Journal of Theoretical Biology 336 (2013) 44–51

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

Basic rules for polarised cell growth

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HIGHLIGHTS

- Model provides a framework for exploring basic rules of polarised growth.
- Links wall material to deposition self-similar shape.
- Accurately predicts self-similar geometry in a range of organisms.
- Predicts the location of the region of maximal wall deposition in a range of organisms.

ARTICLE INFO

Article history:
Received 30 April 2013
Received in revised form
25 June 2013
Accepted 27 June 2013
Available online 10 July 2013

Keywords:
Curvature
Mathematical model
Tip growth

ABSTRACT

Growth by cell elongation is a morphological process that transcends taxonomic kingdoms. Examples of this polarised growth form include hyphal tip growth in actinobacteria and filamentous fungi and pollen tube development. The biological processes required to produce polarisation in each of these examples are very different. However, commonality of the polarised growth habit suggests that certain "basic physical rules" of development are being followed. In this paper we are concerned with trying to further elucidate some of these basic rules. To this end, we focus on a simple and hence ubiquitous description of the polarised cell, its geometry, and using a mathematical model investigate how geometry and the deposition of new wall material could be related. We show that this simple model predicts both cell geometry and the location of maximal wall-deposition in a range of examples.

1. Introduction

Growth by cell elongation is a morphological process that transcends taxonomic kingdoms. Examples include hyphal tip growth in actinobacteria and filamentous fungi, plant root-hair formation, pollen tube development and the development of neurons in animals (see e.g. Read and Steinberg, 2008; Flärdh, 2003; Rounds et al., 2011; Cáceres, 2012 and the reference therein). In microorganisms, such as fungi and bacteria, these structures have developed almost surely because they afford an evolutionary advantage, producing a growth habit well-suited to exploiting physically complex environments and facilitating the (internal) redeployment of nutrients over long spatial scales. For pollen tubes and neurons, again the polarised growth form allows for the efficient transfer of materials (sperm cells) and information (electrical impulses) over large spatial distances. The biological processes required to produce this polarised growth form are clearly very different when manifested in plant, bacterial, fungal or mammalian cells. Even within different classes of the same organism, the transport of vesicles containing wall-building materials to the growing tip can be achieved by very different mechanisms. For example, in pollen tubes the circulation of vesicles is in entirely opposite directions in angiosperm and gymnosperm (Kroeger and Geitmann, 2012).

Despite their biological differences, the basic mechanics of tip formation are similar in many cases including fungi, bacteria and pollen tubes—a soft region in the cell wall is located at or near the apex. This soft tip is stretched by internal forces and thus driven forward. A combination of turgor pressure, the developing cytoskeleton and the structure of the cell wall itself make up the driving forces (Read and Steinberg, 2008; Kroeger et al., 2011; Winship et al., 2010). Sub-apically, the wall stiffens and thus a tube-shaped cell is formed. The commonality of polarised growth structures across these diverse organisms suggests that certain "basic physical rules" are being followed that are in some sense independent of the precise mechanisms of delivery (Campàs et al., 2012). Moreover, if we compare even fungi and actinobacteria, it is clear that these rules are scaleable—tip growth is similar, despite the orders of magnitude difference in cell size (Davidson, 2010).

At a fundamental level, modelling tip growth processes require descriptions of (i) the cell wall and (ii) the delivery of materials to maintain the cell wall and produce new growth (Dumais et al., 2006).

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0022-5193/$ - see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.jtbi.2013.06.039

To mathematically describe the cell wall, both geometrical and biomechanical models have been developed. The former allows for the most basic, but qualitatively accurate description of possible self-similar tip-like shapes (e.g. Bartnicki-Garcia et al., 1989). More detailed biomechanical models take account of, for example, wall-material delivery and the balance of forces on the cell-wall, which is assumed to be a thin, differentially elastic or elasto-plastic membrane (e.g. Dumais et al., 2006; Goriely and Tabor, 2003; Dumais et al., 2004; Rojas et al., 2011). In these latter models, the tip shape is not predetermined, rather it evolves naturally through the mathematical rules for the material properties. See Goriely and Tabor (2008) for a comprehensive review of both approaches in modelling fungi and actinomycetes and Kroeger and Geitmann (2012), Geitmann (2010) and the references therein for pollen tube growth. Bernal et al. (1997) provide an overview of the transfer of modelling ideas from inert to biological materials in determining possible tip morphologies. More detailed properties of wall development continue to be investigated, for example in Eggen et al. (2011), the maturation of wall building material in fungal hyphae is explicitly modelled. Moreover, a model for pollen tube growth that encompasses both material deposition and wall deformation has recently been presented in Rojas et al. (2011). In this paper we are concerned with trying to elucidate some basic physical rules for polarised growth. Given that the delivery mechanism of wall-building materials and the properties of the wall itself can be very different in different organisms, we focus on a simple and hence ubiquitous description of the polarised cell: its geometry. However, the model analysed here lies at the interface between the approaches discussed above in that it relates the geometry of the tip to the deposition of wall-building materials in a mechanistic way. By developing a model first proposed in Goriely et al. (2005) as a way of describing hyphal tips of filamentous fungi and bacteria, we construct a basic description of how geometry and the deposition of new wall material could be related in a wider class of organisms.

The paper is organised as follows. In Section 2, we discuss the formulation of the model. To assist the reader and to provide sufficient clarity for the subsequent discussion, this includes a brief review of the basic model formulation given in Goriely et al. (2005). Then, in Section 3, we present an extension of this model and construct and analyse general forms for expressions determining the relationship between tip geometry and wall-material deposition. Finally, in Section 4, we present some examples of tip geometries and discuss how they are described by the model. We draw some brief conclusions and in particular note that the model is not only capable of capturing tip geometry, but also accurately predicts the location of maximum wall deposition in a wider class of organisms.

2. Construction of the model

2.1. Basic description

It is a common feature of polarised growth in many organisms that a self-similar shape is formed at the apex of the cell that moves forward with constant average velocity. It is well-known that many organisms including fungi and pollen tubes can exhibit both random fluctuations in extension rate and pulsatile growth (see e.g. Rojas et al., 2011; Sampson et al., 2003), but the *average* velocity can be reasonably assumed constant. Thus, it is assumed that the medial section of the polarised cell can be described by a curve, C, that translates at a constant speed, U_0, in a given spatial direction. The curve, C, can be parameterized by arc length, s, and time, t, see Fig. 1. A moving frame of reference, (x,y), is associated with the tip, the vertex being located at the origin in this moving

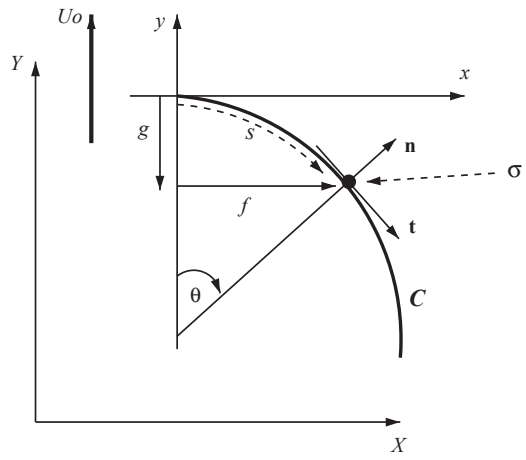

Fig. 1. The curve, C, and the associated variables.

frame. The tip is assumed to be axisymmetric about the y-axis. Hence a three-dimensional representation of the tip can be generated by rotating the curve C around the y-axis through 2π radians. Further assumptions can be made as follows: (i) the arc length, s, can itself be parameterised by the material coordinate, σ, and time, t, i.e. $s=s(\sigma,t)$ and (ii) the tip shape does not explicitly depend on t, i.e. the tip is self-similar and any change in the profile is due to the movement of material points with respect to each other and not through translation of the curve (other than in the Y-direction). Thus, relative to the origin in the fixed frame of reference, (X,Y), the curve can be identified by

$$\mathbf{r}_C(s(\sigma,t),t) := (X(s,t),Y(s,t)) = (X_0+f(s(\sigma,t)),Y_0+g(s(\sigma,t))+U_0t),$$

where (X_0,Y_0) is the location of the origin of the moving frame at $t=0$ (this can be set to be $(0,0)$ without loss of generality), U_0 is the translation speed introduced above and (f,g) is the coordinate of the material point σ on C with respect to the moving frame of reference. The angle θ marked in Fig. 1 is defined to be the angle between the normal $\mathbf{n}$ to the curve at σ and the y-axis. The dynamics of the curve can therefore be expressed as

$$\frac{d\mathbf{r}_C(s(\sigma,t),t)}{dt} = \left(\frac{df}{ds}\frac{\partial s}{\partial t}, \frac{dg}{ds}\frac{\partial s}{\partial t}+U_0\right) =: W\mathbf{t}+U\mathbf{n}, \tag{1}$$

where W and U denote the magnitude of the tangential, $\mathbf{t}$, and normal, $\mathbf{n}$, components of the velocity, respectively, where

$$\mathbf{t} = \left(\frac{df}{ds},\frac{dg}{ds}\right) = (\cos\theta, -\sin\theta) \quad \text{and} \quad \mathbf{n} = (-\sin\theta, -\cos\theta). \tag{2}$$

From (1), and on taking the scalar product with $\mathbf{n}$ and $\mathbf{t}$ in turn, it follows that

$$U = U_0\cos\theta \quad \text{and} \quad W = \frac{\partial s}{\partial t} - U_0\sin\theta. \tag{3}$$

A key assumption of the model is that W can be set to zero. This is in line with the long-standing *normal growth hypothesis*, first proposed in Reinhardt (1892). This hypothesis states that any material point embedded in the cell wall will move normal to the wall. Reinhardt (1892) made this conclusion based on observations and projection methods, but discounted turgor as being the main cause of this phenomenon. It was not until 2000 that the orthogonal movement of particles adhered to the outside (and inside) surface of fungal hyphae was reported (Bartnicki-Garcia et al., 2000). In that paper, the key conclusion was that this orthogonal movement of wall material was a result of turgor pressure (which is by definition orthogonal to the wall and equal at all areas of the tip). Thus it is proposed that the forward motion of the tip shape is a result of this internal pressure and the anisotropic delivery of wall-building materials released from an