case, lobes broaden before the tip-splitting. It is noteworthy that, before the tip-splitting, the tip region flattens considerably as is observed for M.rotata (Fig.3b). By varying the different coefficients a large variety of shapes can be obtained (Pelcé and Sun [18]).

We expect that experiments can tell us about the coefficients α, β and γ. It could be interesting if botanists could measure them as a function of various control parameters such as external ionic concentration (calcium, potassium) and applied stresses. In that case, this kind of models can be the beginning of a macroscopic description for the growth of unicellular algae.

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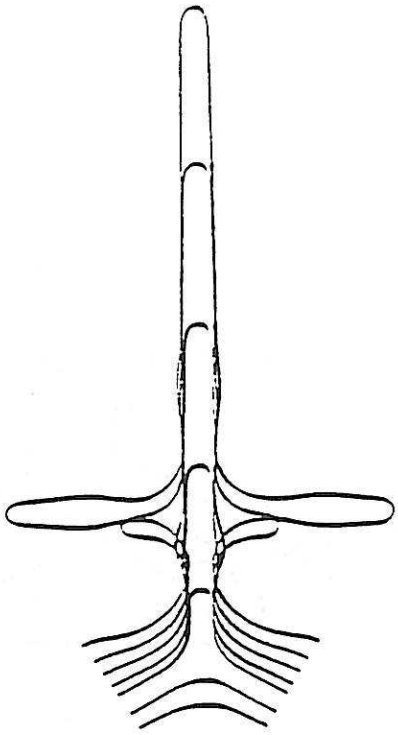
FIGURE CAPTIONS.

Fig.1: Comparison between time-lapse shapes obtained a) from model I $\alpha = 1.5$, $\beta = -1$ $\gamma = 10$ and b) from an experiment on Chara rhizoid [16].

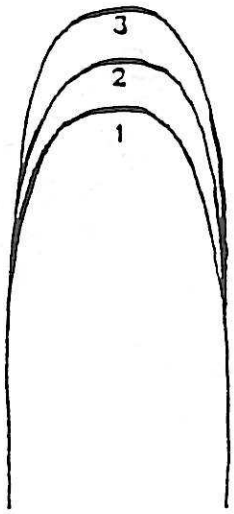
Fig.2: Comparison between time-lapse shapes during development obtained a) from model I $\alpha = 1.5$, $\beta = -1$, $\gamma = 8$ and b) from an experiment on Micrasterias radiata [17]. Consecutively numbered stages are separated from one another by $\Delta t = 2$ in the simulation and 20 min in the experiment. Fig.2b is reprinted from J.Embryol.Exp.Morph. Vol.33, 1, 120 with the courtesy of T.C. Lacalli and the permission of company of biologists LTD.

Fig.3: Comparison between time-lapse shapes during development obtained a) from model II $\alpha = 1.5$, $\beta = -1$, $\gamma = 1$ and b) from an experiment on Micrasterias rotata [17]. Consecutively numbered stages are separated from one another by $\Delta t = 2$ in the simulation and 20 min in the experiment. Fig.3b is reprinted from J.Embryol.Exp.Morph. Vol.33, 1, 120 with the courtesy of T.C. Lacalli and the permission of company of biologists LTD.



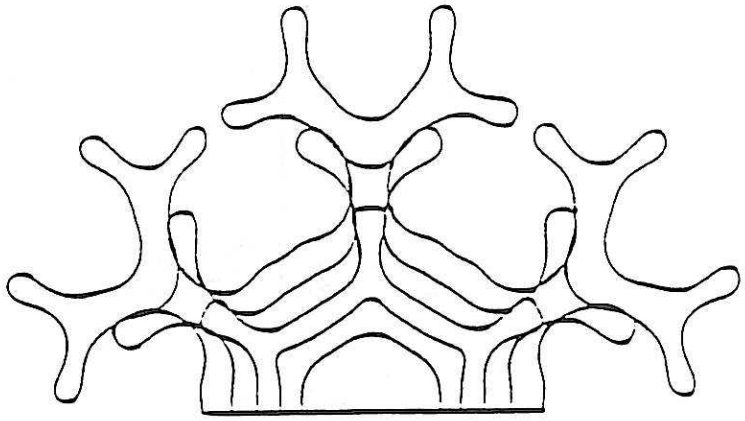
a

10 µm.



b

Fig.1



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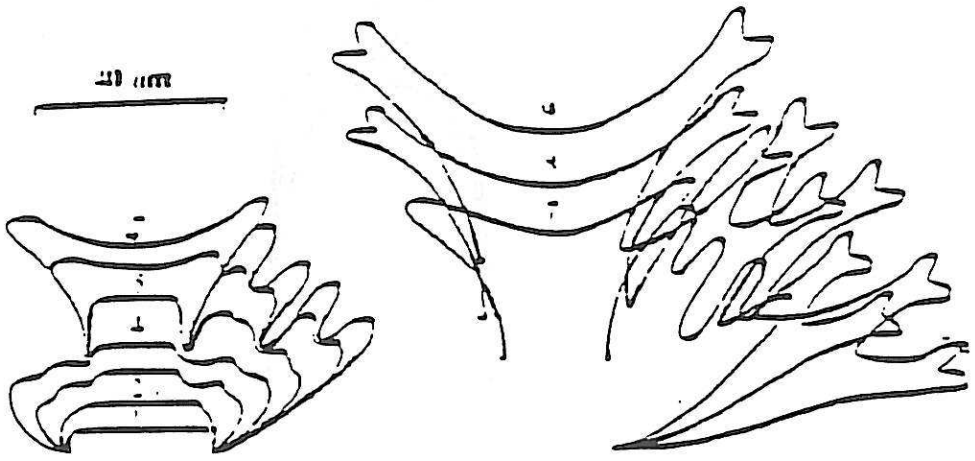

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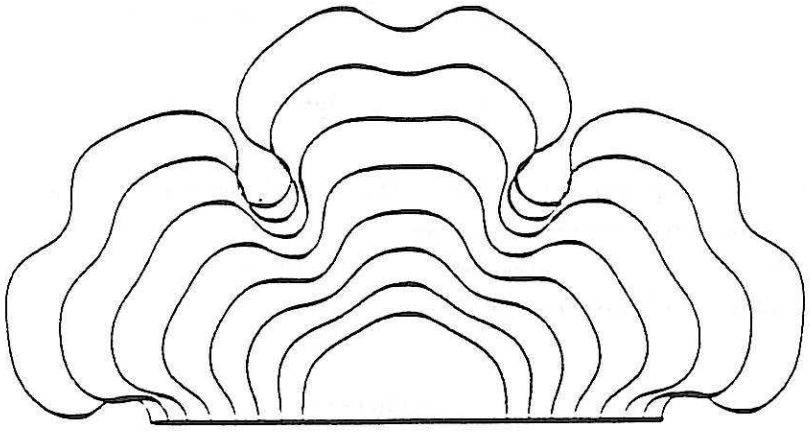
Fig. 2



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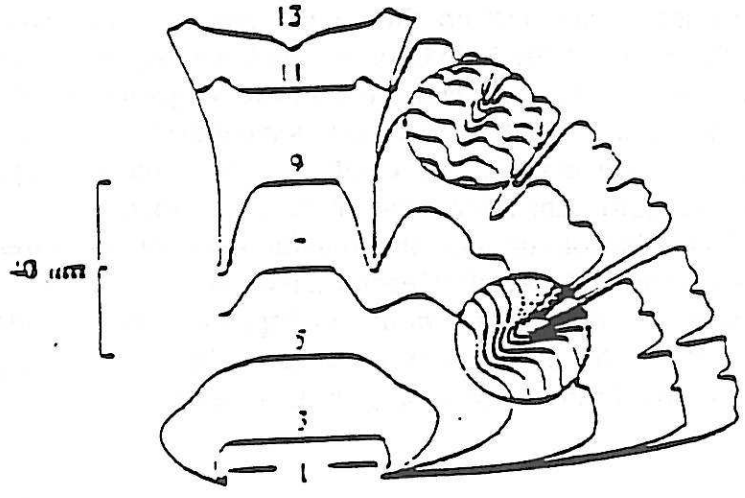

b

Fig.3