

RESEARCH ARTICLE

DERIVATION OF FORMULA OF APPROXIMATE IDEALIZED HYPHAL CONTOUR AS BUILT-IN HYPHAL FITTING PROFILE

M.Z.A.M. Jaffar* and M.B.A. Ayop

Department of Mathematics and Statistics, Faculty of Science, Universiti Putra Malaysia, 43400 Serdang, Selangor, Malaysia.
Department of Mathematical Science, Universiti Teknologi Malaysia. Could you Google full address of this Universiti?
*Corresponding Author E-mail: maizurwatul@upm.edu.my

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ABSTRACT

Hypha consists of two regions; cap (apex) and cylindrical shaft (subapex and mature combined). The hyphal-cap is the most critical part due to its dominant role in the hyphal-wall growth and morphogenesis. Just how the hyphal-wall growth is regulated in order to maintain its tubular shape has been the subject of much research for over 100 years. Here, we derived a formula of approximate idealized hyphal-contour based on gradients of secant lines joining a fixed coordinate at the starting hyphal-shaft to any coordinates on the contour. The formula is capable of being a control for experimental analysis in which it is not limited to one specific shape of the hyphal-like cell. Also, it potentially can play a role as built-in or ready-made hyphal-fitting profile that "best fits" microscopic images of various actual hyphal-like cells. In other words, given a microscopic image of hyphal-like cell, mycologists and microbiologists would not have to wonder about mathematical representation of its contour since the formula has prepared for it.

KEYWORDS

Hyphal tip growth; Gradient; Control hypha; Experimental hypha; Microscopic image

1. INTRODUCTION

Hypha is a single filament in a fungus consisting of two regions; cap (apex) and cylindrical shaft (subapex and mature combined). Hypha grows at its tip and such growth mode is called hyphal tip growth (see Figure 1 (Left)) (Davidson, 2007; Harold, 1997). The cap is the most critical part due to its dominant role in hyphal wall growth and morphogenesis. Penetrating-physical power and powerful tensile strength possessed by hypha is what affords it to exploit physically complex environments. This results in hypha has evolutionary advantage and ecological significance offering an important role in industries useful for human life as well as threaten food security, health and biodiversity (Read and Steinberg, 2008; Boswell, 2007; Flrdh, 2003; Harold, 1997; Davidson, 2007). However, complete details of its complex growth process remains a matter of discussion. Hence, just how hyphal tip growth is regulated in order to maintain its tubular shape has been the subject of much research for over 100 years.

Examining such cell forms has been developed from both biomechanical and geometrical models (Gierz and Bartnicki-Garcia, 2001; Goriely et al., 2005; Goriely and Tabor, 2003; Trinci and Saunders, 1977; Saunders and Trinci, 1970; Bartnicki-Garcia et al., 1989). The former focuses on balance of forces on the cell wall, where the wall is assumed to be a differentially thin elastic membrane. As for geometrical model, it offers the plausible fundamental description of possible hypha-like shapes. For example, geometrical model proposed by a previous researcher, where its key assumption is tip curvature, κ , is proportional to vesicle-incorporation for

wall building process, n (Goriely et al., 2005). Also, tip monotonicity is stated as κp , for $p \geq 1$. In following years, a researcher suggested that $p > 0$ also results in a monotonically increasing function of κ (Jaafar and Davidson, 2013). From what it follows, it serves as a motivation for this study to derive a formula of a two-dimensional approximate idealized hypha as control hypha allowing experimental hypha to be examined from the context of model proposed by (Goriely et al., 2005). The contour generated from the formula evolves naturally from trends of gradients of secant lines along the idealized contour. Tendency of points on idealized cap contour to depart from tangent lines drawn to the contour at those points is represented by exponentiality featured in the formula. The state of idealized hyphal-cap being curved is restricted by a constraint paving the way for tangency-comparison between actual cap contours and idealized cap contour.

The paper is structured as follows. In Section 2, we proposed geometrical setting of two dimensional idealized hypha and associated secant lines. While, Section 3 suggests plausible proportionality of gradient-trends. Next is Section 4, which it analyzes range of tip monotonicity. Finally, Section 5 draws a conclusion of this study and its future study.

2. GEOMETRY OF APPROXIMATE IDEALIZED HYPHAL CONTOUR

Half the approximate idealized hyphal contour denoted by $r(x)$ shown in Figure 1 (Right). Let $(b, r(b)) = (-\pi/2, \pi/2)$ be a fixed coordinate. The secants lines are drawn from the fixed coordinate to any coordinates on

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$r(x)$ denoted by $(x, r(x))$, where, $x \in [-2\pi, 0]$. Hence, gradient is

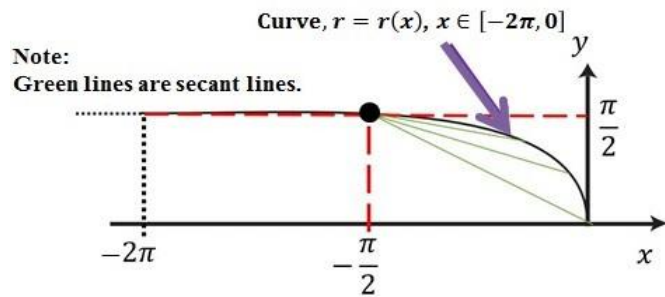
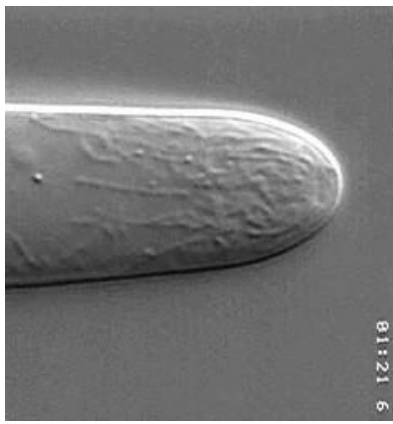


Figure 1: Left: A filamentous fungus known as *Allomyces macrogynus*. Taken from [14] with kind permission. Right: Half the contour of cross-section of the approximate idealized hyphal contour denoted by $r(x)$ and associated secant lines (green).

$$g = \frac{r(x) - \pi/2}{x + \pi/2}, \quad (x \neq -\pi/2). \tag{1}$$

Values of g of the secant lines on $r(x)$ for $-2\pi \leq x \leq 0$ can be generally summarized by

$$g = \begin{cases} 0, & -2\pi \leq 0 \leq -\pi/2 \\ q, & (q \in [-1, 0)) \wedge (-\frac{\pi}{2} < x \leq 0). \end{cases} \tag{2}$$

3. PLAUSIBLE PROPORTIONALITY OF GRADIENT-TREND

Equation (1) offers clues that $g \propto (r(x) - (\pi/2))$ and $g \propto 1 \div (x + \pi/2)$. As for $g \propto (r(x) - (\pi/2))$, its nearest similar trend is curvature. Let $K(x)$ denotes curvature at a point on $r(x)$ defined by $K(x) = 1/p$, where p is radius of a circle (known as radius of curvature) drawn at a point on $r(x)$ that best approximates $r(x)$ at that point. The simplest (and nearest) choice for $K(x)$ is exponential function, that is, $K(x) = \hat{\kappa}(x)(\pi/2) = kx(\pi/2)$, ($k \in R^+$, $-2\pi \leq x \leq 0$). Next, $g \propto 1 \div (x + \pi/2)$ shows that increasing g occurs concurrently with decreasing $(r(x) + \pi/2)$ for $(-\pi/2) < x \leq 0$. To sum up, g on $r(x)$ can be mathematically mimicked by

$$g \approx K(x) \div (r(x) + \pi/2). \tag{3}$$

Equating LHS of (1) with the negative of RHS of (3) and then solving for $r(x)$ gives

$$r(x) \approx \pm \sqrt{(\pi/2)^2 - (\pi/2)\hat{k}(x)(x + (\pi/2))}, \tag{4}$$

which represents a formula of half the contour of cross-section of the approximate idealized hypha where the starting hyphal shaft is at $x = -\pi/2$.

4. APPROXIMATE IDEALIZED HYPHAL CONTOUR

Recalling (4), $\hat{k}(x)(\pi/2) = k^x(\pi/2)$, ($k \in R^+$, $-2\pi \leq x \leq 0$). The state of the approximate idealized cap is being curved lies in choosing k . For this reason, we investigated the approximate idealized hyphal-cap constraint

denoted by $w^*(x)$ focusing on $-\pi/2 \leq x \leq 0$ due to the growth activity is concentrated within such an interval. Following that, firstly,

$$0 \leq (\pi/2)\hat{w}(x)(x + (\pi/2)) \leq (\pi/2)^2. \tag{5}$$

Next, for $-\pi/2 < x \leq 0$, it is observed that $(x + (\pi/2)) \geq 0$. For this reason,

$$\hat{w}(x) \leq (\pi/2)^2 \div ((\pi/2)(x + (\pi/2))) = (\pi/2) \div (x + (\pi/2)), \tag{6}$$

where $-\pi/2 < x \leq 0$. For instance, $B(x) = (\pi/2) \div (x + (\pi/2))$ is sandwiched between $A(x) = 2 \div (x+2)$ and $C(x) = 1.2 \div (x+1.2)$, where A, B and C share one common feature, namely, the y -intercept is 1. Next, based on (4), for $-\pi/2 \leq x \leq 0$, if $r(0) = 0 = r(x) \approx \sqrt{(\pi/2)^2 - (\pi/2)\hat{w}(0)(0 + (\pi/2))}$, then $\hat{w}(0) = 1$. At $x = -\pi/2$, $(r(-\pi/2))^2 = (\pi/2)^2 = (\pi/2)^2 - (\pi/2)\hat{w}(-\pi/2)(-\pi/2 + (\pi/2))$. But $\hat{w}(-\pi/2)$ is unclear. With this in mind, investigation of the radicand of (4) is necessary that can be divided by three cases:

Case 1: The Radical is negative.

$$(\pi/2)^2 - (\pi/2)w^*(x)(x + (\pi/2)) < 0, \tag{7}$$

gives

$$w^*(x) > (\pi/2)^2 \div (\pi/2)(x + (\pi/2)) = (\pi/2) \div (x + (\pi/2)), \tag{8}$$

for $(\pi/2 < x \leq 0)$. Notice that $(x + \pi/2) > 0$ till $w^*(x) > 0$. But, $w^*(x) \rightarrow +\infty$ as $x \rightarrow -\pi/2$ and it is only true if it satisfies (7). Note that for $x \leq -\pi/2$, $r(x) = \pi/2$ till $r'(x) = 0$. While, for $-\pi/2 \leq x \leq 0$, it suggests $2r(x)r'(x) = -(\pi/2)(w^*(x)) - w^*(x)(x + (\pi/2))$. Next, at $x = -\pi/2$, $w^*(-\pi/2) = 2(r'(-\pi/2)) \div (\pi/2)$. But, $r'(-\pi/2)$ does not exist and so $w^*(-\pi/2)$ does not exist. No conclusion can be made in this case.

Case 2: The radicand is positive.

$$(\pi/2)^2 - (\pi/2)w^*(x)(x + (\pi/2)) > 0. \tag{9}$$

Thus, $w^*(x) < (\pi/2) \div (x + (\pi/2))$. To get a clue of $w^*(x)$ in this case, any two values of $x \in (-\pi/2, 0)$ were chosen, such as: $w^*(-\pi/4) < 2$ and $w^*(-3\pi/8) < 4$. By induction, $w^*(x) < +\infty$ for $-\pi/2 \leq x \leq 0$. Let $x = x_1$ such that $-\pi/2 < x_1 \leq 0$, thus $w^*(x_1) = (\pi/2) \div (x_1 + (\pi/2))$. Consequently, $x_1 = 1 - (\pi/2) \approx -0.571$. Subsequently, $w^*(1 - \pi/2) < \pi/2$. Therefore,

$(0, 1)$, $(1 - \pi/2, w^*(1 - \pi/2))$, $(-\pi/4, w^*(-\pi/4))$, $(-3\pi/8, w^*(-3\pi/8))$, are not colinear but such points form an exponential-like graph.

Case 3: The radicand is neither negative nor positive

$$-x \leq r(x) \leq \sqrt{(\frac{\pi}{2})^2 - (\frac{\pi}{2})\hat{w}(x)(x + (\frac{\pi}{2}))} \tag{10}$$

Since $-\pi/2 \leq x \leq 0$, then $-x \geq 0$. Simplifying (10) gives $x^2 \leq (\pi/2)^2 - (\pi/2)w^*(x)(x + (\pi/2))$, where $-\pi/2 < x \leq 0$ resulting in $w^*(x) \leq ((\pi-2x) \div \pi)$. From what it follows, $w^*(0) \leq 1$ and $w^*(x) \leq 2$ for $-\pi/2 < x \leq 0$. Since $w(x)$ is not linear as concluded in Case 2, its closest expression is $w^*(x) = w^{-x}$, where

$$w^*(x) \approx \begin{cases} 1, & x = 0 \\ 2, & x > -\pi/2 \end{cases} \tag{11}$$

Solving for w in (11) at $x > -\pi/2$ gives $w = 2^{2/\pi}$. However, recall that Spitzenkörper lies within approximately at $-\pi/4 < x \leq 0$, where it represents high-curvature region of $r(x)$ which is in agreement with physiology of hyphal cells. Here, we choose $x = \pi/5.2465$ since $\pi/5.2465 > \pi/2$ and so $w = 2^{5.2465/\pi}$. To summarize,

$$w^*(x) \approx 2^{-\frac{(5.2465x)}{\pi}} = \begin{cases} 1, & x = 0 \\ 2, & x > -\frac{\pi}{5.2465} \approx -\frac{\pi}{5.2465}, \end{cases} \tag{12}$$

which is an approximate constraint of hyphal-cap contour of (4). Subsequently, as guided by (12) and basic mathematical rule of hyphal-shaft contour, namely, $r'(x) \approx 0$ for $x \leq -\pi/2$, it is observed that $82 \leq k \leq 82.3$. Choosing $82 \leq k \leq 82.3$ results in $r'(-\pi/2) \leq -0.0004$ which ensures that $r(x)$ at $-2\pi \leq x < -\pi/2$ is closer to 0.

5. DISCUSSION

The formula stated in (4) displays the two-dimensional hyphal-contour, where the starting hyphal-shaft contour is at $x = -\pi/2$ as proposed by (Goriely et al., 2005). Also, notice that the starting hyphal-shaft contour is actually length of hyphal-cap contour, L_c , here, $L_c = \pi/2$. Furthermore, radius of hyphal-cap contour, is denoted by R_c , that is, $R_c = \pi/2$ as well. While, the exponentiality, k^x ($k \in \mathbb{R}^+$), in (4) reflects the state of the hyphal-cap contour being curved. In reality, L_c and R_c of actual hyphal contours are not necessarily equal to $\pi/2$. Differences in size and in shape depend upon species and other factors influencing the growth. Speaking of species, it was observed that re- placing $L_c = \pi/2$ with either $L_c > \pi/2$ or $L_c < \pi/2$ with a suitable k still ables for $r(x)$ to produce different sizes and shapes of hyphal-like contours. This tells that the formula can also be used as control for experimental results of other hyphal-like cells such as pollen tube, root hair and neurons in animals. Besides that, the formula stated in (4) can also act as a built-in hyphal-fitting profile making it easy for mycologists and microbiologists to quickly find the "best fit" to microscopic images of various actual hyphal-like cells. This means that mycologists and microbiologists should not be concerned about finding a mathematical expression that "best fits" the contour of the given microscopic image. Instead, mycologists just have to adjust L_c and k to smooth the profile and improve its appearance. Therefore, (4) can be rewritten generally as

$$r(x) \approx \pm \sqrt{(L_c)^2 - (L_c)k^x(x + (L_c))}, (k \in \mathbb{R}^+, -2\pi \leq x \leq 0). \quad (13)$$

In the light of the above, this profile illustrates relationship between L_c and k . Caution should be taken when plotting (4) in order to study the relationship due to graphical illusion. Such an illusion appears that the profile idealistically obeys its idealistic basic mathematical rules that state $0 \leq r(x) < \pi/2$ and $r(x) = \pi/2$ for $-\pi/2 \leq x < 0$ and $-2\pi \leq x \leq -\pi/2$, respectively. The illusion is immediately crushed by examining the $r'(x)|_{-2\pi \leq x \leq -\pi/2}$, where $r'(x)$ can never be equal to zero but closer to zero since $r'(x) = -(1/2)k^x$. Another important observation is just because the hyphal-cap contour satisfies its constraint, $w'(x)$, does not necessarily mean the hyphal-shaft contour satisfy its basic mathematical rule. The hyphal-shaft contour violates its idealistic rule when $r'(x) \neq 0|_{-2\pi \leq x \leq -\pi/2}$. This actually boils down to choosing a suitable k , which means $r'(x)$ is closely approaching 0 as k increases.

6. CONCLUSION

The formula derived in this work refers to approximate idealized hyphal-like contour, which is based on gradients of secant lines. Its capability of being a control for experimental analysis is not limited to one specific

shape of the hyphal-like cell. Also, it potentially can play a role as built-in hyphal-fitting profile that "best fits" microscopic images of various actual hyphal-like cells.

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