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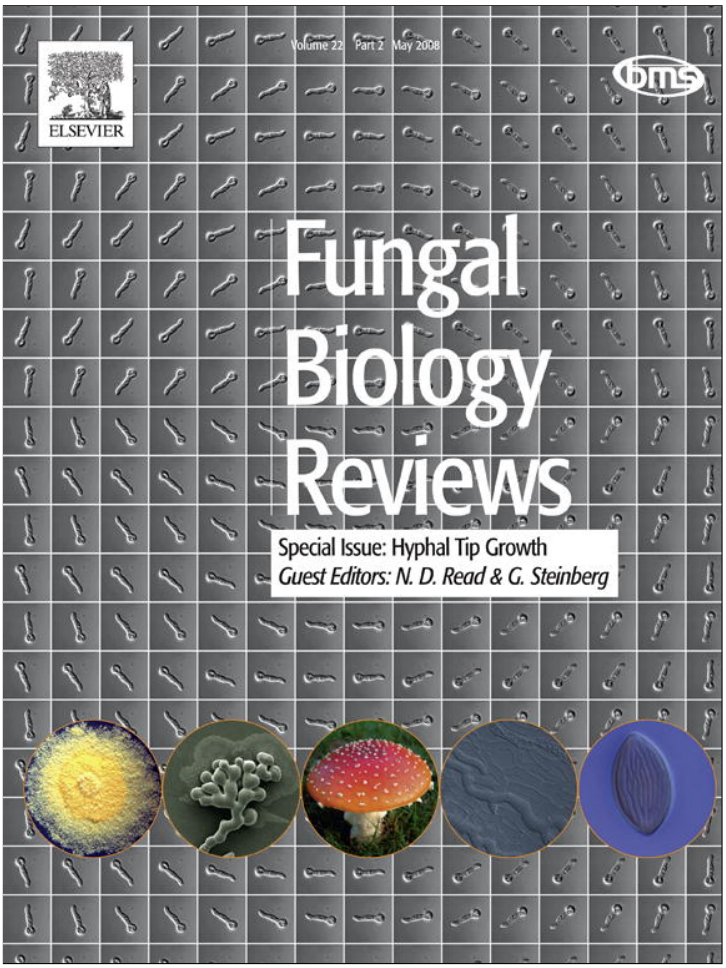

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Review

Mathematical modeling of hyphal tip growth

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ABSTRACT

The mathematical modelling of growing filamentous cells has been approached in a variety of ways ranging from simple geometric to biomechanically based models using exact, nonlinear, elasticity theory for shells and membranes in which a growth mechanism is included, and alternative approaches using visco-plasticity theory. We describe how the nonlinear elastic model is able to capture essential biomechanical mechanical features of the growth of a broad array of filamentous cells including fungi, actinomycetes, pollen tubes, and root hairs. A comparison between this approach and visco-plasticity based models is made.

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1. Introduction

Filamentous cells such as fungi, actinomycetes, root hairs, and pollen tubes have long been a topic of interest and the subject of experimental studies, e.g. a study of root hairs with excellent illustrations can be found in Duhamel du Monceau's dissertation (1758). In more recent times, the growth of such cells has been the subject of mathematical modeling to provide quantitative descriptions of their temporal evolution and morphology. Despite many fundamental differences in cellular structure, life cycles, size, and function, there appear to be certain common characteristics in the growth of these diverse cells at the morphological level. Typically, the growth is apical, i.e. the growth extension is at the tip of the cell and the building of new cell wall occurs mainly in the vicinity of the tip. This experimentally confirmed picture of the growth has its origins in the old, but widely accepted, ''soft-spot'' hypothesis (Koch 1994) in which the hyphal tip is considered to be more stretchable than more distal regions, which become asymptotically rigid. The fact that cells grow with this general morphology implies an intrinsic anisotropy to the process (since if the growth was isotropic the cell would swell out spherically under the effect of turgor pressure). The source of this anisotropy and the interplay between the anisotropy of the stresses, namely the longitudinal (meridional) and azimuthal (hoop) stresses - which is a characteristic of axisymmetric elastic shells - and anisotropy of the material properties of the cell wall has been a topic of considerable interest for some time. This issue has been studied with ever increasing experimental sophistication and is the topic of many papers and review articles in the field of hyphal growth modeling.

Although the specific shapes of the tips vary for different cells there can be periods in which the tip growth appears ''self-similar'', i.e. at each time step the newly grown tip looks like a translation of the tip shape at the previous instant. Another quite common feature appears to be that of ''normal'' growth, namely that labelled points on the tip appear to move in a direction normal to the tip surface as it grows. The possibility of such a growth pattern was discussed well over a hundred years ago by Reinhardt (Reinhardt 1892) and has been confirmed in experimental studies of fungi (Bartnicki-Garcia *et al.* 2000) and root hairs (Shaw *et al.* 2000) in more recent

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times. Despite these apparent commonalities in growth morphology there are huge differences in the biological mechanisms that drive the growth. For actinomycetes it is generally accepted that turgor pressure is still the principal driving force, whereas for fungi the role of turgor has been the topic of some debate (Money 1997, this issue; Harold 2002); although the current indications are that turgor forces are the dominant effect and that the cytoskeleton does not play a direct mechanical role (Geitmann 2006). The mechanisms by which new wall building material is transported to the tip in actinomycetes and fungi is also very different. For the actinomycetes this is probably achieved by some form of (not well understood) diffusive mechanism, while for fungi the cytoskeleton plays a significant role and the possibility of a vesicle supply centre in hyphal tip growth has been proposed (Bartnicki-Garcia *et al.* 1989).

Mathematical models of hyphal growth range from simple geometrical models to sophisticated mechanical ones. In this article we will focus on the mechanical models and refer the reader to a variety of papers investigating geometric approaches (Trinci & Saunders 1977; Saunders & Trinci 1970; da Riva Ricci & Kendrik 1972; Bartnicki-Garcia *et al.* 1989; Gierz & Bartnicki-Garcia 2001; Goriely *et al.* 2005). The mechanical models aim to capture the tip growth through a proper description of the physical stresses and strains experienced by the growing hypha. Some quite different approaches have been proposed. One way of achieving irreversible extension, which is taken as a manifestation of growth, is to employ the ideas of (linear) plasticity theory; an approach that has been used for cells ranging from plant cells (Proseus *et al.* 1999) to root hairs (Boudaoud 2003; Dumais *et al.* 2006). An alternative approach, taken by the present authors, has been to use the techniques of exact, nonlinear elasticity - which enables one to follow large deformations of the cell wall - and to model the actual growth mechanism by a certain incremental process in which mass is added to the elastically strained cell wall. We use the term morpho-elasticity to describe the process of incremental growth in response to elastic deformation. The self-consistent inclusion of growth into the formalism of continuum mechanics is a delicate matter and one of real biomechanical importance since it is also relevant to fundamental processes such as bone and arterial growth (Taber 1995; Humphrey 2003). Overall, we will show that it is possible to formulate quite general mechanical models that can describe generic growth morphology and hyphal mechanics of a wide variety of cells. We will compare our modelling approach with recent visco-plasticity models (Dumais *et al.* 2006) and suggest that at the level of linear (infinitesimal) elasticity theory they are essentially equivalent.

2. Basic principles of the mechanics and mathematical modelling of hyphal growth

Modelling of hyphal growth brings together the communities of microbiologists and applied mathematicians: each expert in their own fields but not necessarily so in the other. Accordingly for this review we thought it would be useful to summarize some of the basic continuum mechanical principles that need to go into a self-consistent biomechanical model of hyphal growth, and how these fundamental concepts translate into mathematical and computational models. Here our discussion is almost entirely qualitative with the minimum of equations. A continuum mechanical model has three components: (i) geometric, (ii) mechanical, and (iii) constitutive. The first component is purely geometric and involves setting up a coordinate system that can be used to measure the strains (the relative displacement of material points under deformation). For a planar sheet a Cartesian or polar coordinate system is appropriate. For an axisymmetric shell a more sophisticated curvilinear coordinate system is required. A commonly used system is shown in Fig 1. The initial positions of uniformly spaced material points along the meridional direction are usually given in terms of arc length. The overall geometry of the shell is conveniently characterized in term of the two principle curvatures: the curvature in the meridional direction, denoted as κ_s and the azimuthal curvature, usually denoted as κ_φ. The second component is the purely mechanical one in which Newton's laws are used to balance the stresses (the internal elastic forces), represented in the same coordinated system as used to describe the shell geometry, with the applied forces. At this point it is important to distinguish between a shell and a membrane. A shell is a two-dimensional sheet of small but finite thickness that can support bending moments. By contrasts membranes cannot support bending and their description only involves the transverse stresses. Accordingly

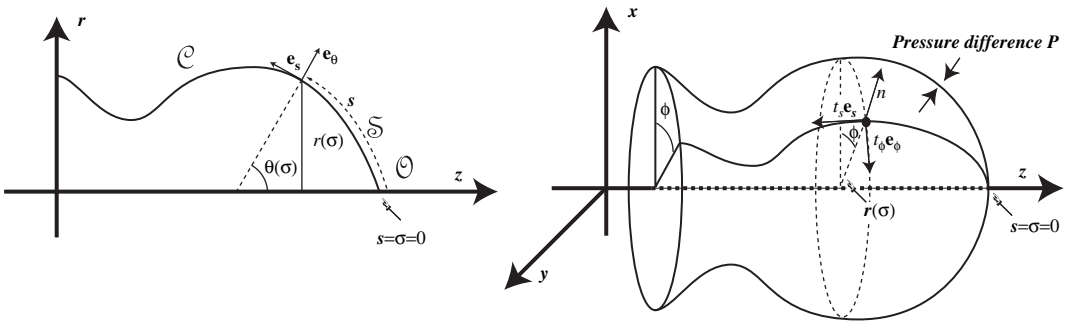

Fig. 1 – Basic hyphal geometry. The origin of the z-axis is set at the hyphal tip. Arc-length, s, to a given material point is measured from the top of the shell, r(s) is the radial distance from the vertical axis to that point, and n denotes the normal direction. The hyphal wall is taken to be axisymmetric, i.e. a curve C in the plane r–z is rotated around the z-axis to produce the surface S in 3D where φ is the azimuthal angle.

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a membrane is usually considered as a purely two-dimensional material. Examples of systems modelled as membranes range from simple soap bubbles to red blood cells. A few points about the applied forces are also in order. As with all vectorial quantities, forces can be resolved into components: in the case of an axisymmetric shell these are the force components normal to the shell surface and the forces tangential to the surface. Internal pressure, which in the case of cells is the turgor (the difference of internal and external pressure) is a purely normal stress and is generally considered to be the primary driving force for growth. However, at the level of mechanical equilibrium, one simply writes down the balance between the total normal stress and the total applied force whatever its origin is: it could just be the turgor or, possibly the combination of turgor and some cytoskeletal force (although, as mentioned above, the latter is currently believed to be negligible relative to the turgor). It is important to remember that filamentous cells are typically burrowing through media such as soil in the quest for nutrients. This means that the shell will experience external tangential stresses corresponding to the friction between the cell and the surrounding medium. A complete model needs to be able to include such tangential stresses. The third and critical component of the model is the constitutive relationships that connect the deformation and the stresses. It requires the postulation of an elastic energy, or plastic flow rule, and is where the mechanical properties of the deforming material appear in the theory. In classical elasticity theory the use of a Hookean elastic energy results in the well known linear relationships between the stresses and strains. For an isotropic elastic material these are characterized by the bulk and shear modulus which are frequently written in terms of the Young's modulus, often denoted as E, and the Poisson ratio, which is often denoted as σ. The latter plays an important role in elasticity theory and represents the ratio of elastic deformation in transverse directions, e.g. the transverse contraction of a rod as it is extended.

The extension of plant cells and other cells has often been modelled through the use of classical plasticity theory - well described in the definitive text by Hill (1950). Plastic materials are taken to deform (or ''flow'') once a certain measure of the shear stresses exceeds some critical yield stress. There are a number of key assumptions in classical plasticity theory: (i) plastic flow is irreversible – one cannot tell whether a material has undergone a ''plastic deformation'' until the external loading has been removed; (ii) plastic deformation is generated by shear and hydrostatic pressure plays little role in the deformation; (iii) plastic flow is usually assumed to be incompressible; (iv) the actual deformation of the material is governed by its elastic material properties which are taken to be the same as the bulk material. The constitutive relations are now between the rates of strain and the stresses. The simplest model sets the increment of the rate of strain proportional to the total stress, which captures the fact that plastic deformation is dependent on the loading history. This linear relationship can be cast in a form reminiscent of fluid flow (e.g. the Bingham fluid model) but the analogy should not be interpreted too literally (Hill 1950). A more complete, but still linear, constitutive relationship, includes contributions from the stress increments, thereby capturing the purely elastic part of the deformation (the Levy-von Mises model). But in either case it is the elastic properties of the material that condition the overall deformation.

Our entire discussion so far has been set in the framework of the classical theories of elasticity and plasticity: these are strictly linear theories in which the strains are, in fact, assumed to be very small: an approximation that appears to be far more satisfactory for typical engineering materials than for soft tissues found in biomedical and biological applications. In this latter context one can use the well developed theory of exact elasticity theory, well described in the definitive text by Ogden (1984), that enables one to study nonlinear elastic deformations and allows for a wide choice of elastic free energy functions far more general than the classical Hookean energy. Within the exact framework it is also possible to include, in a thermodynamically self-consistent way, a number of ansatz corresponding to the combination of material growth and elastic deformations. Unfortunately, the development of a satisfactory nonlinear plasticity theory has still proved to be elusive.

3. Hyphal tip growth

Although this is primarily an article about fungal growth the universal features of tip growth morphology makes it appropriate to say a few words about the growth of filamentous actinomycetes, such as *Streptomyces coelicolor* A3(2) – a topic of considerable interest to microbiologists since the nineteenth century (Reinhardt 1892). The cell wall structure of these gram positive prokaryotic cells is dominated by a network of peptidoglycan polymers. In a typical growth cycle the streptomycete spores bud into long filamentous hyphae that grow in and on the nutrient source. Apical growth in this ''vegetative'' phase is energetically more efficient than growth along the entire filament since the latter would result in increased friction with the medium. A typical filament of *Streptomyces coelicolor*, at this stage is less than 1 μm in diameter and can grow to lengths of 50–100 μm. That the hyphal growth of streptomycetes in the vegetative phase is concentrated at the tip has been amply demonstrated in a variety of studies tracking the presence of tritiated N-acetyl-D-flucosamine (GlcNAc), a precursor of peptidoglycan. Gray *et al.* (1990) used this technique in their study of *Streptomyces coelicolor* A3(2) to demonstrate that the bulk of the labelled material was incorporated close to the hyphal apex. These and other experimental studies of hyphal extension in *S. coelicolor* show that the main factors determining growth in the vegetative phase are: (i) turgor pressure, (ii) addition of newly synthesized wall-building material in the apical extension zone, and (iii) the rigidification of the distal cell wall. Thus the overall picture of the growth mechanism consistent with these observations is a continuous and complex process in which wall building materials are transported to, and incorporated into, the tip which is stretched by the turgor pressure generated by the intracellular fluid; and that as the tip is continually stretched and rebuilt the more remote portions of the hyphal wall become (relatively) rigid (Prosser & Tough 1991). In other words, the generic pattern of hyphal growth assumed for many filamentous cells.

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Filamentous fungi are typically at least an order of magnitude bigger than the streptomycetes and their complex, multi-layered, cell-wall structure usually consists of a network of chitin with cross-linking β-glucan chains plus other components. Studies of *Neurospora crassa* showed that the incorporation of tritiated wall precursors decreased rapidly from the hyphal tip (Gooday *et al.* 1980) – again demonstrating apical hyphal growth dynamics. For most fungi turgor pressure also appears to be a factor in the growth process but there is some experimental evidence indicating that Oomycetes continue to grow even when they do not maintain turgor (Money 1997). But for all fungi it seems clear that the cytoskeleton plays a central role in the growth process especially in transporting wall building materials to the tip; although a complete understanding of the different roles played by actin filaments and microtubules in the tip growth process is still evolving (Sampson & Heath 2005). A striking result concerns that of orthogonal cell wall expansion. By tracking carbon particle markers on the tip of *Rhizoctonia solani* Bartnicki-Garcia *et al.* (2000) were able to show that the markers moved in a direction perpendicular to the surface of the hyphal apex, thereby confirming the old prediction of Reinhardt (1882). Their results also support the view that turgor pressure is still a major driving force in the hyphal growth process. However, for all these complexities and subtleties, the overall picture parallels that of hyphal growth in filamentous bacteria: namely apical growth driven by a complex process involving transport of wall building materials and a tip straining mechanism.

Root hairs have been one of the most enduring topics of study in microbiology with scientific publications dating back almost two hundred and fifty years. As with filamentous fungi it was established long ago that the cell wall expansion is concentrated at the tip. More refined microscopic studies have also shown that the expansion is both inhomogeneous (the rate of expansion being maximal around the tip) and anisotropic (the meridional expansion being greater than the circumferential expansion); the latter observation suggesting a varying stiffness of the cell wall – perhaps due to a corresponding variation in cellulose microfibril cross-linking. Recent experimental studies of *M. truncatula* root hair growth also support the notion of orthogonal growth in the growing tip (Dumais *et al.* 2006).

4. Nonlinear elastic models of hyphal tip growth

Here we will summarize the results of our morpho-elastic approach to modelling hyphal tip growth; namely the use of exact nonlinear elasticity theory incorporating material growth. Our current model (Goriely *et al.*, in prep.) corresponds to a more refined version of our earlier work (Goriely & Tabor 2003) and now represents the hyphal wall as a shell, as opposed to a two dimensional membrane. It can therefore support bending as well as stretching, is formulated to allow for quite general elastic free energy functions, and incorporates the effects of tangential stresses on the cell wall thereby providing a phenomenological representation of the effects of friction between the growing hypha and the external environment.

In our models the hyphal wall is represented as an elastic shell whose basic geometry is shown in Fig 1. The shape, which is assumed to be rotationally symmetric about the z-axis, is described in terms of the deformation variables

$$\lambda_s = \frac{ds}{d\sigma},\ \lambda_\varphi = \frac{r(\sigma)}{r_0(\sigma)} \tag{1}$$

where s is the arc-length in the deformed configuration and σ is the material coordinate, that is the arc-length of the reference configuration defined by its radius $r_0(\sigma)$. The variables λ_s and λ_φ measure, respectively, the meridional and azimuthal stretches of the shell - these are related to, but not the same as, the elastic strains and are not assumed to be small. For an incompressible shell the third deformation variable, λ_3, measuring changes in the normal thickness of the shell, is simply related to λ_s and λ_φ through the incompressibility condition $\lambda_s\lambda_\varphi\lambda_3 = 1$. If we were to elect to set $\lambda_3 = 1$ this would be equivalent to representing the material as a strictly two dimensional membrane of (arbitrary) constant thickness. The geometric variables satisfy the equations

$$\frac{dr}{ds} = \cos\theta,\ \frac{dz}{ds} = -\sin\theta \tag{2}$$

and the principal curvatures of the shell are given by

$$\kappa_s = \frac{d\theta}{ds},\ \kappa_\varphi = \frac{\sin\theta}{r} \tag{3}$$

The mechanical equilibrium, including bending moments and external tangential stresses corresponding to frictional effects, is governed by a complex set of differential equations representing the balance of stresses. We again emphasize that at the mechanical level all that the shell ''recognizes'' is the balance of the stresses, not the origins of those stresses.

In order to close the system of mechanical and geometric equations constitutive relations must be introduced. These are developed through the introduction of an elastic free energy function, W, specified as energy per unit volume,

$$W = W(I_1, I_2, I_3) \tag{4}$$

where I_1, I_2, I_3 are the strain invariants of the deformation tensor which, for this axi-symmetric problem, takes the form

$$F = \begin{pmatrix} \lambda_s & 0 & 0 \\ 0 & \lambda_\varphi & 0 \\ 0 & 0 & \lambda_3 \end{pmatrix} \tag{5}$$

The corresponding invariants are

$$I_1 = \lambda_s^2 + \lambda_\varphi^2 + \lambda_3^2,\ I_2 = \lambda_s^2\lambda_\varphi^2 + \lambda_s^2\lambda_3^2 + \lambda_\varphi^2\lambda_3^2,\ I_3 = \lambda_s\lambda_\varphi\lambda_3 \tag{6}$$

The incompressibility condition implies that $\lambda_3 = 1/(\lambda_s\lambda_\varphi)$ and that W does not depend on the third strain invariant, $I_3 = 1$. The meridional and azimuthal stresses can be expressed in terms the derivatives of W with respect to the stretches λ_s and λ_φ (Rivlin & Thomas 1951). The choice of W depends on the problem at hand. A popular choice for elastomers is the Mooney-Rivlin model

$$W = C_1(I_1 - 3) + C_2(I_2 - 3), \tag{7}$$

where C_1 and C_2 are certain elastic parameters. When $C_2 = 0$, Eq. (7) reduces to the so called neo-Hookean model, and for small deformation C_1 is related to Young's modulus, E, by $E = 6C_1$. We note that despite its linearity in the invariants the Mooney-Rivlin potential, and its neo-Hookean limit, is still capable of describing finite deformations. A variety of nonlinear material responses can be captured by considering more

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general functional forms of W, e.g. the Fung energy used for modeling soft tissue (Fung 1993).

Fundamental to any modelling of hyphal tip growth is the representation of the cell wall anisotropy. This will depend on the cell wall architecture and, in particular, the orientation of the chitin microfibrils. Possibilities range from (completely) random orientation of microfibrils leading to isotropic material properties, to a situation in which the microfibrils are aligned differently in both the plane of the cell wall and normal to the wall leading to fully anisotropic material properties (Dumais *et al.* 2006). In our model we take a simpler, phenomenological, approach that captures the essential soft spot hypothesis by simply prescribing the elastic response of the cell wall to vary along the meridional direction such that the distal regions of the hypha are practically rigid while the regions near the tip have a much smaller elastic modulus corresponding to a more flexible material. At this level of modelling one observes by scaling that a softer material response can, in effect, be interpreted as an increase in turgor pressure, and vice-versa.

The inclusion of growth effects in exact elasticity is, as mentioned above, a highly nontrivial topic. For a recent discussion and applications, see Ben Amar and Goriely (2005). In an earlier paper on hyphal growth (Goriely & Tabor 2003) we introduced a simple way of representing the growth process. There the hyphal wall was modelled as a two dimensional membrane and because of the axi-symmetric symmetry of the problem it becomes, effectively, a one-dimensional problem. Thus the growth of the cell wall becomes a problem of representing the growth of a material line and is simply achieved by the reparameterization of the curve, i.e. after each deformation of the wall the material points are redistributed uniformly: thereby resetting the arc-length along the wall for the next deformation step.

5. Results

Here we focus on some new results provided by our more general formulation (Goriely *et al.*, in prep.) in which the hypha is represented as an elastic shell including the possibility of bending moments and external tangential stresses. We show the effect on tip shapes resulting from external friction due to the medium, an examination of the normal growth hypothesis, and we also revisit the concept of a self-similar propagation of the hyphal tips.

First, we consider the evolution of a soft tip in the absence of surface friction. Using the membrane equations, a neo-Hookean energy, and an initially spherical shell with a soft

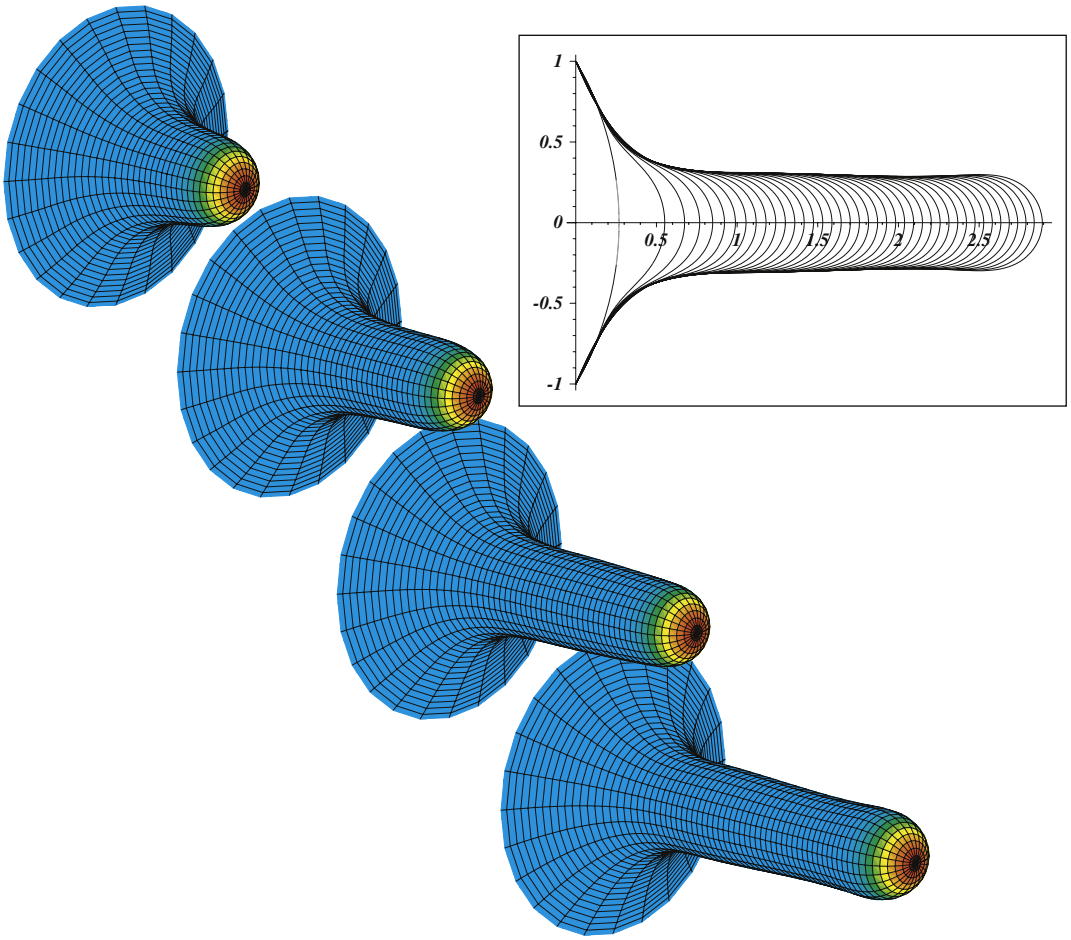

Fig. 2 – Evolution of a tip in 2D and 3D. This simulation is performed in the absence of external surface friction.

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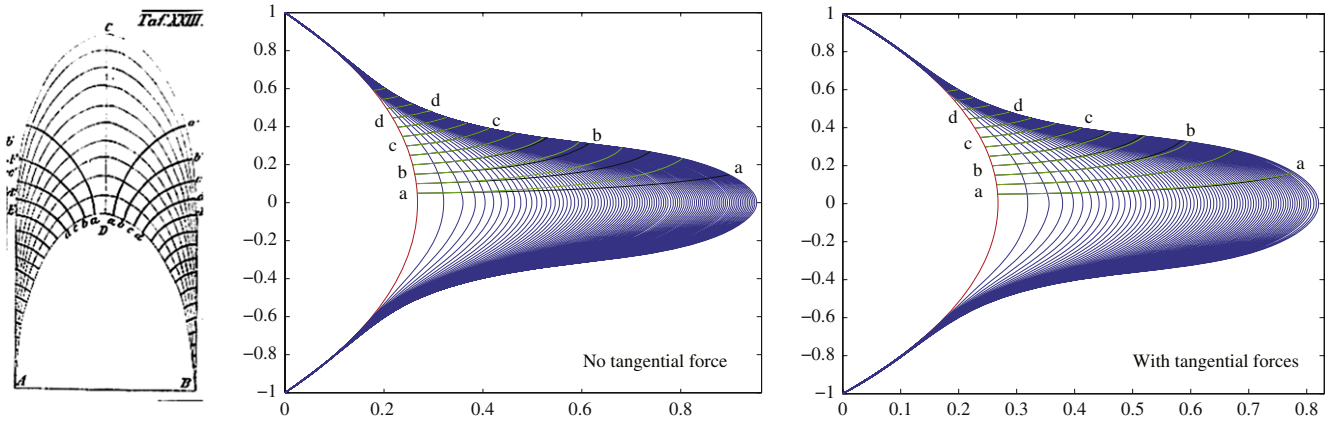

Fig. 3 – Effect of surface friction and the normal growth hypothesis. As friction increases, the tip flattens out and trajectories of normal points becomes increasingly normal (green: normal lines to the curves, black: material lines) consistent with Reinhardt's hypothesis (Drawing on the left).

spot, we can simulate the initial phases of hyphal growth a typical growth pattern over N time steps is shown in Fig 2.

We now consider the effect of external surface friction by increasing the value of the external tangential shear stress, τ_s, acting on the wall. In Fig 3 we show two different tip shapes with vanishing and non-vanishing surface friction. Note the flattening out of the tip as the surface friction increases. This theoretical prediction of tip flattening appears to be consistent with recent experimental results (Bowen *et al.* 2007). Furthermore, we can test the normal growth hypothesis by tracking the paths of material points on the tip surface and comparing them with what would be the equivalent normal paths. As we see in Fig 3 the particle trajectories do not follow normal paths for $\tau_s = 0$, but that as τ_s is increased the particle trajectories become ''normal''. This is a striking result and to the best of our knowledge has not been discussed before. Yet the reason for this may be quite straightforward: without having to work against external forces there is no energetic reason for the tip expansion to follow a normal path, but once such forces are included, such paths are the most work-efficient ones to follow.

Third, we consider the evolution of the tip shape during growth. To do so, we draw the evolution of the tip in a reference frame moving with the tip as seen in Fig 4. This analysis confirms our previous observation that over long-time simulations the tip propagation appeared to be self-similar, namely that at each time step the newly grown tip looks like a translation of the tip shape at the previous instant. This suggests that in the course of apical growth dynamics it is this (temporal) self-similarity, which will depend delicately on the local environmental conditions and material parameters, that characterizes the propagation rather than a specific mathematical form of the tip shape.

6. Discussion

Hyphal tip growth modelling encompasses different levels of description: the biomechanical level which aims to describe hyphal growth and morphology based on mechanical principles; the biophysical level which aims to translate the structural details of the cell wall into macroscopic material properties that must be incorporated in the mechanical models; and the biochemical level which aims to understand the molecular basis for the detailed structure and expression of the cell. Our results and those of others suggest that the biomechanical description is capable of describing many of the observed features of hyphal growth, and that the addition of biophysical information about the cell wall structure can give further insights into the growth process and, given sufficient information about the cell wall structure, help distinguish details of that process in different cells. In our bio-elastic modelling the ability to include external tangential stresses reveals a significant result; namely that the long-accepted normal growth hypothesis is conditioned by those stresses as a means of achieving the most work efficient tip propagation.

At the biomechanical level different modeling approaches are possible: the hyphal tip propagation and tip morphologies that our model of elastic growth can generate look similar to those produced by the visco-plastic modeling due to Dumais *et al.* (2006). In the latter work a hypha is represented as a plastically deforming dome whose equator is attached to a non-growing cylinder of fixed radius. Both the dome and the

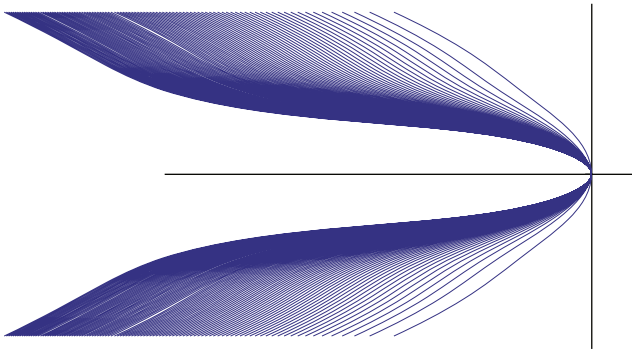

Fig. 4 – Evolution of tip shapes in the reference frame of the moving tip. As the tip grows, its shape evolves towards a self-similar shape.

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cylinder are maintained at a prescribed constant thickness. As the tip advances forward under plastic deformation the equatorial line where the dome and cylinder join is moved forward to follow the advance of the tip. The representation of the hypha as a two dimensional membrane with axisymmetric geometry results in a problem that is effectively one dimensional, namely all the pertinent variables are just functions of the meridional arc-length. With this choice of geometry, and under the assumption of a simple linear flow rule, explicit formulae for the meridional and azimuthal stresses, the strain rates, and corresponding displacement velocities can be obtained. Thus, for a given initial tip shape it is possible to determine if an effective stress exceeds a prescribed yield stress: if so, the linear plastic flow rules are used to compute the corresponding strain rates, and hence the displacement velocities. Given the velocities at each point, it is then possible, by simple time-stepping to compute the displacements of these points over a small time interval. In this approach the deformed meridian is (numerically) remeshed with uniformly spaced points; thereby redefining the arc-length for the ''next'' propagation step. This is analogous to our own approach in which the ''growth'' of the elastically deforming tip is represented by a reparameterization of the meridional space curve representing the tip profile. This also suggests why in the limit of infinitesimal displacements our nonlinear elastic growth model, in which growth is represented by means of a space-curve reparameterization, and their linear plastic flow model, can produce similar looking tip morphologies and tip propagation. Nonetheless, when the hyphae are treated as (true) shells undergoing larger displacements expressed by nonlinear constitutive relations and subject to external surface stresses, the two approaches become very different.

Acknowledgments

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