



Fungal dynamics: how real fungi grow

On the previous page we established that the fundamental cellular component of fungi is the hypha, and that the crucial features of this that determine the way it grows are (a) extension growth occurs only at the hyphal apex; (b) cross walls always form at right angles to the long axis of a hypha; (c) nuclear division is not necessarily linked to “cell” division; (d) formation of hyphal branches is the only way to increase the number of growing points.

Filamentous hyphal growth is inherently suited to kinetic analysis, and the mathematics of hyphal tip extension is well established. Direct observation and measurement established a number of general relationships that are expressed in **equation (1)**,

$$\bar{E} = \mu_{max} G \quad (1)$$

where \bar{E} is the mean extension rate of the colony margin; μ_{max} is the maximum specific (biomass) growth rate; and G is the hyphal growth unit length.

G is defined as the average length of a hypha supporting a growing tip according to **equation (2)**:

$$G = \frac{L_t}{N_t} \quad (2)$$

where L_t is total mycelial length, and N_t is number of hyphal tips (= number of branches).

The hyphal growth unit is approximately equal to the width of the peripheral growth zone (more accurately, the *volume of the hyphae within that zone*), which is a ring-shaped peripheral area of the mycelium that contributes to radial expansion of the colony.

Equation (1) is the crucial understanding because it contains all of the elements necessary to completely define mycelial morphology – hyphal length, number of branches and growth rate, and if you want more detailed information or explanation you should refer to the publications cited in the following **information box**.

The influences of several external factors on the direction of hyphal growth and branching are also well understood. These cause so-called **tropisms**, which are evidenced as growth **towards** (that's called a **positive [+ve] tropism**) or **away from** (described as a **negative [-ve] tropism**) the source of the signal.

Despite the fact that the fundamental hyphal growth equation can be written with confidence, and that it is relatively easy to understand the most likely effects of tropisms, it is not easy to use these understandings to form a mental picture of the behaviour of a *large population of hyphal tips*, or the way that the hyphal network is established.

Essential reading about filamentous hyphal growth:

To learn more about fungal growth kinetics we suggest you start with **Liam McNulty's** review, which is on the website http://www.davidmoore.org.uk/Sec02_00.htm.

For more detail, view Chapter 4: *Hyphal cell biology and growth on solid substrates* of our **21st Century Guidebook to Fungi** at http://www.davidmoore.org.uk/21st_Century_Guidebook_to_Fungi_PLATINUM/Ch04_00.htm.

And here are three of the original scientific publications you can download from this site:

Trinci, A.P.J. (1974). A study of the kinetics of hyphal extension and branch initiation of fungal mycelia. *Journal of General Microbiology*, **81**: 225-236.

Trinci, A.P.J., Wiebe, M.G. & Robson, G.D. (1994). The mycelium as an integrated entity. In: *The Mycota* vol. I (eds. J.G.H. Wessels & F. Meinhardt), pp. 175-193. Springer-Verlag: Berlin & Heidelberg. ISBN-10: 3540577815, ISBN-13: 978-3540577812.

Trinci, A.P.J., Wiebe, M.G. & Robson, G.D. (2001). Hyphal growth. In: *Encyclopaedia of Life Sciences*. John Wiley & Sons, Ltd. DOI: <http://dx.doi.org/10.1038/npg.els.0000367>.

What is required is a *mathematical model that represents growth of hyphal apices in a way that lends itself to computer visualisation*. There are several models describing the growth of fungal mycelia in the literature. As well as incorporating the equations dealing with general parameters (such as mass, total length of hyphae, total number of tips, etc.), some authors have implemented algorithms for the simulation of morphogenesis.

Computer programs, written using these algorithms, have produced images of the growing and branching mycelia the routines generate that can be compared with images of real fungi. So they go some way towards satisfying the need for a representational model.

Unfortunately, most of the *older growth models only simulate growth of mycelia on a single plane*, mainly because the authors were concentrating on simulating growth on agar-solidified media. But two-dimensional space has some specific features that reduce the value of the simulations obtained. In particular, in a rigidly two-dimensional world a hypha cannot cross the path of another hypha, because in two dimensions such an event is a collision between the two hyphae. In two dimensional space turning up or down to avoid a collision is not an option because the vertical direction (the **z axis**) does not exist.

However, in the real three-dimensional world crossing the path of another hypha is not a problem because the approaching hyphal tip can extend above or below the original hypha, and may be some distance above or below the original hypha. Consequently, modelling hyphae growing on a flat plane may be able to approximate the growth of a circular colony but it does not provide a realistic simulation of living fungi.

Our purpose was to create a system that would provide life-like simulations of the *three dimensional growth of fungal mycelia* that used existing factual knowledge of the growth patterns of living fungal mycelia.

We structured the mathematical model so that what is known about regulation of fungal growth can be applied by the user to control the hypothetical (virtual or cyber-) hyphal apex.

This is most easy to do with a **vectorial model** so that the growth vector of the apex can then be influenced by external (= tropic) factors. It is then a matter of reducing the known hyphal growth control factors to mathematical representations that can be used to inform the growing apex and modify its growth vector.

In the model (as in life) the hyphal filament is the growth vector of the apex. In fact, *the hyphal filament is the historical record of the successive positions in space previously occupied by the growing apex.*

On the next two pages we describe (first as a verbal description, then as the mathematical description) the computer model that provides a life-like tool that enables the user to experiment on the impact of tropisms by actually **visualising on screen the virtual hyphal growth patterns**. We call it the *Neighbour-Sensing mathematical model of hyphal growth*. This model:

1. is vector based
2. calculates the effect of surroundings on the growth vector of each apex
3. calculates the effect of surroundings on the probability of branching
4. creates a real-time visualization.