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Review

Mathematical modelling of mycelia: a question of scale

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ABSTRACT

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Recent advances in systems biology have driven many aspects of biological research in a direction heavily weighted towards computational, quantitative and predictive analysis, based on, or assisted by mathematical modelling. In particular, mathematical modelling has played a significant role in the development of our understanding of the growth and function of the fungal mycelium. One of the main problems that faces modellers in this context is the choice of scale. In the study of fungal mycelia, the question of scale is expressed in an extreme manner: Their indeterminate growth habit ensures that the investigation of the growth and function of mycelial fungi has to consider scales ranging from the (sub) micron to the kilometer. An excellent and extensive review of the applications of mathematical modelling to fungal growth, conducted up to the mid-1990s, can be found in Prosser (1995). In this article, we will concentrate on work since that date, with the emphasis being on recent developments in understanding fungal mycelia at all scales.

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1. Introduction

Recent advances in genomics and the subsequent, reactive development of “systems biology” have driven many aspects of biological research in a direction heavily weighted towards computational, quantitative and predictive analysis. Mathematical modelling has played a key role in this development as it provides a powerful and efficient method of investigation that can provide deep insight into the complex interactions between biological systems and their environment. Given the ubiquitous use of mathematical modelling as an adjuvant experimental tool, it is of no surprise that it has played a significant role in the development of our understanding of the growth and function of the fungal mycelium. Indeed, modelling techniques have been employed in this area for many years. An excellent and extensive review of the applications of mathematical modelling to fungal growth, conducted up to the mid-1990s, can be found in Prosser (1995). Consequently,

in this article we will concentrate on developments in this area since that date, with the emphasis being on recent work.

In his seminal paper on morphogenesis, Turing (1952) wrote, “[a mathematical model] is a simplification and an idealisation”. This succinctly captures the aim of mathematical modelling. It is not the goal of the mathematical modeller to form an extremely complex system of equations in an attempt to mirror reality. All that achieves is the replacement of one form of impenetrable complexity with another. Instead, the aim is to reduce a complex (biological) system to a simpler (mathematical) system where the rigorous, logical structure of the latter can be used to identify, isolate and investigate key properties. However, as Einstein is famously quoted “everything should be made as simple as possible, but no simpler”. Hence, mathematical modelling is not about what to include, but instead, what can be omitted, where the art is in achieving a meaningful balance between the two.

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One of the main problems that faces modellers is the choice of scale. Clearly, it must first be decided what specific biological questions are to be addressed. It must then be decided at what scale these questions are most likely to be expressed. Once this has been set, the modeller can then construct a meaningful framework at the appropriate scale. This is precisely the method used in the application of mathematical modelling to e.g. physical science and engineering problems. For example, in fluid dynamics, when one is concerned with the macroscopic properties of fluid flow, then usually the Navier Stokes equations form the basis for mathematical models. These equations describe the fluid as a continuum: if one is solely concerned with the macroscopic properties of flow, there is no direct requirement to model the movement and interaction of individual water molecules making up that flow (although the Navier Stokes equations are in some sense derived from a knowledge of these interactions).

Of course, in some cases it is advantageous to attempt to construct models that operate at a range of scales by the transfer of information across scale boundaries. Indeed, this problem of *multi-scale modelling* of biological systems is currently the subject of intense interest and some such models for mycelial development and function have been constructed, as discussed below.

2. Modelling at the extremes of scale

In the study of fungal mycelia, the question of scale is expressed in an extreme manner. The indeterminate growth habit of the mycelium can produce massive organisms (one clone of *Armillaria gallica* has been measured to have spread over 15 hectares of forest, [Smith et al. 1992](#)), whilst the modular building block of these structures, the fungal hypha, is only a few microns in diameter. To model the interaction of such extremes of scale is an almost overwhelming task. However, significant developments in modelling mycelial fungi have been made by focusing on selected ranges.

At the macro-scale it is the interaction of fungi with the environment that forms the main focus. For example, in [Parnell et al. \(2006\)](#), the coexistence of fungicide-resistant and sensitive strains of a fungal crop pathogen is addressed via a model comprising ordinary differential equations. A threshold value for the fraction of fields sprayed in a given region is identified above which it is predicted that fungicide-resistant strains will always be able to establish themselves (yielding the possibly counter-intuitive result that region-wide spaying may not necessarily be the best policy). The variables in the model developed by [Parnell et al.](#) represent the density (number) of fields in a given region that are infected by or free from either strain of pathogen (see also [Bailey & Gilligan 1997](#); [Webb et al. 1999](#); [Gilligan & Kleczkowski 1997](#); [Parnell et al. 2005](#)). Explicit spatial variation in model variables at this scale has also been considered by [Stacey et al. \(2004\)](#), who adopt a similar, but spatially extended, approach to the study of the spread of *Rhizomania* (see [Fig. 1](#)).

In [Lamour et al. \(2000, 2002\)](#), modelling is again at the macro-scale but here it is the production of fungal biomass by consumption of substrates, which forms the focus. Carbon and nitrogen are isolated as two important growth limiting

factors and a model is developed that analyses the absorption from the substratum of these elements (in the form of more complex compounds) by the developing mycelium. Thus the external substrates carbon and nitrogen are internalized to form internal metabolites, which are then available to the mycelium to produce and maintain biomass. As in the first models discussed above, the model comprises ordinary differential equations and thus considers densities (of internal and external substrates and biomass) with no explicit spatial resolution, but from which total quantities per unit area could be derived. Using the model, conditions are predicted under which a sustainable invasion of a generic fungal species can be maintained in a previously uninfected area.

At the other extreme of scale, much modelling work has been and still is devoted to the investigation of the development of hyphal tips and also to a lesser degree, to tip branching and anastomosis. Two main hypotheses regarding the formation and advancement of hyphal tip formation have developed in parallel over the past two decades. The steady-state (SS) theory of [Sietsma and Wessels \(1994\)](#) proposed that plastic wall material is continually deposited at the hyphal apex and cross-linked into a more rigid form over time. The second hypothesis revolves around the concept of a vesicle supply centre (VSC) ([Bartnicki-Garcia et al. 1995](#); [Gierz & Bartnicki-Garcia 2001](#)). This theory predicts that the Spitzenkörper or equivalent structure acts as a distribution point for vesicles containing cell wall synthesizing materials. It suggests that a gradient of exocytosis would be created as this vesicle assembly point, which moves with the growing hyphal tip. It is this gradient that is hypothesized to be responsible for the shape of the apical dome. There is still debate as to how the tip is actually driven forward, but turgor pressure is assumed to play some role as discussed in detail in [Bartnicki-Garcia \(2002\)](#) (see also [Regalado et al. 1997](#)) where it is also proposed that a model combining elements of the VCS model (to explain the spatial organization of the fungal tip) and the SS model (to account for the temporal control of wall flexibility) presents a more realistic approach. A detailed and extensive account of the development of the various theories regarding hyphal tip growth is given in [Bartnicki-Garcia \(2002\)](#). (See also [Goriely & Tabor \(2003a, b\)](#) for the modelling of related hyphal growth dynamics in actinomycetes, where turgor pressure is known to play a more identifiable role in hyphal extension.) Very recently the VSC model has been extended by [Tindemans et al. \(2006\)](#) to include important details of the diffusive transfer of the vesicles from the Spitzenkörper to the hyphal wall and their subsequent fusion with the cell membrane ([Fig. 2](#)). These theories have been developed and tested using mathematical modelling, and supported by appropriate experimental results.

The mathematical modelling of hyphal branching has also gained attention. For example, in [Regalado et al. \(1997\)](#), [Regalado \(1998\)](#), [Regalado and Sleeman \(1999\)](#), a model is derived in which the cytoskeleton is described as a viscoelastic fluid. Viscoelastic forces are coupled to a conservation equation governing vesicle dynamics. The results of this work strongly suggest that the formation of the Spitzenkörper and the series of dynamical events leading to hyphal branching, arise as a consequence of the bias in vesicle motion resulting from interactions with the cytoskeleton (see [Fig. 3](#)). In [Regalado \(1998\)](#)

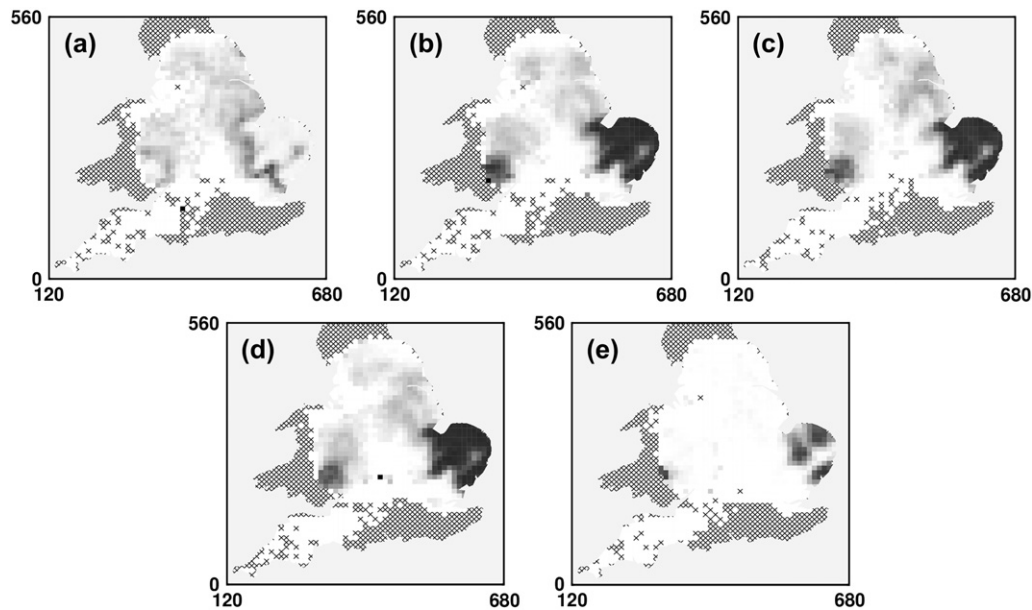


Fig. 1 – The spatial distribution of *Rhizomania* in sugar beet in the south of the UK in the year 2050 as predicted by the model of Stacey *et al.* (2004). Maps a and b show the distribution of asymptomatic (but infested) and symptomatic farms, respectively. The distribution of symptomatic farms if: c containment; d restriction of within-farm transmission and; e restriction of between-farm transmission to 10 % of its standard level, are implemented from the year 2000. From Stacey *et al.* (2004) with kind permission.

the model is used to explain how the Ca^{2+} status at the tip may be responsible for the apical accumulation of vesicles and for an increase in the cytosol osmotic pressure, accompanied by the contraction of the cytoskeleton.

3. Modelling at the single colony scale

At the intermediate or “single colony” scale, the interaction of the microscopic, modular components of the mycelium to produce centimeter-scale growth dynamics is striking. Indeed, the images of mycelial growth and interaction at this scale reported by Rayner and co workers in the 80s and early 90s (see e.g. Raynor *et al.* 1995) provided impetus for redevelopment of mathematical modelling at this scale, which continues to this day. The modelling approach adopted at this scale generally falls into two categories. One approach is to assume that the mycelium is a continuum, the properties of which can be viewed in some sense as an average of the properties of the individual components (much like in the fluid dynamics example given above). Such models have their roots in the earlier work of Edelstein and co-workers see e.g. Edelstein (1982), Edelstein and Segel (1983), Edelstein-Keshet and Ermentrout (1989). The models developed and analysed in e.g. Davidson (1998) and the references therein, Regalado *et al.* (1996) and more recently by Stacey *et al.* (2001), Lopez and Jensen (2002), Boswell *et al.* (2002, 2003a, b) and Falconer *et al.* (2006) all fall into this category. In these studies, systems of equations (non-linear partial differential equations) are derived that represent the (implicit or explicit) interaction of fungal biomass and at least one growth-limiting substrate (e.g. a carbon source) as well as other factors (e.g. toxins).

Such an approach is ideal when modelling dense mycelia, for example growth in Petri dishes or on the surfaces of solid substrates such as foodstuffs, plant surfaces and building materials. This modelling strategy has, for example, allowed the study of biomass distribution within the mycelium in homogeneous and heterogeneous conditions, translocation in a variety of habitat configurations as well as certain functional consequences of fungal growth, such as acid production. A recent model developed by Boswell *et al.* (2003a, b) is the distillation of much of the modelling work conducted over the previous 10 years. Hence, we describe their approach in some detail below, as it contains generic elements of the structure and development of this class of model.

A second category of model is based on a discrete modelling approach, in which individual hyphae are identified. These discrete models generally take the form of computer-generated simulations (see e.g. Soddell *et al.* 1995; Regalado *et al.* 1996; Meskauskas *et al.* 2004a, b) and are often derived from the statistical properties of the experimental system under investigation. These models can yield images that are almost indistinguishable from real fungi and are therefore very appealing. There are significant advances that can be made using this type of model, for example in the testing of hypotheses concerning basic growth architecture. In particular the model developed by Meskauskas *et al.* (2004a, b) can consider different species growing in 3-dimensional space and within a variety of nutrient distributions. This model has been developed into a user-interactive experimental system with example images shown in Fig. 4.

It must be noted, however, that in this modelling category there is the tendency to use non-mechanistic rules to generate hyphal tip extension and hyphal branching, i.e. the underlying

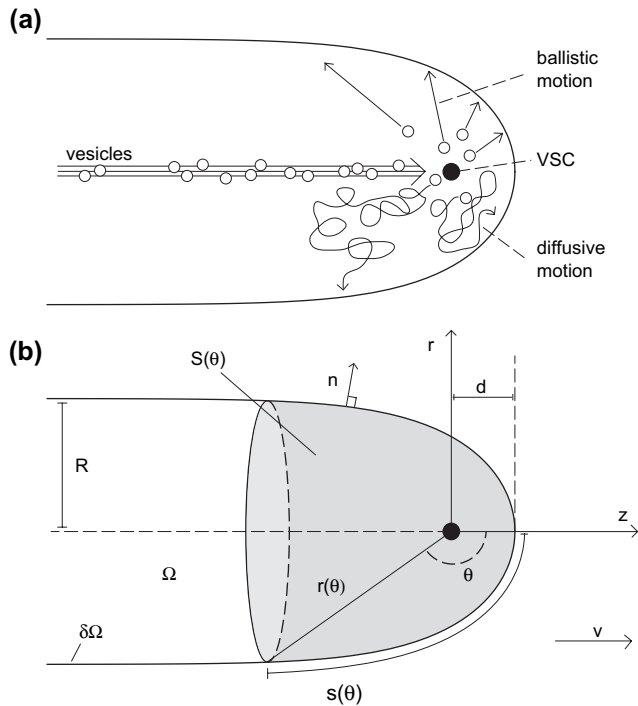


Fig. 2 – (a) Schematic comparison of the ballistic and diffusive vesicle supply centre (Spitzenkörper) models (b) An overview of the mathematical description of the hyphal tip and the variables required for the model of Tindemans et al. (2006). The hyphal tip is modeled as being axially symmetric, with reference direction given as $\theta = 0$. The domain Ω represents the inside of the hypha whilst $\partial\Omega$ represents the hyphal wall/cell membrane complex. $S(\theta)$ is the cap that is formed by the incorporation of vesicles in to the cell wall and whose formation and geometry is determined by the model. From Tindemans et al. (2006) with kind permission.

mechanisms for growth are not modeled directly and are instead replaced by abstract branching and growth rules. Consequently, difficulties arise in attempting to make and test hypotheses concerning changes in growth dynamics and mycelial function in response to external factors. Moreover, because of this abstraction, it is difficult to choose parameter values in any *a priori* meaningful way. Furthermore, because of computational difficulties, it is only very recently that the two key processes of anastomosis and translocation, have been modeled (see Boswell et al. 2006.) These processes are crucial to mycelial development in general and in particular to growth in heterogeneous environments. We outline the construction of the Boswell et al. (2006) model below, which circumvents the above mentioned problems and again provides an insight into certain generic processes in the construction of models in this category.

Other approaches to modelling at this colony scale include the use of ordinary differential equations to model properties such as radial growth rate and its dependence on environmental factors such as temperature and pH (Panagou et al. 2003), and statistical modelling approaches to e.g. investigate the stochastic variability in pathozone behaviour of soil-borne plant pathogenic fungi (Gilligan & Bailey 1997).

4. Example of a Model framework

In Boswell et al. (2003a), the mycelium is modeled as a distribution consisting of three components: *active hyphae* (corresponding to those hyphae involved in the translocation of internal metabolites), *inactive hyphae* (denoting those hyphae not involved in translocation or growth, e.g. moribund hyphae) and *hyphal tips*. An important distinction is made between nutrients located within the fungus (*internal*) and those free in the outside environment (*external*). Internally-located material is used for metabolism and biosynthesis, e.g. in the extension of hyphal tips (creating new hyphae), branching (creating new hyphal tips), maintenance, and the uptake of external nutrient resources. In most environments, a combination of nutrients is necessary for growth (carbon, nitrogen, oxygen, etc.)

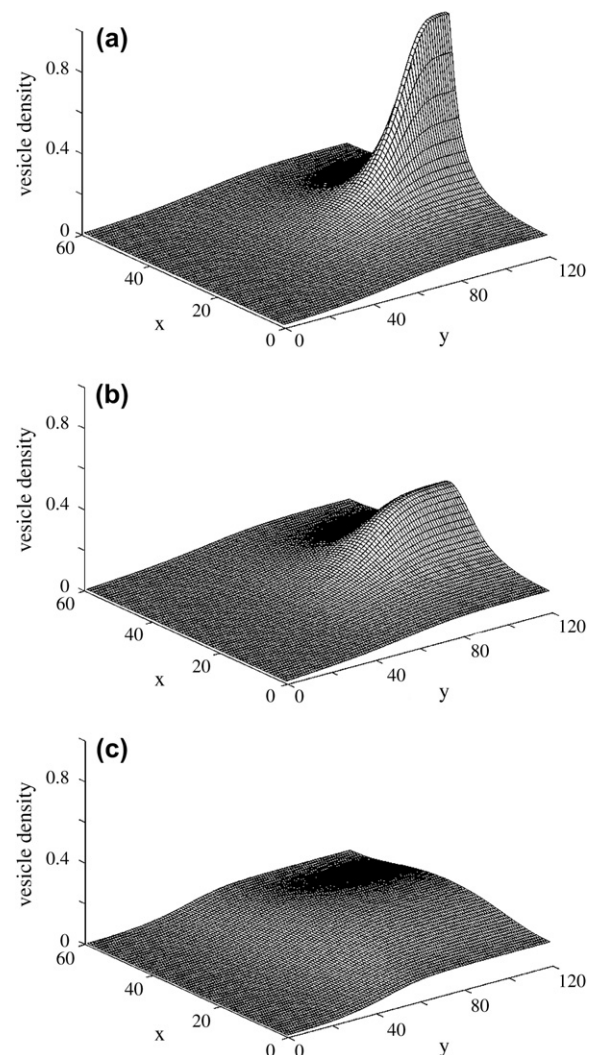


Fig. 3 – The model proposed by Regalado et al. (1997) details how branching is initiated by the splitting of the Spitzenkörper via mechano-chemical deformation of the cytoskeleton. Initial vesicle cluster (a), collapses (b, c) before reorganizing as two new aggregations centres (d, e) predicting the initiation of apical branching. From Regalado et al. (1997) with kind permission.

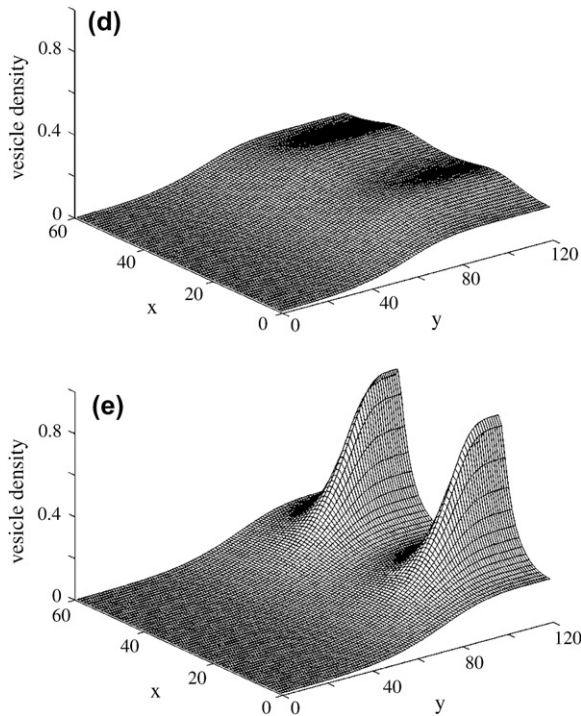


Fig. 3 – (Continued)

but, for simplicity, in the model system it is assumed that carbon, given its central role in growth, is the single generic element limiting for growth. The model is based on the physiology and growth characteristics of the ubiquitous soil-borne saprophyte, *Rhizoctonia solani* and it is to the results of growth experiments using this fungus that the model has been initially compared. However, many aspects of the model (and results thereby obtained) are applicable to a large class of fungi growing in a variety of habitats.

In terms of the five variables outlined above, the model has the following structure:

change in active hyphae in a given area	= new hyphae (laid down by moving tips) + reactivation of inactive hyphae – inactivation of active hyphae,	(1)
change in inactive hyphae in a given area	= inactivation of active hyphae – reactivation of inactive hyphae – degradation of inactive hyphae,	(2)
change in hyphal tips in a given area	= tip movement out of/into area + branching from active hyphae – anastomosis of tips into hyphae,	(3)
change in internal substrate in a given area	= translocation (active and passive mechanisms) + uptake into the fungus from external sources – maintenance costs of hyphae – growth costs of hyphal tips – active translocation costs,	(4)
change in external substrate in a given area	= diffusion of external substrate out of/into area – uptake by fungus.	(5)

It is commonly observed that hyphal tips have a tendency to move in a straight line but with small random fluctuations in the direction of growth (due to the manner new wall material

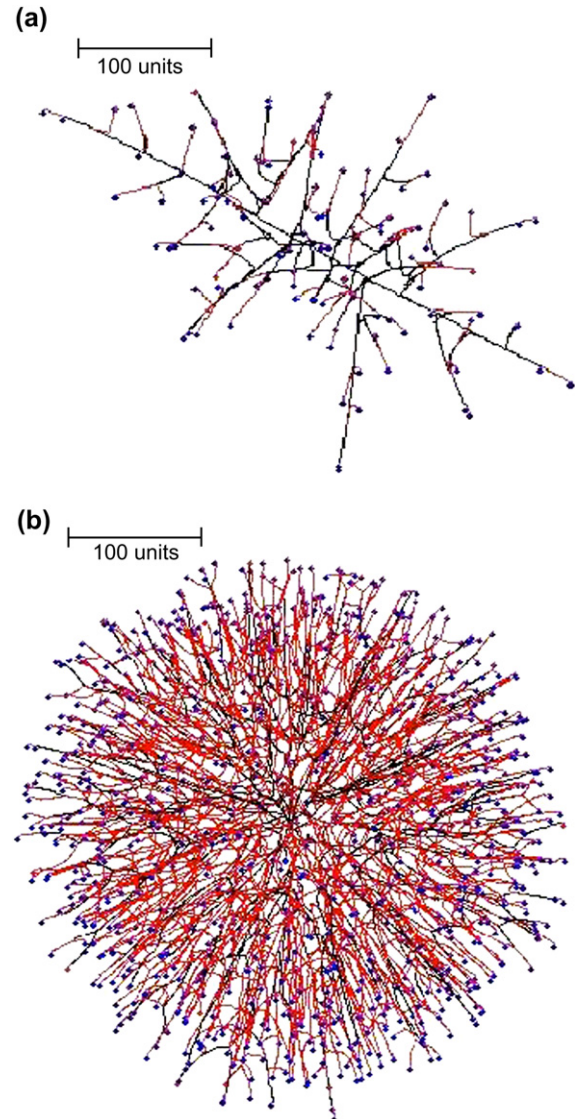


Fig. 4 – The development of a model *Trichoderma* colony as generated by the neighbour-sensing model of Meskauskas et al. (2004a,b). Images (a) and (b) give two snapshots of the continuous development of the colony produced by the online interactive modelling tool available at the <http://www.world-of-fungi.org>. Blue dots represent hyphal tips, red lines represent new “active” hyphae and black line represent older “inactive” hyphae. With kind permission of Professor David Moore.

is incorporated at the tip) and that the rate of tip growth depends on the status of internally-located material. The model includes these important growth characteristics. It has been widely reported that hyphal branching in mycelial fungi is related to the status of internally-located material: turgor pressure and the build-up of tip vesicles have been implicated (Webster 1980; Gow & Gadd 1995). Thus, the branching process is modeled as being proportional to the internal substrate concentration. In mycelial fungi, the uptake of nutrients mainly occurs by active transport across the plasma membrane.

Hence, in the model system, the uptake process depends not only on the concentration of the external substrate, but also on the concentration of the internal substrate (i.e. the energy available to drive the active uptake) and on the amount of hyphae (i.e. membrane surface area). It is known that many species of fungi possess both active (i.e. metabolically-driven) and passive (i.e. diffusive) translocation mechanisms for carbon (see e.g. Olsson 1995). Active substrate translocation, unlike diffusion, depletes the energy reserves within the mycelium and is modeled as a process that moves internal substrate towards hyphal tips since they represent the major component of mycelial growth and are therefore likely to be the largest net energy sinks.

Many of the features discussed above are generic to the relevant class of models, but the explicit inclusion of the two distinct mechanisms for translocation is unique to the Boswell *et al.* construction.

5. A continuum approach

As a first step, it can be assumed that the variables in the model system are *continuous* (i.e. can be viewed as densities) and as such, a system of partial differential equations is formed. However, the true, branched (fractal) nature of the mycelial network is not disregarded entirely in the formulation of Boswell *et al.* (2003a): this is taken into account by

modelling translocation so as to best represent movement inside a branching (fractal) structure (essentially, it is assumed that the *transit time* of vesicles transported around the network is less than if they were diffusing in free space).

Although the core of the model is formed from a consideration of the general growth characteristics of mycelial fungi, as mentioned above, for direct comparison with experimental observations, the results were obtained in conjunction with experiments using *Rhizoctonia solani* Kühn anastomosis group 4 (R3) (IMI 385768) (see Boswell *et al.* 2002).

The model equations were solved in a standard manner, on a computer using a finite-difference approximation, which involves dividing time and space into discrete units. A square grid is superimposed on the (continuous) growth domain so that each square (or “cell”) in the grid contains a quantity of active and inactive biomass, hyphal tips, and internal and external substrate. Thus the densities and concentrations of the model system are stored on the computer in a series of two-dimensional arrays. These quantities change in subsequent time steps, as determined by the model equations, according to the status of each “cell” and that of its neighbouring “cells”. Thus, both local concentrations and gradients of concentrations of the five model variables can be considered. By repeatedly applying the above process using finer grids and smaller time steps, the numerical approximation obtained progressively resembles the true solution of the model equations.

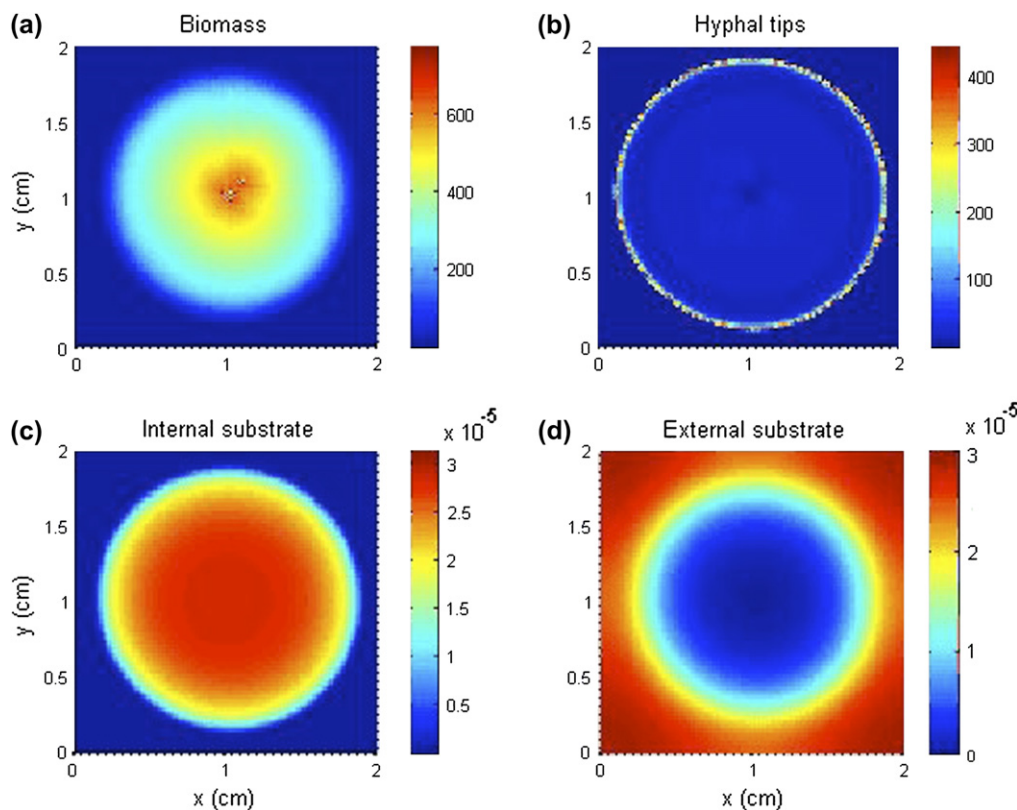


Fig. 5 – Qualitatively and quantitatively accurate prediction by the model of Boswell *et al.* (2003a) of the development of a radially symmetric colony of *Rhizoctonia solani* on a uniform nutrient. The images (a)–(d) show the biomass densities (cm hyphae cm^{-2}), hyphal tips (cm^{-2}), internal substrate and external substrate (mol cm^{-2}), at the time representing 5 d (spatial scale represents cm, colours represent appropriate quantities, values given by the colour bars).

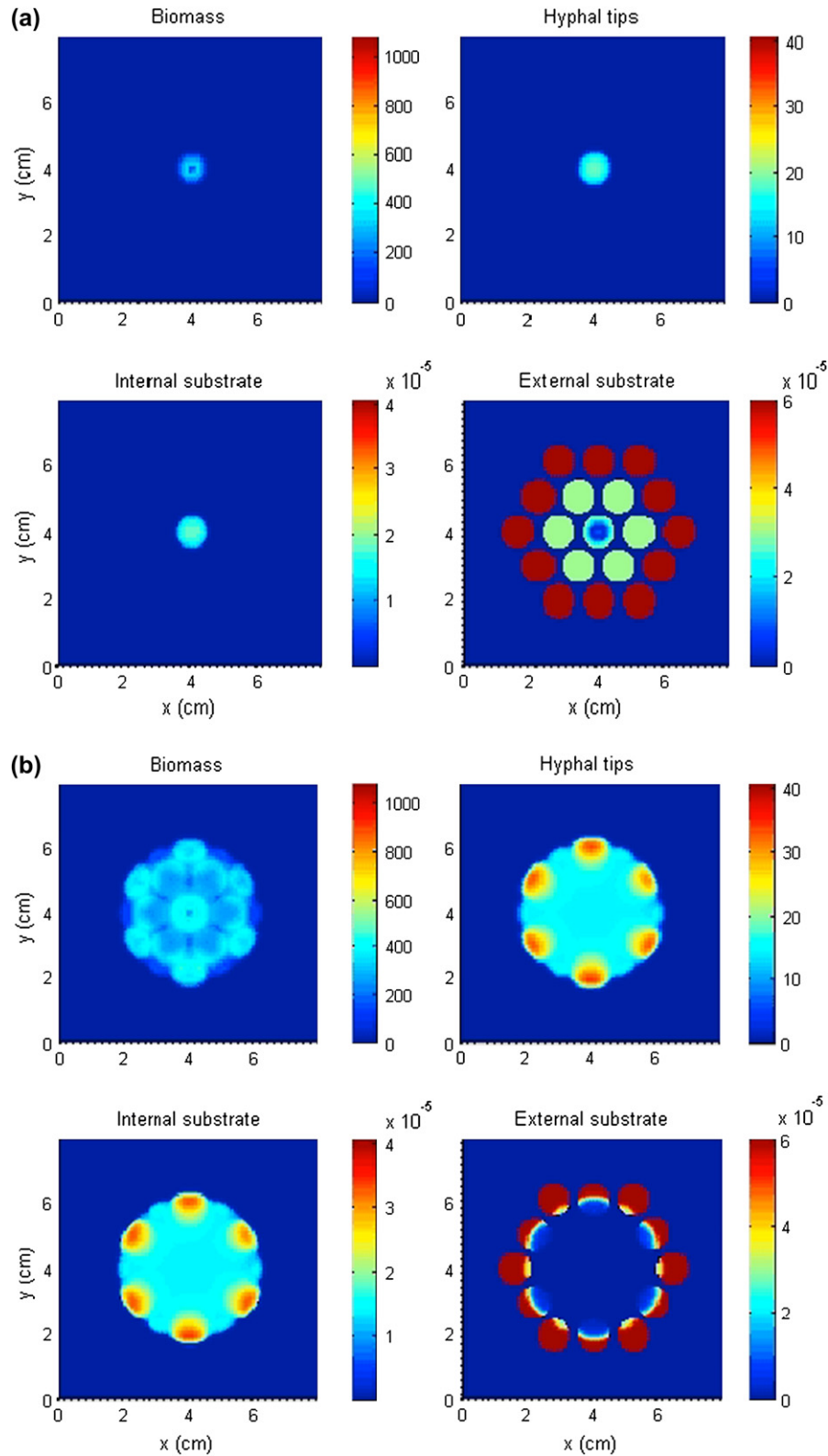


Fig. 6 – The model of [Boswell et al. \(2003a\)](#) is used to predict the development of a fungal colony on the tessellated agar system of [Jacobs et al. \(2002\)](#). The specific distribution considered here represents the exterior ring of droplets amended by the addition of glucose whilst the internal droplets are standard MSM agar. This configuration is reflected in the distribution of model external substrate as seen in [Fig. 6\(a\)](#). Here the figure shows the development of the model solution shortly after the initial inoculation of the central droplet. [Fig. 6\(b\)](#) and [\(c\)](#) show the distribution after 3 and 7 d respectively. Notice that the model accurately predicts that the biomass bridges the air gaps between the droplets and colonizes the entire distribution. External substrate absorbed from the outer ring of droplets is used by the model fungus to recolonize the inner droplets where previously, the local substrate concentration was not sufficient to support dense growth.

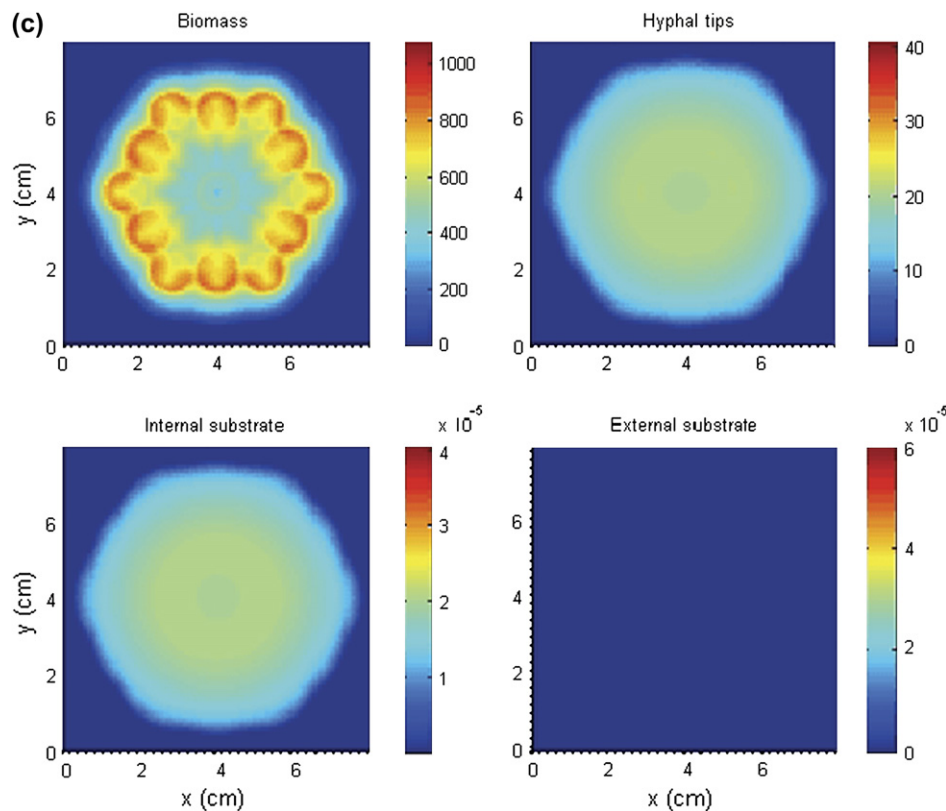


Fig. 6 – (Continued)

A simple quantitative test of the model's predictive power is given by comparing the colony radial expansion, measured experimentally, to the biomass expansion obtained from the solution of the model equations. The total hyphal density (i.e. active and inactive hyphae) is shown in Fig. 5 and is in good qualitative and quantitative agreement with experimental values obtained (see Boswell *et al.* 2002, 2003a). The model extends the experimental data by predicting the development of hyphal tip density and external and internal substrate concentration in “real time”.

The model can easily be adapted to consider nutritionally heterogeneous environments, for example, the tessellated agar droplet system discussed by Jacobs *et al.* (2002) in which 19 agar droplets were pipetted onto a Petri dish in a hexagonal pattern. Different combinations of amendments to these agar droplets were considered. The model can be applied without alteration to a subset of these tessellations, corresponding to the four configurations constructed using standard MSM and glucose-amended MSM. The model predicts general growth characteristics that are similar to those observed experimentally (Fig. 6) and again extends these results by, for example, explicitly mapping internal substrate concentrations and, in “real-time”, the acidification of the environment.

6. Explicit modelling of the network

When growth is sparse, a continuum approach is less relevant. In this case, a discrete modelling approach is more

appropriate in which individual hyphae are identified. As discussed above, the derivation of meaningful rules for growth and function and the parameterisation of such rules for discrete models is problematic. To overcome these difficulties, a discrete model that is directly derived from the continuum model described above has been developed by Boswell *et al.* (2006). This discrete model is therefore based on the underlying processes of the growth and interaction of the fungus with its environment and explicitly includes anastomosis and translocation, thus allowing growth to be appropriately and accurately simulated in both uniform and heterogeneous environments. Moreover, the parameter values used in the discrete model are exactly those used in the calibrated and tested continuum model. In this approach, space is modelled as an array of hexagonal “cells” and the model mycelium is defined on the embedded triangular lattice (i.e. the lattice formed by connecting the centres of adjacent hexagonal cells). Time is also modelled as discrete steps and the probabilities of certain events occurring during each time interval (the *movement* or *transition probabilities*) are derived from the assumptions used in the previously described (continuum) approach: essentially they are derived from the finite-difference discretisation used to numerically solve the continuum model (see Boswell *et al.* 2006). This discretisation procedure allows certain key processes, including hyphal inactivation and reactivation, branching and anastomosis to be treated in a more detailed manner than is possible in the continuous formulation.

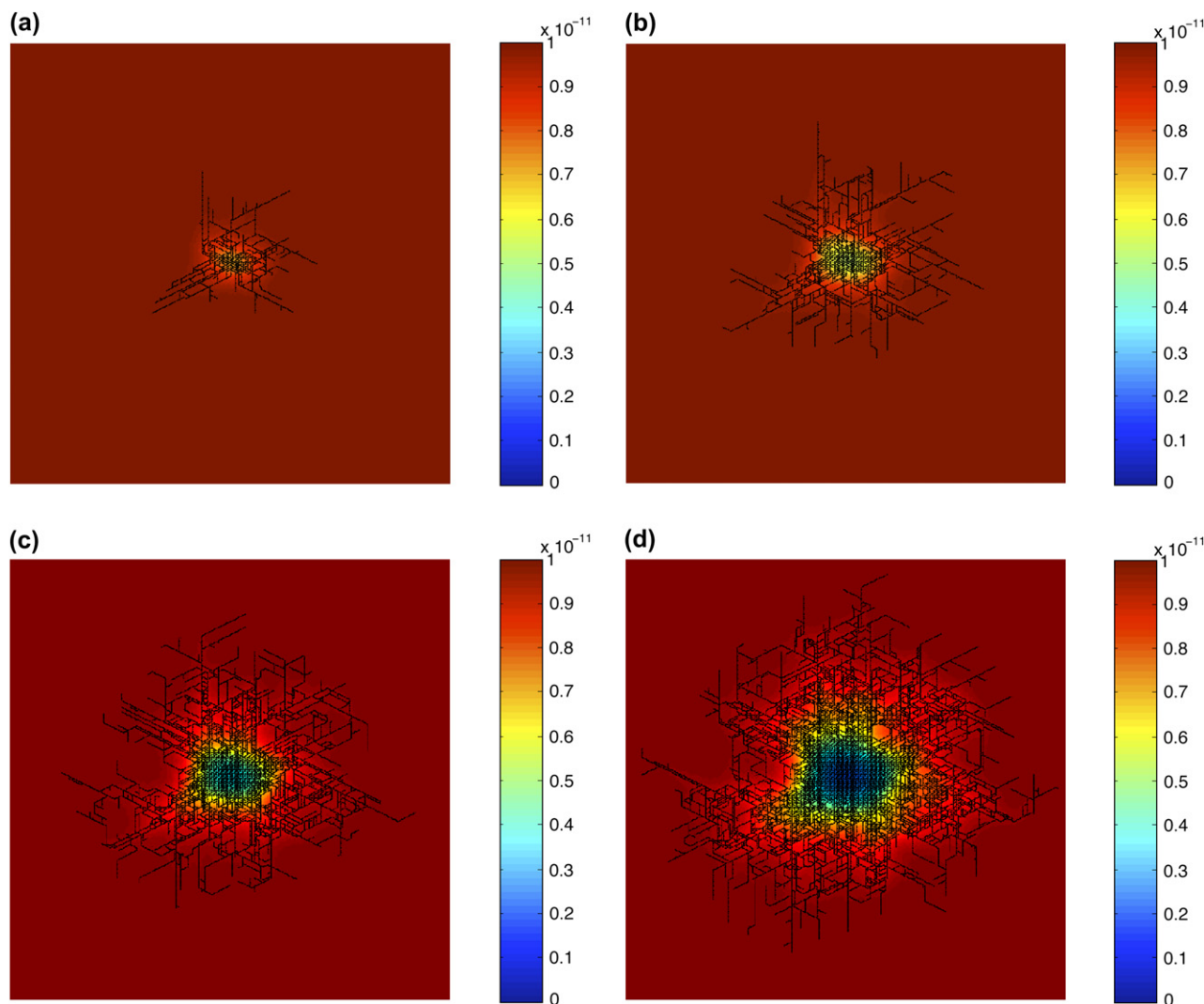


Fig. 7 – Model mycelial growth generated by the hybrid model of Boswell *et al.* (2006). The developing hyphal network is represented by dark lines and is given at snapshots in time representing approximately (a) 8 hours (b) 16 hours (c) and (d) 1 d. The model network develops by utilizing the external substrate supply. The subsequent depletion of the external substrate is shown by the colour scale (mol cm^{-2}).

Uniform substrates

The discrete model replicates many of the important qualitative features associated with mycelial growth in uniform conditions (Fig. 7). Moreover, quantitative features such as *fractal dimension* (how well the network fills space) are also consistent with experimental observations and a predictive relationship between substrate concentration and fractal dimension is derived in Boswell *et al.* (2006).

Growth in soils

Soils exhibit spatio-temporal, nutritional and structural heterogeneity. The structural heterogeneity in soils is determined by the relative location of soil particles and the resulting pore space. Nutritional heterogeneity is strongly modulated by the ground-water distribution, which itself depends on the

architecture of the pore space. All of these factors greatly influence fungal growth and function (see e.g. Otten *et al.* 2001; Harris *et al.* 2002; Otten & Gilligan 2005). In non-saturated soils, water films prevail around pore walls and larger pores are air-filled. Nutrients (with the exception of oxygen) are in general confined to such water films. Water surface tension ensures these nutrients diffuse within the film but not across its outer surface. Experimental studies of mycelial growth in soils typically consist of examining thin slices of soils (see e.g. Harris *et al.* 2002). These soil slices are in essence a two-dimensional object and hence various properties, such as the fractal dimension of the growth habitat and the location and abundance of biomass within the growth habitat, can be easily compared between the model and experimental systems. Boswell *et al.* (2006), constructed artificial structures that emulate heterogeneous porous media, such as soils, by randomly “removing” (possibly overlapping) hexagonal blocks of cells from

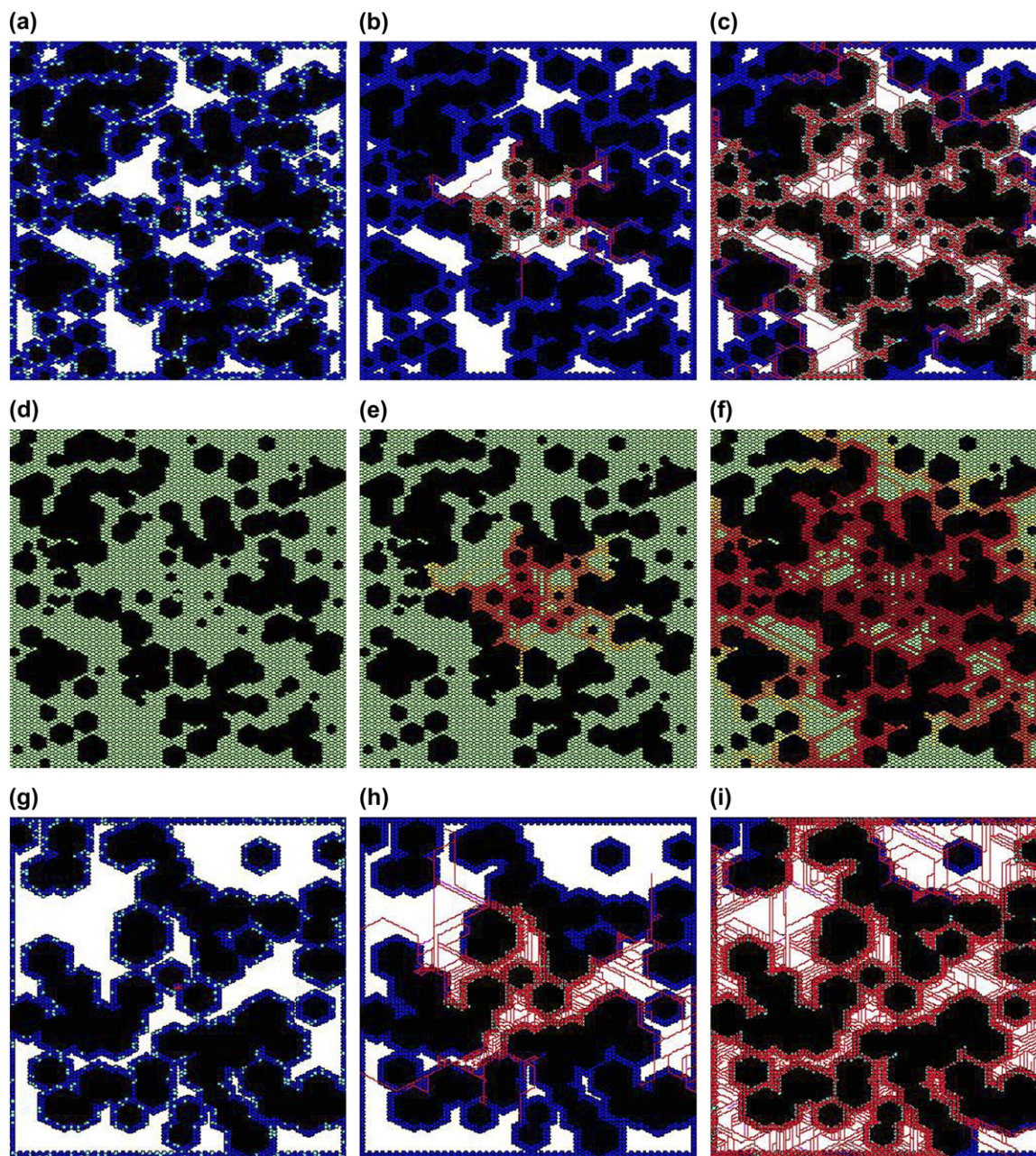


Fig. 8 – Model mycelial growth generated by the hybrid model of Boswell *et al.* 2006, (a)–(c) and corresponding acidification of the environment (d)–(f) up to 7 d after inoculation. The developing hyhal network is represented by dark lines. The black cells denote soil particles, the dark and light blue cells respectively denote the water film containing high and low amounts of substrate, and the white regions correspond to air-filled pore spaces. The acidity predicted by the model is shown using a universal pH indicator and ranges for pH 7 (green) to pH 3 (dark red). Typical biomass growth in a similar environment but with reduced water surface tension is shown in (g)–(i) at the same times as above. Redrawn from Boswell *et al.* (2006).

the growth domain. The distribution of the remaining habitat, which corresponds to the pore space, may be connected or fragmented. Fundamental properties of the model pore space, such as its fractal dimension, can be computed, enabling qualitative and quantitative comparisons with real soil systems as indicated above.

Using the model the spatio-temporal development of the model mycelium and the predicted acidification of the surrounding environment can be studied in “real-time”. Thus it

is seen that early biomass growth is confined to the region representing the water film (Fig. 8a, b). A small number of tips escape from this region, extend rapidly across the model pore space, and locate new substrate resources, which are subsequently colonised and exploited (Fig. 8c). Corresponding acidification of the environment can also be predicted by the model (Fig. 8d–f). Surface tension of the water film was observed to play a significant role in determining biomass and acidity distribution. Reducing surface tension in the model

results in a greater biomass distribution in the pore space and a faster overall biomass expansion (Fig. 8g-i).

7. Conclusions

The indeterminate growth habit of mycelial fungi ensures that the investigation of the growth and function of these organisms has to consider scales ranging from the (sub) micron to the kilometer. As seen in many of the papers cited here, accurate modelling involves the transfer of information across scales. However, the construction of a single “multi-scale, gene-to-landscape” model is certainly some way off, and indeed such a model may not be necessary to address many important questions regarding mycelial growth and function. In fact, for the reasons given in the introduction, it may not even be desirable to attempt to construct such a mathematical system. What is more important is a meaningful construction that can address relevant questions at the relevant scale.

Although not common place, it is clear that mathematical modelling is being successfully employed as an efficient and accurate experimental tool at all scales of investigation. It will without doubt be a key element in the further development of our basic understanding of fungal physiology and morphology, the role fungi play in nutrient cycling, epidemiology and biogeochemistry and in the successful biotechnological application of fungi to areas such as biocontrol and bioremediation.

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