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# Biomass recycling and the origin of phenotype in fungal mycelia

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Fungi are one of the most important and widespread components of the biosphere, and are essential for the growth of over 90% of all vascular plants. Although they are a separate kingdom of life, we know relatively little about the origins of their ubiquitous existence. This reflects a wider ignorance arising from their status as indeterminate organisms epitomized by extreme phenotypic plasticity that is essential for survival in complex environments. Here we show that the fungal phenotype may have its origins in the defining characteristic of indeterminate organisms, namely their ability to recycle locally immobilized internal resources into a mobilized form capable of being directed to new internal sinks. We show that phenotype can be modelled as an emergent phenomenon resulting from the interplay between simple local processes governing uptake and remobilization of internal resources, and macroscopic processes associated with their transport. Observed complex growth forms are reproduced and the sensitive dependence of phenotype on environmental context may be understood in terms of nonlinearities associated with regulation of the recycling apparatus.

**Keywords:** fungal colony; physiological model; fungal interactions; indeterminate

## 1. INTRODUCTION

Fungi are one of the most important components of the biosphere. They are essential for the growth of over 90% of all vascular plants (Allen 1993), and play an essential role in the ecosystem services associated with soil processes valued at $90 trillion per annum globally (Boumans 2002). Estimates suggest that there may be as many as 1.5 million species of fungi globally (Hawksworth 1991). In a cubic centimetre of field soil there could be 25 km of fungal hyphae (Young & Crawford 2004), and in a 1 ml suspension of leaf litter as many as 150 species can coexist (Bills & Polishook 1994). Given their status as a separate kingdom of life, their abundance and their functional importance, it is surprising that, compared with higher organisms, we know relatively little about the properties of fungi that maintain this level of diversity and how diversity relates to function. Despite a large body of qualitative studies at many scales, we lack the unifying quantitative framework that is required to synthesize existing knowledge to address these challenges and to make predictions required for management.

At a fundamental level, one of the reasons for this level of ignorance is the defining feature of fungi: their indeterminate growth form (Rayner 1994; Sturrock *et al.* 2002). A mycelium, or fungal colony, has no characteristic scale above that of an individual hypha (the basic unit of the mycelium) and can potentially persist indefinitely, reproducing when environmental circumstances are favourable. The connected nature of the mycelial network means that local behaviour can, and is, affected by conditions in remote parts of the colony via mechanisms including translocation (White *et al.* 1998; Bown *et al.* 1999; Olsson 1999). Therefore, the behaviour of the colony is dependent on the interaction between genotype and a complex spatial convolution of environmental conditions across the whole mycelium. Add to this the complexity introduced by considering the diverse nature of interactions that occur among mycelia of the same and different species and it becomes clear that the challenges of finding a unifying framework that links biological processes operating over multiple scales and with varying constancy to ecosystem behaviour are considerable (White 2004).

Indeterminacy, non-local behaviour and the need to address community-scale dynamics conspire to make it difficult to determine the appropriate choice of scales to include in any framework. Theoretical approaches to date fall into one of three categories: those that model the microscopic scale; those that model the macroscopic scale; and those that aim to explain macroscopic form in terms of microscopic processes. Microscopic models focus on the hyphal-scale or single-cell scale. These models are designed to elucidate the mechanisms of hyphal tip growth, branching, anastomosis (hyphal fusion) and septation (compartmentalization of hyphae). For example, Bull & Trinci (1977) describe the basic branching events of hyphae. Prosser & Trinci (1979) describe internal accumulation of growth precursors that trigger hyphal branching. However, these models do not address how the collective behaviour of hyphae effects colony-scale macroscopic growth. Davidson *et al.* (1996) present a colony-scale model based on a diffusible, replenishing substrate, an agent converting substrate into energy that drives the proliferation of biomass, and diffusion of an activator. Davidson *et al.* (1996) show that by varying key parameters many of the observed morphological patterns produced by growing fungal colonies may be obtained. Although phenomenological, the model illustrates the important point that relatively few processes can be orchestrated by different contexts to

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produce wide-ranging phenotypes, and this capacity must be embodied in any general representation. Bown *et al.* (1999) chose a multi-scaled approach to examine the relative contribution of local and non-local effects on the dynamics of a two-species fungal microcosm. This model represents implicitly the physiological processes that are important in the outcome of individual fungal interactions. The analysis shows that the outcome of interactions at the local scale depends on the larger scale context, and so the behaviour that emerges cannot be understood in terms of the behaviour of isolated modules, highlighting the need to link across scales.

Recent theoretical approaches couple two or more characteristic scales in the hope of understanding what drives colony growth dynamics. These models have evolved from early work by Edelstein (1982) and Edelstein & Segel (1983) describing colony-scale growth in terms of hyphal density and density of hyphal tips, accounting for different hyphal mechanisms such as lateral and dichotomous branching, anastomosis and translocation of metabolites within the mycelium. Davidson & Olsson (2000) and Boswell *et al.* (2002, 2003) developed this work further by producing a model based on directed growth of fungal hyphae and includes more realistic, bidirectional translocation mechanisms. Boswell *et al.* (2002) identify vacuolation as an important process; however, the 'inactive hyphae', those hyphae not involved with translocation, are degraded into the environment and therefore not recycled by the colony. These models have been useful in investigating the interplay between active and passive translocation within the mycelium for homogeneous and heterogeneous environments, and suggest that passive translocation is used for random exploration while active translocation is used for resource exploitation (Boswell *et al.* 2002). Stacey *et al.* (2001) also extend the work of Edelstein (1982) to address transmission rates of fungal soil-borne pathogens from infected to susceptible plant. The model scales up from hyphal growth and branching to the scale of the colony. Finally, a rather different vectorial-based mathematical model has been produced by Meskauskas *et al.* (2004). This model simulates growth of hyphae in up to three dimensions and can simulate fruiting bodies.

A major limitation of many of the approaches used to date is that they do not describe the capacity of fungi to reuse their own hyphal material, referred to hereafter as biomass. Fungi are able to persist in dynamic, heterogeneous environments because of a capacity to take locally immobilized internal resources (e.g. those incorporated in structural or storage elements) and remobilize these into a form capable of being reused locally or directed to new internal sinks (e.g. sites of hyphal tip growth). This is one of the most important processes promoting indeterminate growth, but current theoretical approaches fail to embrace this process and thereby do not contribute to our understanding of fungal growth and development. Another limitation that obstructs more effective interaction between theory and experiment is the lack of an explicit physiological basis for the proposed processes. Therefore, although models are formulated to link across scales, they often exploit arbitrary functions and parameter values, are generally limited to qualitative testing and only rarely *explicitly* incorporate measurable physiological processes. Finally, very few approaches are designed to include the complex interactions that occur between individual hyphae and mycelia, and the effect these have on biomass distribution.

Here, we consider a physiologically based model for mycelium growth that supports interpretation of macroscopic patterns in terms of observable microscopic processes. The impact of colony-scale context on local behaviour within the mycelium is explained in terms of the dynamics of resource uptake, and biomass remobilization and movement, a manifestation of the hyphal-scale behaviour of fungi. Furthermore the model is simple enough to extend to study the link between the dynamics of biomass distribution and the structure and function of fungal communities.

## 2. MODELLING FRAMEWORK

Much that concerns the spatio-temporal dynamics of remobilization of internal resources in fungi is unknown (Carlile *et al.* 2001; Read & Hickey 2001), and a major rationale for the current work is to explain as much as possible about mycelial form and function by incorporating only essential processes. This approach both aids understanding and facilitates experimental testing of hypotheses. Clearly, the model can subsequently be made more sophisticated by including additional processes as required.

The fungal mycelium is represented by two 'types' of biomass: immobile and mobile. The immobile biomass can be in one of two states: non-insulated and insulated, where $b_n$ and $b_i$ denote the respective biomass per unit area. Non-insulated biomass is assumed to represent hyphae capable of significant uptake of external resource and corresponds mainly to active hyphal tips within a colony. Behind the tips, the cell wall and membrane change in character, and uptake is greatly reduced or absent (Carlile 1995) and is, in this sense, insulated. Common macroscopic manifestations of insulation include the formation of fully anastomized centres of colonies in nutritionally depleted environments, and the formation of cord-like structures by some species in hostile environments (Rayner *et al.* 1999). The rate of uptake of resource is assumed to be proportional to local immobile biomass concentration and external substrate concentration denoted by $s$. The specific rate of uptake for non-insulated biomass, $\lambda_1$, is assumed to be larger than that for insulated biomass, $\lambda_2$. We have assumed that there is a small uptake of substrate by parts of the mycelium represented by insulated biomass. This is used as a surrogate for underlying mechanisms responsible for the initiation of new hyphal tips from insulated biomass in response to availability of new resources (see below). The expansion of non-insulated biomass is represented as a diffusion process with a constant diffusion coefficient, $D_b$, corresponding to the constant linear extension rate of the hyphal front that is observed in colonies larger than the hyphal growth unit (Prosser & Trinci 1979). Non-insulated biomass is converted into insulated biomass at a constant rate, $\zeta$, corresponding to the process of apical extension and sub-apical rigidification (Saunders & Trinci 1979).

The integrated uptake of the mycelium is redistributed along with remobilized elements to growing tips via the movement of an internal mobile biomass component with

concentration denoted by $n$. At this stage, we consider only that component of mobile biomass implicated in local biomass production. An explicit account of the various forms of mobile biomass (e.g. vesicles) and mechanisms for their movement, while possible in principle, would introduce excessive complexity that would obstruct our initial aim of determining the key processes. Key movement mechanisms include passive diffusion, active transport, pressure driven bulk flow, vacuolar compartmentalization and vesicle trafficking (Olsson 1999). These are encapsulated in the model by a single process governing reallocation of immobile biomass. The precise mechanisms of transport and aggregation of mobile biomass, and in particular vesicles in hyphae, are not fully understood (Read & Hickey 2001). We have previously implicated complex interactions between the cell wall and the actin network in the organization of vesicles including the formation of the Spitzenkorper (Regalado & Sleeman 1999). Such detailed level of description is inappropriate in an approach designed to elucidate colony-scale behaviour. However, the observed movement of cytoskeletal- and wall-building material and its organization in tip-growth regions is an important process to incorporate. To proceed in the development of the model linking local hyphal-level processes to colony and community-scale features, we make the following testable hypotheses relating to the processes associated with biomass recycling and transport.

(i) Mobile biomass is assumed to diffuse in the colony and the interaction between cytoskeleton elements and transport is encapsulated in a diffusion coefficient, $D_n$, which depends on local concentration of mobile biomass. Nonlinear dependence of this kind occurs when diffusion takes place in a medium with limited transport pathways. We assume the following simplified nonlinear form

$$D_n = \begin{cases} 10^{-7} D_\mathrm{b} & n > n_0 \\ D_\mathrm{b} & n < n_0 \end{cases}. \tag{2.1}$$

The threshold concentration of mobile biomass, $n_0$, is set to a constant.

(ii) Immobile biomass is mobilized locally at a prescribed specific rate, and the mobilization process is assumed to require elements of the mobile biomass. We therefore take the mobilization rate to be proportional to the local mobile biomass concentration in the hyphae (i.e. the ratio of mobile to immobile biomass)

$$\beta\pi, \quad \text{where } \pi = \left[\frac{n}{b_\mathrm{n} + b_\mathrm{i}}\right], \tag{2.2}$$

such that if the ratio is lower (higher), the rate of mobilization per unit biomass will be proportionately lower (higher) as a direct result of a dilution (concentration) effect. Note that if the mobile biomass concentration is zero, the mobilization rate is zero. Such behaviour is consistent with a mechanism for mobilization involving assisted transport of elements of the mobile biomass across a membrane, e.g. active transport. We assume that the coefficient for the rate of mobilization $\beta$ takes the value of parameters $\beta_\mathrm{n}$ or $\beta_\mathrm{i}$ for regions comprising non-insulated biomass and insulated biomass, respectively.

(iii) Mobile biomass is assumed to be locally immobilized at a rate per unit biomass given by

$$\alpha\pi^\theta, \tag{2.3}$$

where the coefficient for the rate of immobilization $\alpha$ assumes the value of parameters $\alpha_\mathrm{n}$ or $\alpha_\mathrm{i}$ in regions comprising non-insulated and insulated biomass respectively, and $\theta$ is a constant. For $\theta > 1$, equations (2.2) and (2.3) mean that for sufficiently low values of $\pi$ (i.e. $\pi < (\beta/\alpha)^{1/(\theta-1)}$) there is a net mobilization of biomass, and this switches to a net immobilization at higher values of $\pi$. By varying $\theta$ we change the sensitivity of this switch to the mobile biomass concentration, and explore the possible importance of nonlinearity in the immobilization process that might result from regulatory processes. We set $\alpha_\mathrm{i} = \beta_\mathrm{i} = 0.5$ for most of the analysis presented here (except figure 2*a*–c) and so study the effect of varying the immobilization and remobilization rates in non-insulated biomass (i.e. hyphal tips) on colony form. Mobile biomass is converted into immobile biomass with efficiency denoted by $\gamma$ to account for metabolic cost of inter-conversion and the possibility that not all mobile biomass is allocated to immobile biomass production.

(iv) Finally, mobile biomass is assumed to be produced at a rate that is proportional to local uptake.

The set of physiological processes described above corresponds to a vector of ten parameters: $\alpha_\mathrm{n}$, $\beta_\mathrm{n}$, $\alpha_\mathrm{i}$, $\beta_\mathrm{i}$, $\gamma$, $\theta$, $\lambda_1$, $\lambda_2$, $D_\mathrm{b}$ and $D_n$. These parameters can be regarded as having a genotypic origin in the sense that they are constants that characterize functions mapping environmental context onto mycelial phenotype. For convenience, we therefore subsequently refer to them as genotypic parameters of the mycelium. Each can, in principle, be directly measured. Here, the environment of a mycelium can be modified directly by adjusting substrate level and replenishment rate.

The resultant set of equations describing uptake, biomass production and recycling, and the transport of mobile biomass can be written

$$\left.\begin{aligned} \frac{\partial b_\mathrm{i}}{\partial t} &= \zeta\left[\frac{\partial}{\partial x} D_\mathrm{b} \frac{\partial b_\mathrm{n}}{\partial x} + \gamma(\alpha_\mathrm{n}\pi^\theta - \beta_\mathrm{n}\pi) b_\mathrm{n}\right] + \gamma(\alpha_\mathrm{i}\pi^\theta - \beta_\mathrm{i}\pi) b_\mathrm{i}, \\ \frac{\partial b_\mathrm{n}}{\partial t} &= (1-\zeta)\left[\frac{\partial}{\partial x} D_\mathrm{b} \frac{\partial b_n}{\partial x} + \gamma(\alpha_\mathrm{n}\pi^\theta - \beta_\mathrm{n}\pi) b_\mathrm{n}\right], \\ \frac{\partial n}{\partial t} &= \frac{\partial}{\partial x} D_n(n) \frac{\partial n}{\partial x} - (\alpha_\mathrm{n}\pi^\theta - \beta_\mathrm{n}\pi) b_\mathrm{n} \\ &\quad -(\alpha_\mathrm{i}\pi^\theta - \beta_\mathrm{i}\pi) b_\mathrm{i} + (\lambda_1 b_\mathrm{n} + \lambda_2 b_\mathrm{i}) s, \\ \frac{\partial s}{\partial t} &= \omega(s_\mathrm{m} - s) - (\lambda_1 b_\mathrm{n} + \lambda_2 b_\mathrm{i}) s, \end{aligned}\right\} \tag{2.4}$$

where we have assumed that local external substrate concentration is replenished at a rate ($\omega$) proportional to the difference between local substrate concentration and the prescribed maximum level. The system of equations was discretized on a square lattice of 128×128 cells, and solved using the Crank Nicholson implicit method (Press 1992), in conjunction with successive

over-relaxations, as this guarantees stability. Zero flux boundary conditions were imposed.

## 3. RESULTS

The model explores the range of growth forms resulting from different realizations of processes associated with biomass recycling, and for different environmental contexts. By altering genotypic and environmental parameters separately we probe the different contributions of genotype and environment to phenotype. Many growth forms that are widely observed and reproduced in earlier more phenomenological models (Davidson *et al.* 1996) can be reproduced, emerging from interactions among genotypic parameters relating to biomass recycling (figure 1) and the environmental context of the mycelium (figure 2). In the following descriptions, $D_b = 10^{-7}$, $\xi = 0.01$, $\lambda_2 = 0.01$ and $D_n \max = 10^{-7}$. For $\xi$, we assume the rate of insulation of hyphae is constant among species. We also assume constancy in the surrogate signalling mechanism $\lambda_2$, controlling initiation of new hyphal tips from insulated biomass in response to availability of new resources. Finally, it is assumed that the maximum rate of diffusion of mobile biomass is comparable to that of biomass spread, allowing hyphal tips to be fuelled with resource necessary for apical extension.

### (a) *Initiation of growth*

The model predicts a critical level of resource (1 unit per cell) below which the fungal individual displays a modest diffusive wavefront exemplifying explorative behaviour. Above this critical level the wavefront propagates autocatalytically, typifying exploitative behaviour. In both cases, wavefronts travel at the same speed and the quantity of biomass accumulated is consistent with literature (Bezzi & Ciliberto 2003). Three parameters were identified as being responsible for exploitative behaviour: the amount of resource in each cell, the biomass conversion efficiency ($\gamma > 0.2$), and the initial inoculum value. The subsequent form of the wavefront is sensitively dependent on the values for genotypic parameters and the environment.

### (b) *Impact of genotype*

In modelled systems where biomass conversion efficiency, $\gamma$, is low (0.2) and where mobilization rate, $\beta_n$, is high (0.8) a ring-like form is produced (figure 1*a*). The colony centre has exhausted its resource, while the biomass on the periphery of the colony is exploiting newly encountered resource. Biomass in the centre of the colony is declining through remobilization and is transported to the colony periphery. This type of behaviour is commonly observed in a number of different systems (Dowson *et al.* 1989). If $\gamma$ is increased (0.8) a plateau-like profile is obtained (figure 1*b*). There is still loss at each time step due to the biomass conversion efficiency parameter, but that loss is significantly less than in the previous simulation. The replenishment of external substrate offsets this loss, supporting further growth. If the replenishment parameter is set even higher a centrally peaked biomass distribution is obtained.

A qualitatively different wavefront is obtained, using the same set of parameters to define the fungal individual as in figure 1*b*, by increasing the degree of nonlinearity in the immobilization rate, $\theta$ (see equation (2.3)). Instead of obtaining the profile in figure 1*b*, defined concentric circles with some centralized local aggregations are obtained (figure 1*c*). Rings are produced as a result of nonlinearities in the remobilization apparatus in the following way. For $\theta > 1$, there is a switch from net mobilization to net immobilization when the mobile biomass concentration increases above a threshold (see §2 above). For high local uptake, the mobile biomass concentration will increase until there is a net immobilization of biomass into new tip growth. This rapid increase in tip production leads to local depletion of external resource, and this in turn will cause the local mobile biomass concentration to decrease until it falls below the critical value and net mobilization of biomass results. There will be a reduction in tip production and therefore uptake until the hyphae grow into a region of higher external resource when the process repeats. Central aggregations occur as a result of replenishment and through amplification of local uptake 'hotspots' by the same process. By decreasing the mobilization rate, $\beta_n$, and increasing the immobilization rate, $\alpha_n$, the switch point moves to progressively smaller values of the mobile biomass concentration. This results in progressively longer periods of immobilization and shorter periods of mobilization and so the rings of high biomass become thicker and more frequent until they eventually disappear (see figure 1*d–f*). These concentric rings are exhibited by, for example, cultures grown in the lab of *Neurospora crassa* and *Streptomycetes rutgersensis* (Deutsch *et al.* 1993), and have been produced by other models such as Davidson *et al.* (1996), although the parameters that cause the heterogeneous structures are not elaborated on in terms of biological processes.

### (c) *Impact of environment*

The macroscopic structure obtained is also intimately dependent on the typically heterogeneous environment, where biomass recycling and nutrient reallocation according to local supply and demand becomes crucial. Figure 2*a–c* illustrates a fungal individual growing in a heterogeneous environment. To focus on the effect of environment, we remove the nonlinear behaviour of recycling (setting $\theta = 1$) and take $\alpha_i = 0.1$ and $\beta_i = 0.9$, so that there is net mobilization of biomass as a result of recycling. This is consistent with biological processes such as autolyses, essential for long-term survival in heterogeneous environments. Initially the fungus exploits the external resource located directly under the inoculum (figure 2*a*). Once a second resource 'hot spot' is located, investment into and consequent exploitation of that external resource is effected via reallocation of biomass (figure 2*b*). Finally, the fungal individual will grow out and explore from the newly found resource (figure 2*c*).

Figure 2*d* shows a fungal individual with the same genotypic parameters as figure 1*c*, with external substrate replenishment rate $\omega = 0$. Here, the inner structure is heterogeneous but the concentric rings are less defined and many more local hyphal aggregations are obtained. Heterogeneous and homogeneous profiles similar to those reproduced here have been obtained in laboratory experiments (Sharland & Rayner 1989*a*,*b*). With the parameter set of figure 2*d*, but with the underlying resource at a much lower concentration, a qualitatively different distribution of biomass is obtained with no local aggregations (figure 2*e*). This occurs because the external

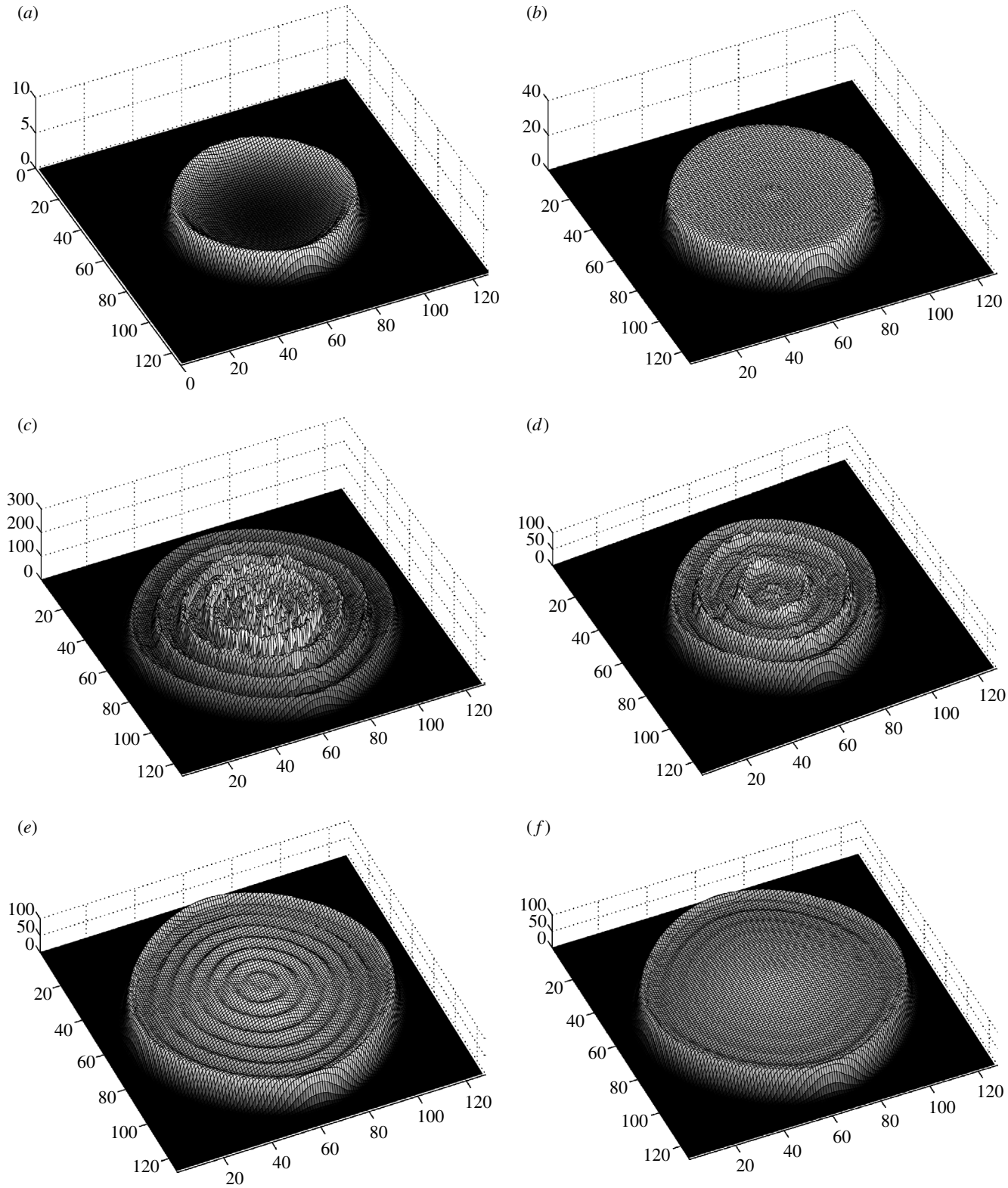


Figure 1. Impact of fungal physiological traits on the emerged biomass profile. (*a*) Propagation of fungal 'fairy ring'; $\alpha_n=0.2$, $\beta_n=0.8$, $\alpha_i=0.5$, $\beta_i=0.5$, $\gamma_1=1.0$, $\gamma_2=0.2$, $\theta=1.0$, $\lambda_1=0.95$, $\lambda_2=0.01$, $D_b=10$, $D_n$ max$=10$, $\zeta=0.01$, $\omega=0.01$, time ($t$)$=20$. (*b*) Biomass conversion efficiency is greater than in (*a*) producing a 'plateau-like' profile; same trait set as (*a*) but $\gamma_2=0.95$, $t=15$. (*c*) Hyphal aggregations appear due to biomass recycling, in particular a high mobilization rate and nonlinear term; same trait values as (*b*) apart from $\theta$ and replenishment rate $\alpha_n=0.2$, $\beta_n=0.8$, $\alpha_i=0.5$, $\beta_i=0.5$, $\gamma_1=1.0$, $\gamma_2=0.95$, $\theta=3.0$, $\lambda_1=0.95$, $\lambda_2=0.01$, $D_b=10$, $D_n$ max$=10$, $\zeta=0.01$, $\omega=0.1$, $t=15$. (*d*) Reduction of mobilization rate and an increase in immobilization rate reduces hyphal aggregations; same trait values as (*c*) apart from $\alpha_n$ and $\beta_n$—$\alpha_n=0.4$, $\beta_n=0.6$, $\alpha_i=0.5$, $\beta_i=0.5$, $\gamma_1=1.0$, $\gamma_2=0.95$, $\theta=3.0$, $\lambda_1=0.95$, $\lambda_2=0.01$, $D_b=10$, $D_n$ max$=10$, $\zeta=0.01$, $\omega=0.1$, $t=15$. (*e*) Further reduction of mobilization and increase in immobilization rate eliminates hyphal aggregations; same trait values as (*d*) apart from $\alpha_n$ and $\beta_n$—rate $\alpha_n=0.5$, $\beta_n=0.5$, $\alpha_i=0.5$, $\beta_i=0.5$, $\gamma_1=1.0$, $\gamma_2=0.95$, $\theta=3.0$, $\lambda_1=0.95$, $\lambda_2=0.01$, $D_b=10$, $D_n$ max$=10$, $\zeta=0.01$, $\omega=0.1$, $t=15$. (*f*) Once immobilization rate is greater than mobilization rate the concentric rings and hyphal aggregations disappear; same trait values as (*e*) apart from $\alpha_n$ and $\beta_n$—$\alpha_n=0.6$, $\beta_n=0.4$, $\alpha_i=0.5$, $\beta_i=0.5$, $\gamma_1=1.0$, $\gamma_2=0.95$, $\theta=3.0$, $\lambda_1=0.95$, $\lambda_2=0.01$, $D_b=10$, $D_n$ max$=10$, $\zeta=0.01$, $\omega=0.1$, $t=15$.

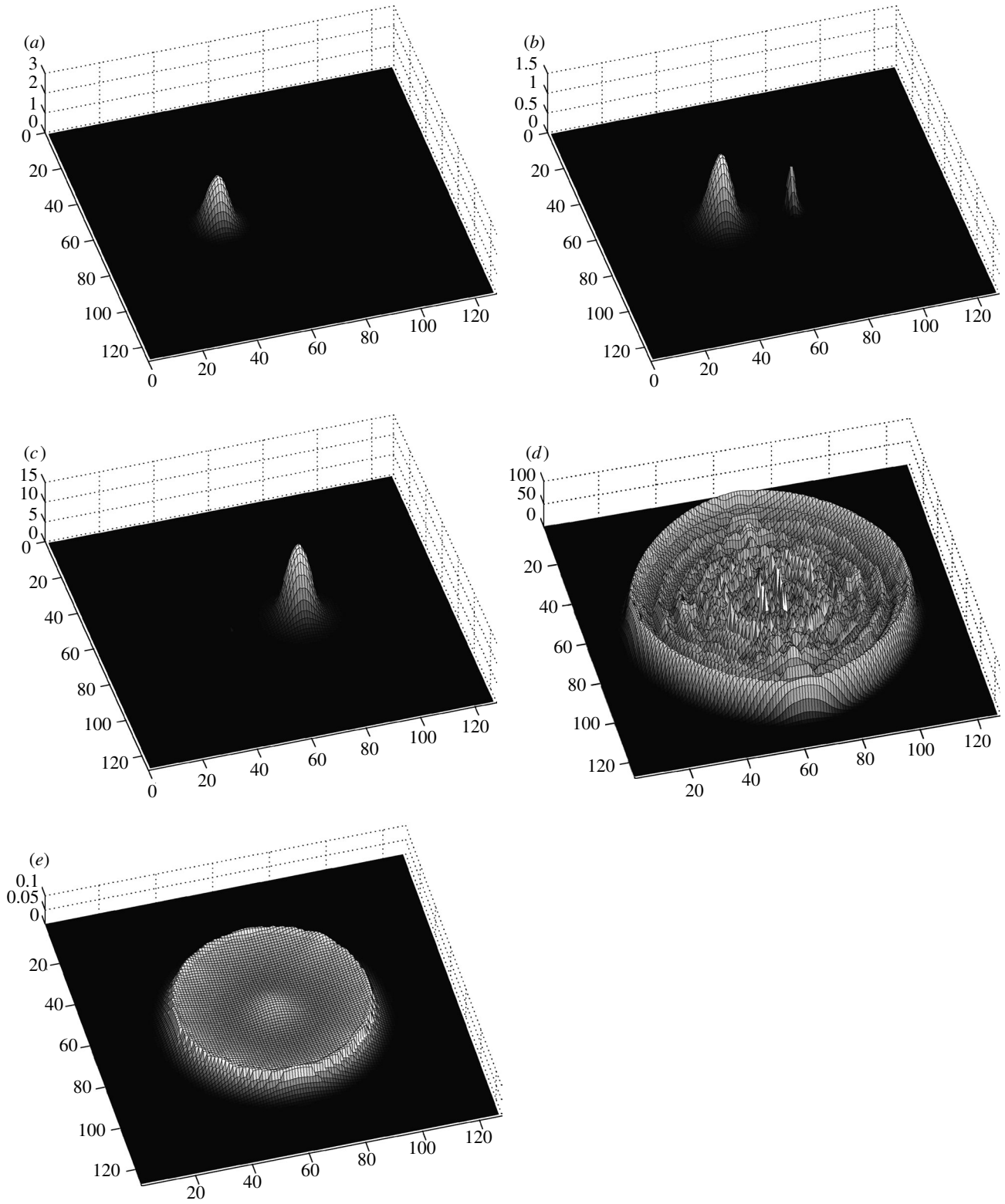


Figure 2. Impact of the environment on emerged biomass profiles. (*a*) Outward growth from an initial resource; fungal individual in heterogeneous environment $\alpha_n=0.8$, $\beta_n=0.2$, $\alpha_i=0.1$, $\beta_i=0.9$, $\gamma_1=1.0$, $\gamma_2=0.4$, $\theta=1.0$, $\lambda_1=0.95$, $\lambda_2=0.01$, $D_b=10.0$, $D_n$ max$=10.0$, $\zeta=0.01$, $\omega=0.01$, time $(t)=10$. (*b*) Detection of second resource; fungal individual in heterogeneous environment $\alpha_n=0.8$, $\beta_n=0.2$, $\alpha_i=0.1$, $\beta_i=0.9$, $\gamma_1=1.0$, $\gamma_2=0.4$, $\theta=1.0$, $\lambda_1=0.95$, $\lambda_2=0.01$, $D_b=10.0$, $D_n$ max$=10.0$, $\zeta=0.01$, $\omega=0.01$, time $(t)=50$. (*c*) Reallocation of hyphal biomass leading to exploitation of second resource hot spot; fungal individual in heterogeneous environment $\alpha_n=0.8$, $\beta_n=0.2$, $\alpha_i=0.1$, $\beta_i=0.9$, $\gamma_1=1.0$, $\gamma_2=0.4$, $\theta=1.0$, $\lambda_1=0.95$, $\lambda_2=0.01$, $D_b=10.0$, $D_n$ max$=10.0$, $\zeta=0.01$, $\omega=0.01$, time $(t)=70$. (*d*) Effect of no replenishment; fungal individual has the same trait set as in figure 1*c* but $\omega=0$, $t=15$. (*e*) Effect of initial resource concentration; fungal individual has same trait set as in (*a*) but the amount of resource in each cell is substantially less, $t=30$.

substrate, which is converted into mobile biomass and then biomass, is at a lower concentration. Therefore, the effect of the nonlinearities is small and the diffusive process can smooth out any small variations.

## 4. DISCUSSION AND CONCLUSIONS

We present a model for the phenotype in fungal mycelia that incorporates, for the first time, the processes associated with recycling and transport of biomass that

are fundamental to indeterminate organisms. Observed colony-scale features are reproduced and can be interpreted as emerging from a relatively simple interaction between localized processes governing recycling of mobile biomass, and colony-scale transport. Broad ranges of observed phenotypes arise from different realizations of these processes as characterized by different associated parameters, and from different environmental contexts. Recycling of biomass is described by rules that implicate only the local internal conditions in the mycelium. Coherence and symmetry of patterns at the scale of the mycelium are mediated by subsequent transport of mobile biomass that result from the recycling process. Symmetry is lost when assumed nonlinearities in biomass recycling become dominant. Such nonlinearities might have their origins in regulatory processes affecting the immobilization of mobile biomass for the local production of biomass. The model clearly shows how local, hyphal scale processes and transport are involved in the production of colony-scale features.

Clearly there are many processes and features of real fungi that have been ignored in the current implementation. Notwithstanding this, the results here show that apparently complex behaviour can result from simple local rules spatially mediated by internal transport, and additional sophistication will not affect this general conclusion. However, in order to develop the study to look more closely at functioning and community dynamics, a number of key processes will have to be incorporated. Mobile biomass has been defined in a very generic sense in the current model to be associated only with transport and immobilized biomass production. However, mobile biomass involves a complex mix of components in real mycelia and each will be used for different, or a range of, purposes. These include the use of resources in increasing bioavailability of external substrate, in signalling at the hyphal level, in reproduction, etc. Fungal interactions involve a complex cascade of signalling and antagonistic responses that determine the outcome beyond those incorporated here.

To progress, a much closer dialogue between experimental and theoretical mycologists is required that focuses on the crucial role that biomass recycling plays in mycelia. The present study points to the need for more detailed and quantitative observation of the dynamics of remobilization and transport of mobile biomass. Increased development and application of real-time *in vivo* techniques capable of studying the consequences of colony-scale context for hyphal-scale processes associated with biomass recycling, linked to the development of testable models, could lead to a revolution in understanding of the origin of phenotype in growing and interacting mycelia.

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