Model for growth and morphology of fungal mycelium

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The growth process of fungal hyphae involves transport of nutrients from the sub-apical region of the fungus to the growing tip of hyphae. At the tip domain, the intracellular organelle-Spitzenkorper uses the nutrients that are packaged as membrane bound vesicles to synthesize fresh cell wall. This in turn leads to elongation and branching of the hyphae and formation of a single colony mycelium. To gain insight about the growth process and temporal evolution of morphology of the single colony mycelium, we propose a driven lattice gas model which incorporates the processes of vesicle supply dependent linear extension and branching of the tips of the hyphae, apart from process of motor driven transport of vesicles along the hyphae towards the growing tips. We first analyze the growth and transport process in the primary hypha modeled as a growing 1-d lattice, which is subject to particle (vesicle) loss due to presence of dynamically created branching sites. Using an analytical Mean-Field approach, we show that the spatial profile of vesicles along the growing lattice is an exponential distribution, while the length grows logarithmically with time and compares reasonably well with the Monte Carlo (MC) simulations for the process. Using MC simulations, we also obtain the probability distribution of length of the hypha, and find that it tends to a Gaussian distribution function at late times. In contrast, we find that probability distribution function of the time required for growth to a specific length is a broad log-normal distribution. We simulate the resultant 2-d morphology generated by the growing primary lattice, quantifying the motility behavior and morphological characteristics of the colony in terms of measures such as the Center of Mass, Radius of Gyration and Aspect Ratio. Analysis of the temporal behavior and morphological characteristics of the resultant 2-d morphology reveals a wide variability of these characteristics which depend on the input parameters which characterize the branching and elongation dynamics of the individual hyphae. By calibrating the input parameters for our model, we make some quantitative comparison of the predictions of our model with the observed experimental growth characteristics of fungal hyphae and the morphological characteristics of single colony fungal mycelium.

I. INTRODUCTION

Fungi is an integral part of the nutrient cycle in ecosystems and they serve as important model systems for genetic research due to their relative simplicity as an eukaryotic cellular system [1, 2].

Fungi exhibit filamentous growth process. The basic filament structure of Fungi- the hyphae, grow by means of extension and branching at the their tip, giving rise to a multicellular complex network -mycelium [1, 3]. In order to develop a comprehensive understanding of the morphology of the entire mycelium, it is pertinent to develop an understanding of the transport and branching process of the individual fungal hypha and the morphological features of colony formed as a result of such a growth process. Depending on the scale of description of the growth phenomenon, theoretical models for growth and transport in individual hypha and fungal colonies belong to the categories of tip-scale models [4, 5], intermediate scale models [6–9], and macroscale models [2, 10]. The tip-scale models such as vesicle supply center (VSC) model focus on aspects of extension and shape of the hyphal tip [4, 5] and the typical length scales of description is $\sim 100\mu$m. For this model the connection of the growth or branching process with the process of vesicle supply from the sub-apical region of the fungi is not explicitly taken into account [5, 9]. On the other hand the macroscale models focus on description in terms of effective interaction of fungal colony as a whole with the environment, without explicitly taking into account the metabolic processes at play for the individual hypha that constitute the colony [10, 11]. The model that we study belongs to the category of intermediate scale description, wherein, we focus on motor driven process of growth and branching in individual hyphae which is fed by a single source of nutrients and generates a single colony mycelium. Much of the previous work in the domain of such intermediate scale description of fungal growth has taken recourse to continuum models and focused on the details of bio-mechanics, without explicitly considering the role of molecular motors [9, 10]. In contrast we investigate the role of molecular motors using a model of driven lattice gas.

Driven lattice gas models have provided useful description for plethora of biological processes encompassing transport across biomembranes [12], dynamics of ribosomes in m-RNA [13], motor driven intracellular transport [14, 15], transport in fungal hyphae [8, 19, 20] and other driven phenomenon [20, 21]. In particular, a driven lattice gas model - Dynamically extending exclusion process (DEEP) has been adopted for modeling extension of fungal hyphae [8, 19]. For DEEP, particles hop unidirectionally on the lattice, interacting with other particles via hard-core repulsion, and the particles at the growing end
of the lattice dynamically create a new lattice site, leading to the overall extension of the lattice [8, 19]. While this model has been able to relate the growth of the fungal hyphae with the supply of nutrients, one inadequacy has been that the process of branching and related loss of the transported particles has not been taken into account. For instance for aerial hyphae of sporangiophore, branching is indeed observed. Further, the elongation process of the individual hypha is such that there is a slow down of their growth rates as their length increases [9, 30]. This is in contrast to the results obtained for DEEP, which predicts a growth rate of the hypha that is uniform, without any slowdown [8, 19].

Our minimal model is a generalization of the Dynamically extending exclusion process (DEEP), encompassing the process of both linear growth and branching. Also in contrast to continuum bio-mechanical models [9], which involves many parameters, our coarse grained description involves very few input parameters e.g; nutrient supply rate, growth rate at the tip, branching rate, and flow rate of nutrients to the different branches of the growing lattice. One experimental system that serves as a paradigmatic example is the fungus Nuerospora Crassa [31–32]. For this system, the material necessary for growth of the hyphae is packaged as vesicles and supplied by a single source located in the sub-apical region of the fungi [31–32]. The transport of these vesicles is done by molecular motors, which walk along the parallel array of microtubule filaments, carrying these vesicles to the tip of the hypha [33, 34]. In the apical region of the tip, the intracellular organelle- Spitzenkorper is involved in synthesis of new cell wall from the vesicles, leading to growth [31]. Apart from linear elongation process of the hyphae, lateral branching process of the fungal hyphae is also observed [9, 30, 32]. The process of branching and elongation of a single primary hypha, fed by a single source of nutrient generates a single colony mycelium. We study the morphological characteristics and growth pattern of such colonies on a surface using a 2-d minimal model. 2-d growth processes have been studied for randomly branched polymers [35–37] and growth of cell colonies [38]. In this context, variants of lattice animal models such as Eden Aggregation process have been used to characterize the growth processes on discrete lattices [38–44], while continuum models such as Flory Theory for branched polymers have been developed to study polymerization process under different conditions [35–37]. The connections between these discrete lattice animal models with the polymerization models have also been studied [39, 47]. There is however one crucial distinction of these models with the model that we study in this article. In particular for our model, the elongation and branching process at individual sites of the colony is coupled to supply of nutrients at those sites, and is in contrast to growth process of branched polymers and lattice animals for which growth process at the sites are not subject to such a constraint.

In Section II we first describe the 1-d minimal model for the growth and transport in the primary hypha, specifying the dynamical rules for growth and set up the corresponding equations of motion for the system. Further we also specify the dynamical rules governing the development of the 2-d mycelium arising from the branching process of the hyphae.

In Section III we obtain the mean field (MF) analytical solutions of the length of the individual primary hypha as a function of time as well as the spatial profile of the transported cargo along the hypha. We then compare these results with the Monte Carlo (MC) simulation results. By performing MC simulations, we also obtain the probability distribution of lengths of the primary hypha, and the probability distribution of the time required for growth up to a specified length of the hypha.

In Section IV we discuss the results for the spatial and temporal features associated with single colony mycelium that is generated from the elongation and branching process of the primary hyphae.

In Section V we calibrate the input parameters of the model to reproduce the quantitative measures associated with the growth characteristics of the individual fungal hypha and single colony mycelium, that are observed in experiments.

In Section VI we summarize our results and discuss the insights gained from the findings of this model in understanding the growth and morphological characteristics of single colony mycelium.

II. MODEL

In general, process of linear growth and lateral branching (in same plane) of the primary fungal hypha would generate a 2-d morphology. We first describe the 1-d model for growth and transport behavior of the primary hypha. Subsequently we would discuss the generalized model for describing the 2-d morphology of the hyphal colony emerging due to the lateral branching process and linear extension of the fungal hyphae.

A. Effective 1-d model for growth for primary hypha

We consider the initial state of the fungal hypha to be an object of 1-d spatial extension with an initial specified length $\epsilon$ and which we refer to as the primary hypha. From the perspective of the linear extension of this primary hypha, the effect of branching manifests as a process of material loss along the hyphae during the process of its growth. We represent this growing primary fungal hypha as a 1-d discrete lattice. At any instant of time $t$, the total number of lattice sites is $N$ corresponding to a length $L = \epsilon N$ (Fig.1). Vesicles required for growth are represented by particles, which are transported by molecular motors along the lattice from left to right. First we describe the dynamics of the particles at the lattice
FIG. 1. Schematic of the dynamical processes for (a) Growing primary hypha is represented as 1-d growing lattice. With a rate $\gamma$, an occupied tip site (T) becomes two normal empty sites while with rate $1 - \gamma$ two empty lattice sites are created with the preceding site transforming into a defect site (D). The particle entry rate at first site (E) is $\alpha$, particle hopping rate is 1 for a normal (non-defect) site and loss rate of particles at defect site is $\delta$. (b) Single colony mycelium represented as a 2-d lattice with entry rate $\alpha$, branch site creation rate $1 - \gamma$, hopping rate of 1 for a normal (non-branching) site and particle flow rate to secondary branch is $\beta$. For the branching sites, hopping rate on the same branch is $1 - \delta$ and overall growth rate at tip is 1. Here (E) denotes the site of entry, (T) denotes tip site and (B) a branching site.

boundaries. At left end of the lattice, at site $i = 1$, particles enter the lattice with a rate $\alpha$ provided the boundary site is vacant. At the boundary site on the right, at site $i = N$, which corresponds to the tip of the hypha, two processes can occur: (a) If the tip site at $i = N$ is occupied by a particle then with a rate $\gamma$ an additional empty lattice site to the right is created, and the site $i = N$ also become empty. This process leads to overall increment of the length of the lattice from from $L$ to $L + \epsilon$, while the total number of lattice sites is incremented from $N$ to $N+1$. This dynamics of lattice growth is exactly same as that of DEEP [8, 19]. (b) With a rate $1 - \gamma$, an occupied tip site $i = N$ not only creates a new empty lattice site to the right, but the lattice at $i = N$ becomes an empty defect site. The overall extension rate of the lattice is 1. These defect sites correspond to the branching sites that would get created dynamically. If one considers the full 2-d morphology resulting from this growth process then the defect sites would correspond to the branching sites for which the vesicle supply from the static end of the hyphae would be split between the two branches, leading to eventual growth of these two separate branches. However from the perspective of the primary hypha, the effect of branching would manifest as loss of vesicle at the defect sites. Thus effectively at any instant of the time, the 1-d lattice, representing the primary hypha would comprise of bulk normal bulk sites (N), defect sites (D), apart from the boundary sites at the growing tip (T) and boundary site at the non-growing end (E), which corresponds to the site where vesicle is diverted. Particles in the bulk of the lattice interact with each other via excluded volume effect, thus restricting the maximum occupancy per lattice site to 1. For any normal bulk site $i$, the particles hop unidirectionally to the adjacent site to the right, with rate 1 provided the site at $i + 1$ is vacant. At the defect site, with a rate $\delta$ there is a loss of particle from the site, while with a rate $1 - \delta$, the particles hop to the site $i + 1$, provided it is empty. This completes the specification of the dynamics of the 1-d model. All the dynamic processes for this dynamic lattice model are schematically depicted in Fig. 1(a).

B. 2-d model for single colony mycelium

We consider the growth process of single colony on a square lattice, arising due to the branching and elongation process of the fungal hyphae constituting the colony. We consider an initial starting configuration of the colony which is a fungal hypha, and represented by a 1-d lattice of length $\epsilon$ placed along the $x$ axis at the origin. The processes of particle entry at the left boundary is same as that of the 1-d model, with the particles entering at left end of the lattice located at $(0, 0)$, with a rate $\alpha$ provided the site is vacant. If there is particle at the tip site, two processes occur: (i) Pure Linear Extension: With a rate $\gamma$, a new lattice site is created in the original direction of movement of the particle, provided that the site is not occupied by the colony itself. The underlying assumption made here is that presence of the colony obstructs and arrests the linear growth process of an hyphal tip. (ii) Branching and extension: With a rate $1 - \gamma$, two new empty lattice sites are created- an empty lattice in the original direction of movement of particle, and an empty site perpendicular to it. One of two perpendicular direction is chosen randomly with equal probability. Again this process is subjected to the constraint that it occurs only if the adjacent site in the direction of growth and the adjacent sites in the perpendicular direction are not occupied by the colony itself. Such branching process would transform the tip site (T) at time $t$ into a branching site (B) at time $t + 1$. It would also create two new tip sites in the direction of original movement of particle and in a direction perpendicular to it. Both these processes would lead to growth of the single colony comprising of these hyphae. Thus at any instance of time any site in the bulk of the colony would either be a branching site (B) or a normal site N (a site without any branching). At any instance a particle on a normal site will hop unidirectionally with rate 1 to the adjacent site in the original direction of motion of particle provided it is empty. For
a particle on a branching site, with a rate $\delta$ the particle would hop on to the other branch site provided the adjacent site on the branch is empty, while with rate $1 - \delta$ it would continue to hop to adjacent site in the original direction of movement provided that site is empty. A typical configuration is schematically depicted in Fig. 1(b).

C. MC simulation of the process

For determining the density and current profiles on hypha, Monte Carlo (MC) simulations have been performed to simulate the various processes for the 1-d model described in subsection II A using a procedure if random update of the sites. For simulating the configurations for the 1-d model, the initial starting configuration is a 1-d lattice with number of sites (N = 1) which is occupied by a particle at $x = 0$. For the 2-d model, the initial starting configuration is also a 1-d lattice with a particle occupying site specified by coordinates $x = 0$, $y = 0$, and the initial growth direction being along $+x$ direction. We adopt a synchronous update procedure for updating the lattice sites for the 2-d model \[17\]. At any instance of time $t$, for a given configuration, all the lattice sites are updated simultaneously according to the rules of dynamics specified in subsection II B. Ensemble averaging is done typically for 5000 samples for the 1-d model and for 100 samples for the 2-d model, starting with the same initial configuration.

III. CHARACTERISTICS OF SINGLE HYPHA

Having described the 1-d model for growth of the primary hypha in section II A, we now discuss the growth characteristics that we obtain for this minimal model.

A. Survival probability and density profile

For the 1-d model for hyphal growth, we consider an ensemble of similarly prepared system. We define survival probability $P(i|j)$ with $i > j$ as the probability of a particle in site $j$ to reach site $i$ without leaving the 1-d lattice. The loss at any given site on the lattice is due to the presence of defect sites, from which particles are lost from the bulk of the growing lattice with a rate $\delta$. The survival probability can be expressed in terms of product of conditional probabilities as,

$$P(i|j) = \prod_{s=j}^{i-1} P(s+1|s)P(j)$$ \hspace{1cm} (1)

where, $P(s+1|s)$ is the conditional probability for a particle at site $s$ to reach site $s+1$, and $P(j)$ is the probability of occupancy of site $j$. The survival probability $P(s+1|s)$ itself is a random variable which would take values $1$ or $1 - \delta$, depending on whether site $s$ is a normal site or a defect site. Since $P(i|j)$ can be expressed as product of the conditional probability $P(s+1|s)$ which are themselves independent random variables, it follows that the probability distribution function of the survival probability is a log-normal distribution function.

On averaging over the ensemble, the average survival probability for a particle at site $s$ to reach a site $s+1$, $\langle P(s+1|s) \rangle$ can be expressed in terms of the probability of occurrence of defect/normal sites and their respective survival probabilities as follows:

$$\langle P(s+1|s) \rangle = P_N(s+1|s)P(N) + P_D(s+1|s)P(D)$$ \hspace{1cm} (2)

where, $P(D)$ is the probability that the site $s$ is a defect site, $P(N)$ is the probability that it is a normal site, $P_D(s+1|s)$ is the survival probability of the particle at site $s$ to reach site $s+1$ if the site $s$ is defect site, and $P_N(s+1|s)$ is the survival probability of the particle at site $s$ to reach site $s+1$ if the site $s$ is normal site. $P_N(s+1|s) = 1$ due to the fact that for a normal site, a particle definitely hops to the next site without any loss. $P_D(s+1|s) = 1 - \delta$, since with rate $\delta$ particles leave the 1-d lattice and with rate $1 - \delta$ they hop to the adjacent lattice site on the right. Whether a particular site is a defect site or not is solely determined by the relative rates of creating a new defect site at the tip. Thus $P(D) = 1 - \gamma$ while $P(N) = \gamma$. Therefore it follows that, $\langle P(s+1|s) \rangle = \gamma + (1 - \delta)(1 - \gamma)$. We further note that the conditional probability $\langle P(s+1|s) \rangle$ is same irrespective of the lattice position $s$ for any site in the bulk. Thus the expression for

![FIG. 2. (a) Average occupancy of particles ($\rho$) as function of distance from the site of particle entry into the lattice ($x$) for the 1-d model. Solid curves correspond to MF expression in Eq 8 while the circles correspond to points obtained by MC simulation done with random update for 5000 samples. (b) Average length of the growing lattice ($\langle L \rangle$) as a function of time $t$ : The solid curves correspond to MF expression of Eq 8 while circles correspond to MC simulation results for 5000 samples. For the plots, $\alpha = 0.2 s^{-1}$, $\delta = 0.2 s^{-1}$, lattice spacing $\epsilon = 0.4 \mu m$ and overall growth rate at tip is $0.4 \mu m s^{-1}$.

\[5000\]
average survival probability \( \langle P(i|j) \rangle \) assumes the form,

\[
\langle P(i|j) \rangle = P(j)[1 - \delta + \delta \gamma]^{(i-j)}
\]  

(3)

The distance of separation between the site \( i \) and site \( j \) in terms of lattice spacing \( \epsilon \) can be expressed as \( x = (i - j)\epsilon \). Then the expression for the average probability of a particle surviving a distance \( x \) assumes a form,

\[
P(x) = \exp \left( \frac{Kx}{\epsilon} \right)
\]  

(4)

where \( K = \ln[1 - \delta + \delta \gamma] \).

Since the steady state average occupancy at the left end of the lattice at \( x = 0 \) is \( \alpha \), it follows from Eq. (3) and Eq. (4) that the expression for the average occupancy \( \rho(x) \) can be expressed as,

\[
\rho(x) = \alpha \exp \left( \frac{Kx}{\epsilon} \right)
\]  

(5)

In Fig.2(a), we show a comparison of spatial profile of the average occupancy along the growing 1-d lattice obtained by approximate analytical means with the profile obtained by MC simulation for which excluded volume interactions are taken into account explicitly.

B. Temporal behavior of hyphal length

For our model we have set the rate of overall growth rate of the lattice to 1 unit per unit time. This corresponds to a growth rate of \( \epsilon \) per unit time, when the tip site is occupied by a particle. Thus the mean linear growth rate of the length of the lattice \( V \equiv d\langle L \rangle/dt \) can be expressed as,

\[
d\langle L \rangle/dt = \epsilon \rho(L) = \epsilon \alpha \exp[K\langle L \rangle/\epsilon].
\]

With the initial condition of \( L \) being 0 at \( t = 0 \), the expression for the average length of the lattice \( \langle L \rangle \) as a function of time is,

\[
\langle L \rangle = \frac{\epsilon}{|K|} \ln(1 + \alpha|K| t)
\]  

(6)

The corresponding expression for the mean linear growth rate of the lattice length is,

\[
V = \frac{\epsilon \alpha}{1 + \alpha|K| t}
\]  

(7)

In Fig.2(b), we show a comparison of the temporal profile of the average length of the growing 1-d lattice obtained by approximate analytical means with the temporal profile obtained by MC simulations.

C. Probability distribution of Length of primary hypha

For the 1-d model for growth of the primary fungal hypha, after a fixed interval of time \( t \), starting from a single lattice site, the lattice grows to \( N \) lattice sites (corresponding to a length \( L = \epsilon N \)). Since the process of creation of defect site is a random process, the length up to which the hypha grows is itself a random variable. Using MC simulations with synchronous update, we simulate the probability distribution of the length of the growing lattice (in terms of the total number of lattice sites \( N \)) after a fixed interval of time. Fig.3(a) displays the probability distribution of \( N \) for different value of \( t \). For this distribution the actual value of the peak of the distribution is closer to approximate expression of average length obtained from Eq. (6). Fig.3(b) displays the probability distribution functions of the scaled variable \( z = (N - \langle N \rangle)/\sqrt{\langle N \rangle} \), at different times. This distribution tends to a Gaussian distribution. The width of the distribution in terms of scaled variable \( z \) decreases very slowly (\( \sim 5\% \), when \( t \) increase by one order of magnitude). This implies that the relative width of the distribution function of \( N \), and equivalently the relative width of the probability distribution function of \( L \) decreases more rapidly than \( L^{-1/2} \). Thus at late times, the variation of the length of the hypha from average value is small.

![Fig. 3.](image-url)
D. Probability distribution of growth time of hypha

We look at the probability distribution of time $t$ required for growth of the primary hypha to grow up to a fixed length. Fig. 3(c) displays the probability distribution function of time $t$ for different values of total number of lattices sites $N$. The probability distribution function of time is generally a broad distribution, with the most probable value of $t$ significantly different from the mean value of time required for growth of the primary hypha. In Fig. 3(d) we plot the distribution of the $\ln(\tau)$ where $\tau$ is a dimensionless and defined as $\tau = t/1s$. This distribution tends to a Gaussian distribution function indicating that $P(t)$ tends to a log-normal distribution function.

IV. FEATURES OF SINGLE COLONY MYCELIUM

We now focus our attention on the motility and morphology characteristics of a single colony mycelium. We use the 2-d model described in Subsection II B for mimicking the growth processes in single colony mycelium which results from elongation and lateral branching of a single primary hypha with a single source of nutrient. The morphology characteristics, e.g; shape and size of the single colony mycelium is determined by the parameters $\gamma$ which characterizes the propensity for branching in the hypha, $\alpha$ which is a parameter that characterizes the nutrient flow rate to the secondary branch and input rate of nutrients $\alpha$. Depending on the choice of these parameters, the morphology characteristics can vary significantly. For experiments with Neurospora Crassa, the experimentally observed growth rates of hyphae are in the range of $20 - 30 \mu m/min$ \cite{31, 32}. Consistent with this observation we set the overall growth rate in our model system to $0.4 \mu m/s$ and choose a lattice spacing $\epsilon = 0.4 \mu m$, which corresponds to overall growth rate of $1s^{-1}$. This would also imply that the particles in the bulk of the lattice are hopping with rate $0.4 \mu ms^{-1}$ corresponding to hop rate of $1s^{-1}$ that we have set for our model. This choice of hopping rate is comparable to the typical motor velocity of kinesin-1 motors whose velocity is $\sim 0.6 \mu ms^{-1}$ \cite{31}. Fig. 4 displays some of the resultant morphologies and their evolution over time, for different set of parameters. As would be expected, when both the branching rate $\gamma$ and nutrient flow rate to the secondary branch $\delta$ is low, the lateral growth of hyphae is small compared to the longitudinal growth along the direction of growth of the primary hypha, in the initial phase of evolution of the single colony (Fig. 4a) and it continues to persist after 21 hours (Fig.4e). Fig.4b and Fig.4f shows the temporal evolution of the morphology when the branching rate is high and rate of nutrient supply to secondary branches is low, while Fig.4(c) and Fig.4(g) shows the typical morphology when the branching rate is low while the rate of supply to the secondary
branches is high. When both the branching rate and nutrient flow rate to the branches is high, asymmetry of growth along the longitudinal and lateral directions is virtually absent and the single colony mycelium tends to a radially symmetric configuration about its Center of Mass at late times (Fig.4h).

The process of branching in the hyphae has the effect of creating new tip sites (T) which in turn serve as seeds for further elongation and branching process of the mycelium. However as described in subsection II B the tips can elongate or branch only if the adjacent space is not occupied by the single colony mycelium. For the case where the branching rate and δ is high, not only would there be numerous branches which would be created in the mycelium, but there would be a tendency of the growth direction of the tips to change and consequently be obstructed by the pre-existing mycelium. Thus over the course of evolution of the morphology, many of the growing tips (T) would become immobile or jammed, i.e.; these tips would not serve as either elongation or branching site. Along with the different morphologies obtained for the different values of control parameter γ and δ, Fig.4 also shows the immobile and mobile tip sites of the mycelium. However as described in subsection II B, the effect of creating new tip sites (T) which in turn serve as seeding sites. Along with the different morphologies obtained for the different values of control parameter γ and δ, Fig.4 also shows the immobile and mobile tip sites of the mycelium. However as described in subsection II B, the effect of creating new tip sites (T) which in turn serve as seeding sites.

A. Motility behavior of Center of Mass

In Fig.5(a) we display the temporal behavior of the Center of Mass of the growing lattice network (averaged over different samples). Increasing the branching rate 1 − γ and/or δ has the effect of impeding the motility of the center of mass of the single colony mycelium. As expected for early times, for low δ and low branching rates, \( \sqrt{\langle R_{cm}^2 \rangle} \) shows a linear dependence on the \( \tau \). From the log-log plot in Fig.5(b), we can infer that \( \sqrt{\langle R_{cm}^2 \rangle} \sim t^q \) at later times. For all the cases we find that the exponent \( q < 1/2 \) indicating sub-diffusive behavior of the Center of Mass for the regime of time window that we have probed. Fig.5(c) shows the dependence of \( \langle R_{cm}^2 \rangle \) on \( N \). From the log-log plot displayed in Fig.5(d) for different set of input parameters we see that for sufficiently large size \( N \), \( \sqrt{\langle R_{cm}^2 \rangle} \sim N^{\beta} \).

B. Size of the Colony

Radius of Gyration \( R_g \) is one measure which can be used to characterize the typical size of the single colony mycelium. In order to understand the growth characteristics of the size of the single colony we look at the temporal behavior of \( \sqrt{\langle R_g^2 \rangle} \). Fig.6(a) displays the temporal evolution of \( \langle R_g^2 \rangle \). From the log-log plot in Fig.6(b) we can infer that at later times, \( \langle R_g^2 \rangle \sim t^\phi \) with \( \phi < 1/2 \). Fig. 6(c) displays the variation of \( \langle R_g^2 \rangle \) with \( N \) for different set of input parameters. Assuming a power law dependence of \( \sqrt{\langle R_g^2 \rangle} \) on \( N \) of the form \( \langle R_g^2 \rangle \sim N^{2\nu} \), from the log-log plot in Fig.6(d) we extract the exponent \( \nu \) from the slope of the least square fitted straight line. For the range of \( N \) considered for our simulations, the exponent \( \nu \) varies with the chosen inputs parameters \( \delta \) and \( \gamma \). Typically the effect of lowering the branching rate has the effect of increasing \( \langle R_g^2 \rangle \) for a given \( N \). When nutrient supply rate \( \delta \) is made high while branching rate is lowered, the resultant colony becomes more porous, with less dense filling of space. This attribute of the colony is demonstrated by the morphology of the colony shown in Fig. 4(g). This may be understood as follows: When the branching rate is low, very few branches are created. However the the secondary branches are the ones which grows faster. Subsequent branching of these secondary branches eventually results also to formation of closed loop, which arrest further growth of the branches locally due to obstruction. The size of this loop determines the porousness of the colony. Since the size of these closed loops increases when branching rate is decreased and δ increased, the resultant overall morphology becomes more porous. When both the branching rate is high and δ is high, it would be expected that the porosity would be low and the growth of the colony would be a space fill-
FIG. 6. Behavior of Radius of Gyration $G = \sqrt{\langle R_g^2 \rangle}$ for four different parameter values (same as Fig.5). Panel (a) displays the plot of $G$ vs $t$. (b) Plot of $\log(G_1)$ vs $\log(\tau)$, where $G_1 = G/\epsilon$ is the dimensionless Radius of Gyration, and $\tau = t/1$sec, is the dimensionless time. The least square fitted straight line to the data points at later times corresponds to a slope of (i) $\phi = 0.29$, (ii) $\phi = 0.40$, (iii) $\phi = 0.37$ and (iv) $\phi = 0.44$ where $G_1 \sim \tau^\phi$. (c) Plot of $G$ vs $N$. (d) Plot of $\log(G_1)$ vs $\log(N)$ : The least square fitted straight line to the data points at large $N$ corresponds to a slope of (i) $\nu = 0.32$, (ii) $\nu = 0.47$, (iii) $\nu = 0.40$ and (iv) $\nu = 0.48$ where $G_1 \sim N^\nu$. Averaging is done over 100 samples.

C. Shape Characteristics of the Colony

In order to characterize the asymmetry of the morphology of the single colony we define aspect ratio $\xi = \sqrt{\langle Y_2^2 \rangle}/\langle X_2 \rangle$. $\xi$ is a measure of the relative growth in the lateral direction viz-a-viz the extension along the original direction of growth of the primary hypha. Fig. 7 shows the temporal behavior of the aspect ratio. For very late times, the aspect ratio is expected to converge to 1. Indeed, when the branching rate is low and nutrient supply rate to the secondary branches is high, as in Case (iv), the aspect ratio of the colony tends to 1 very rapidly which corresponds to a typical morphology of the colony shown in Fig. 4(h). However when the branching rate is low and $\delta$ is also low, for early times, the lateral extension of the colony (perpendicular to initial growth direction of the original hypha) is much less compared to growth along the original direction along x. Thus even after more than 8 hours of growth, the aspect ratio is much lower than 1, approaching ‘late’ time limit of $\xi = 1$ slowly. Interestingly for a range of intermediate times (up to $30000$ secs) considered in the simulation, when the branching rate is very high, while the nutrient supply rate to the branches is low, as in Case (ii), the aspect ratio $\xi$ even exceeds 1 (Fig. 7). This maybe qualitatively be understood as follows: When the branching rate is high, whilst $\delta$ is low, from the primary hypha, many lateral branches(along y axis) would be generated, and the typical distances between these lateral branches would be relatively small. Over the course of evolution of the colony, these lateral branches would be the sites for secondary branches along x axis- the direction of growth of the original primary hypha. However the growth of these secondary branches would be arrested by the frequent lateral branches arising due to high rate of branching. This is turn would lead to a situation where the overall growth along the x direction(except the primary branch) would be slowed down compared to the unhindered growth of the secondary branches along the lateral direction along
y axis. Such growth process results in a typical morphology of the colony shown in Fig 4(f).

D. Growth sites of the colony

For the 2-d model for the growing colony that we have considered, growth occurs only at the tip sites. While the elongation process shifts the position of the tip site, the branching process results in creation of new tips. Over the course of evolution of the morphology of the colony, many of the tip sites cease to be sites of growth and become immobile as they are obstructed by the part of the pre-existing colony. Fig.8 displays the temporal behavior of $Q$ which is the ratio of the number of mobile tips $N_m$, with total number of tips $N_T$ in a single colony. $Q$ decreases with the passage of time as the colony size increases. Expectedly, the rate of decrease of $Q$ is faster for the case when the branching rate is high and the nutrient supply rate to secondary branches is also high (Case iv) in comparison to the case when both the branching rate and $\delta$ are low (Case i). In fact, at 'late' times, and 'large' N limit, the mobile tips would reside typically on the outer perimeter of the colony while the immobile tips would be part of the bulk (Fig.4h). As the size of the colony grows, the ratio of the number of sites on the outer perimeter with the total number of sites, decreases and consequently we would expect the decrease in $Q$ as we observe in the simulations. In order to quantify the typical scaling behavior exhibited by these mobile tips in the 'large' N limit, we specifically focus on the case where branching rate is high and for which $\delta$ is low, since for this case convergence to 'large' N limit behavior is relatively faster. We define $S$ as the ratio of the number of mobile tips $N_m$ with the total number of lattice sites of the colony $N$. In Fig. 9(a) we show the variation of $S$ with Radius of Gyration $R_g(N)$. From the corresponding log-log plot in Fig.9(b), we can infer $S \sim R_g^{-1}$. This particular scaling behavior maybe understood as follows: For large N limit, the mobile tips reside on the outer perimeter of the colony. Further if the perimeter is an euclidean surface, then the ratio of the perimeter length with Total area should scale inversely with $R_g$ and consequently $S$ itself scales inversely with the Radius of gyration. Since for this case, from our simulations, we know that $R_g \sim N^{1/2}$ (Fig.6, Case iv), it would be expected that $S \sim N^{-1/2}$. Fig.9(c) displays the variation of $S$ with $N$. The corresponding log-log plot displayed in Fig.9(d) indeed confirms this scaling behavior.

V. COMPARISON WITH EXPERIMENTS

The only control parameters of the 2-d minimal model that we have presented are the entry rate $\alpha$, the branching rate $1-\gamma$, and nutrient supply rate to secondary branches $\delta$. In order to make connection with the morphological features observed in experiments, we check whether by calibrating these three input parameters, the model is able to reproduce quantitative measures associated with the growth characteristics of fungal hyphae. Consistent with experiments with fungal hyphae of _Nuecespora Crassa_, we choose overall hyphal extension rate $0.4 \mu m/s$ [31, 32] and set the lattice spacing $\epsilon = 0.4 \mu m$. This would correspond to an overall growth...
rate of 1 lattice unit per second. For experiments with *Neurospora Crassa*, the experimentally observed growth rates of hypha are in the range of $20-30\mu m/\text{min}$ [31,32]. We choose a particle hopping rate of $1s^{-1}$. This would also imply that the particles in the bulk of the lattice are hopping with rate $0.4\mu ms^{-1}$. This choice of hopping rate compares reasonably with the typical motor velocity of kinesin-1 motors [31].

![Graph](image)

**FIG. 10.** (a) Average length of lattice ($L$) as a function of time $t$: The solid curves correspond to MC simulation results for 1-d model. Here, $\alpha = 0.4s^{-1}$. $\delta = 0.2s^{-1}$, $\gamma = 0.998s^{-1}$, lattice spacing $\epsilon = 0.4\mu m$ and velocity at the growing tip is $0.4\mu ms^{-1}$. For these choice of parameters, the hyphal growth characteristics observed experimentally for fungal hypha of *Rhizopus Oligoporous* (Ref.[35,45]), matches reasonably well with the MC simulation results. (b) The 2-d morphology after 5 hours obtained for $\alpha = 0.4s^{-1}$, $\delta = 0.2s^{-1}$, $\gamma = 0.995$, $\epsilon = 0.4\mu m$ and velocity at the tip is $0.4\mu ms^{-1}$. This morphology is similar to the morphology of the single colony hypha obtained in experiments with *Neurospora Crassa* (Ref.[32]).

In Fig.10(a) we plot the temporal behavior of the average length of the primary hypha, using MC simulations of the 1d model discussed in subsection 1A for a particular choice of input parameters. This profile quantitatively reproduces reasonably well the temporal profile obtained experimentally for the hyphal growth of *Rhizopus Oligoporous* [35,45].

In Fig.10(b) we show the morphology of a single sample obtained by MC simulations of the 2-d model discussed in subsection 1B for a particular choice of parameters $\alpha$, $\gamma$ and $\delta$ after 5 hours of growth. This simulated morphology compares well with the morphology observed in experiments with *Neurospora Crassa* after 5 hours of growth [32].

**VI. CONCLUSIONS AND DISCUSSION**

In this article, we have presented a minimal driven lattice gas model which generates the morphological characteristics associated with single colony mycelium arising from the growth and branching process of fungal hyphae, which is fed by a single source of nutrients. While the 1-d model describes the growth characteristics of the primary hypha, the 2-d model provides a description of the entire single colony mycelium that is generated by the elongation and branching process of the fungal hyphae.

The 1-d model predicts a spatial profile of particles which is exponential along the direction of growing primary hypha, and a length of the primary hypha which grows logarithmically with time. Our MC simulation results shows that the sample to sample relative fluctuation of the average length of the primary hypha at late times is small. However we find that the probability distribution of the time required to grow to a specified length is broad and it tends to a log-normal distribution at late times. Although we have not been able to explicitly derive an explicit analytical form of the distribution function of the growth time, we have been able to show that the analytical form of the survival probability of particle to reach distance $L$ along the primary lattice without getting lost from the primary lattice is a log-normal distribution. As an aside, it maybe noted that this kind of log-normal distribution with its implication of huge sample to sample variation of the measured growth time is seen also in context of probability distribution function of tangent-tangent correlation function of a random heteropolymer [49] and spin-spin correlation function for random Ising spin chain [50].

Using MC simulations, we generate the different types of 2-d morphologies of single colony mycelium. We find a wide variability of motility, size and shape characteristics of the 2-d morphology depending on the input parameters, e.g: branching rate $1 - \gamma$, nutrient flow rate to secondary branches $\delta$ and input rate of nutrients $\alpha$. The Center of Mass $R_{cm}$ and the Radius of Gyration $R_g$, of the simulated colony exhibit a sub-diffusive behavior, at later times. Our analysis also reveals a power law dependence of $R_g$ on $N$ of the form $R_g \sim N^\nu$. When both the branching rate is high and $\delta$ is high, for sufficiently high $N$, the behavior of $R_g$ as a function of $N$ is characterized by exponent which seems to converge to $\nu \sim 0.5$, which is similar to the value of the exponent that characterizes the growth process of an Eden cluster in the large $N$ limit [39,43]. A more detailed investigation is needed to confirm whether growth process of our 2-d model, in the limit of high branching rate and high $\delta$ belongs to the same universality class as that of the Eden model [38,39,43]. More generally, it would be interesting to study the similarities and the differences of the asymptotic characteristics of the growing colony at large $N$ and late time limit for this model with other lattice animal models of growth [39,41,43] and polymerization process of branched polymers [35,37,45,46].

We find that by suitable calibration of the parameters of the model, we are able to quantitatively reproduce the observed experimental growth characteristics of the primary hypha of *Rhizopus Oligoporous* [35,45], and we are also able to replicate the morphology characteristics of the single colony mycelium of *Neurospora Crassa* observed in experiments [32].

While in this article, we have restricted ourselves to analyzing the morphology characteristics of the colony for which the tip site stops growing and branching when it encounters obstruction due to the presence of the al-
ready grown lattice, it would interesting to study the morphology characteristics of the colony for the situation for which parts of the growing network is allowed to overlap over each other to form a layered mesh.

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