Numerical Morphological Analysis of Fungal Growth based on a Reaction-Diffusion Model

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The objective of this study was to develop a numerical, reaction-diffusion based model that predicted colony formation by taking into account the influence of nutrients, moisture (water activity), temperature, and the surface characteristics of building materials for various fungi. First, the results of fundamental experiments that measure the growth responses of colony size on culture media under various environmental conditions are presented. Second, the mathematical models that reproduce colony formation on the PDA medium and the numerical simulation intended for the experimental conditions are discussed. Fitting of the model coefficients was performed using the data of the fundamental experiments, and sensitivity analysis was executed. The mathematical models proposed depended on the nutrient concentration and the substrate softness of the surface of the construction materials, and were in reasonable agreement with the experimental data.

Key words: Reaction-Diffusion Model/Fungal Colony Formation/Morphological Analysis.

INTRODUCTION

In recent years, health damage caused by exposure to microorganisms and chemicals has been recognized as a serious problem, and studies in many countries have recognized the association between symptoms of respiratory problems, moisture, and fungal growth in buildings. Fungal growth and infestation in buildings can cause allergies, asthma, and rhinitis. Furthermore, such growth and infestations are closely associated with indoor environmental conditions. In particular, in spaces such as bathrooms where the environment becomes very humid, fungal proliferation and fungal colony formation are visible on the surface of building materials. In particular, the proliferation of darkish molds such as Cladosporium and Exophiala spp are often very evident in indoor environments.

The problems caused by fungi in indoor environments are usually recognized at a stage where colony formation can be observed visually. In other words, fungal growth is detected when the later stage of growth become evident. It is difficult to predict and control the health effects of fungi at an early stage of fungal growth in indoor environments because of the lack of detailed information regarding the mechanisms and numerical models of fungal growth including the germination of spores and subsequent hyphal growth and colony formation. The clarification of the mechanism of fungal growth and the establishment of predictive models would help to improve the health of occupants.

Concerning the proliferation problems of fungal colonies in indoor environments, the growth mechanisms are strongly influenced by the surface temperature, water activity (free water), hydrogen ion exponent (pH), and the amount of nutrients on the growth surface. Moreover, there is clear evidence that the fungal proliferation rate depends on temperature, relative humidity (corresponds to water activity at the equilibrium state), and also the concentration of chemical compounds in the indoor air (Bayer et al.,

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The objective of this study was to develop a mathematical model capable of numerically predicting fungal proliferation on the surface of building materials in indoor environments. Towards this end, the paper has two parts. The first describes the development of mathematical models of fungal growth based on a reaction-diffusion modeling approach. The second consists of fundamental experiments coupled with numerical analysis of the experimental scenarios to examine fungal growth and distribution on agar plates. In general, although fungal proliferation occurs in three dimensions, including on building materials, the mathematical models proposed in this paper assume two-dimensional growth. Results confirming the predictive accuracy of the mathematical models are reported by comparing them with the experimental data.

MATERIALS AND METHODS

Mathematical Models

In the field of life sciences and biology, the basic concept of proliferation or growth can be formulated as mathematical models, and mathematical and theoretical approaches using computer simulation to understand these phenomena have developed into the fields known as mathematical biology and theoretical biology.

Concerning the proliferation of microorganisms such as cells and bacteria, an attempt to express the proliferation patterns of the population/density based on a logistic model has been carried out (Trinci, 1969). Logistic regression is a basic model equation used for the prediction of an increase in the rate of change ($dx/dt$) of microorganism density that decreases with an increase in the density itself ($x$). The general solution of the logistic equation becomes a sigmoid type function. In addition, the Monod equation is a classic expression in these analyses. Meanwhile, Michaelis-Menten kinetics is an expression that is highly effective for the reproduction of synthetic reactions involving molecules and enzyme reaction rates.

In the case of the diverse growth patterns of microorganisms like colonies of bacterial species, the Turing model was proposed as a basic model that reproduces a non-homogeneous/random proliferation pattern from a uniform density distribution (Turing, 1952). This model consists of two determining factors, the activation factor and the control factor, as the governing parameters of microorganism proliferation. This model reproduces a periodic proliferation pattern by reaction-diffusion phenomena, including the interaction between activation and control factors. In general, it is expressed by a partial differential equation, including the time-derivative, diffusion, and generation terms (positive reaction and/or negative reaction) by activation and control factors. In addition, various microorganism growth patterns, such as polka dots, stripe patterns, and reverse polka dots, can be reproduced by coupling various non-linear reaction/diffusion terms. As for the morphological pattern formation of *Bacillus subtilis*, mathematical models based on nonlinear reaction-diffusion models were proposed by Kawasaki et al. (1997) and Mimura et al. (2000), and the qualitative prediction accuracy of these models compare reasonably well with the experiment data.

In the present study, a mathematical model that reproduces fungal proliferation and morphological colony formation was developed based on reaction-diffusion modeling. As already stated, the time series of fungal proliferation can be expressed by a sigmoid type function; therefore, the fungal colony proliferates exponentially when the fungal density is low. Pirt (1965) investigated bacterial colony formation that could be observed visually and pointed out that, rather than an exponential relationship, a straight line relation was confirmed between the colony diameter and elapsed time. This result was based on the assumption that fungal colony formation on rich nutrient medium is caused by proliferation only of the margin; proliferation in the center part of the colony stabilizes and can be disregarded. Referring to the assumptions of Pirt (1965) and the formula of Mimura et al. (2000), the mathematical model of growth in indoor environments in the present study was developed under the following assumptions.

1. The fungus was separated into two states, active and inactive. In this hypothesis, it was assumed that the active fungus moves by diffusion and reaction while generating and producing the inactive fungus at a constant rate. For morphological colony formation the perimeter part was formed by the active fungus and the central part was occupied by the inactive fungus. This modeling followed the assumptions of Pirt (1965) and the formula of Mimura et al. (2000).

2. Fungal proliferation was expressed based on a non-linear reaction-diffusion model. The expression of the effective diffusion coefficient of the active fungus was based on a logistic type expression.

3. Concerning the inactive fungus, which was produced by the dynamism of active fungus, neither extinction nor movement was considered and it accumulated as generated in-place. Using the above assumptions, a nonlinear reaction-
diffusion model was adopted that is expressed by the following partial differential equations.

\[
\frac{\partial u}{\partial t} = \nabla \cdot \left( D_c \nabla u \right) + \theta f(u, n) - a(u, n)u \tag{1}
\]

\[
\frac{\partial v}{\partial t} = a(u, n)u \tag{2}
\]

Here, \( u \) and \( v \) are the densities of the active and inactive fungus, respectively. The total density of the fungus is given by \( (u+v) \). \( n \) is the concentration of nutrients. The first term on the right side in equation (1) expresses the non-linear diffusion term that indicates the random movement of the fungus. The second term shows the reaction and generation term, which depends on the density of the active fungus, nutrient concentration, and other environmental factors. The third term shows the conversion term from active to inactive fungus. The term on the right side in equation (2) expresses the generation term of the inactive fungus transformed from the active fungus.

The diffusion coefficient, \( D_c \), which indicates the motility of the active fungus in equation (1), expresses a logistic type function that depends on the density of the active fungus.

\[
D_c = \sigma' \cdot \sigma \cdot \left( 1 - \frac{u}{d_i} \right) \cdot n \tag{3}
\]

Here, \( \sigma' \) is a scaling parameter and \( d_i \) and \( d_s \) are model parameters of a logistic type expression \((d_i > 0)\). In this study, the analysis was executed by adding the stochastic fluctuation of random movement into the diffusion coefficient, as shown in equation (4).

\[
\sigma' = \sigma_i (1 + \delta), \quad -0.5 < \delta < 0.5 \tag{4}
\]

When the temperature and humidity dependence of fungal growth were expressed, it was assumed that these effects strongly influence the diffusion coefficient \( D_c \). For instance, the effects of temperature and humidity were included in the damping function \( \zeta (T, \phi) \) with diffusion coefficient.

\[
D_{\text{diff.}}(T, \phi) = D_s \times \zeta (T, \phi) \tag{5}
\]

Here, \( T \) and \( \phi \) express the temperature and relative humidity in ambient air, respectively.

The second term of equation (1), \( f(u, n) \) is a model function that indicates the consumption of nutrients by the active fungus. This was a reaction-generation term in which the fungal proliferation was assumed in proportion to the nutrient consumption ratio and contributed to the fungal growth (proliferation) at a fixed constant rate \( \theta \). In the present study, \( f(u, n) \) was formulated using the following Michaelis-Menten kinetics.

\[
f(u, n) = \sigma_j \left( \frac{f_j n}{1 + f_j n} \right) \cdot u \tag{6}
\]

Here, \( \sigma_j \) is a scaling parameter and \( f_j \) and \( f_s \) are model parameters of the expression of Michaelis-Menten kinetics \((f_j > 0)\).

The third term of equation (1), which indicated the transformation from the active to inactive fungus, was formulated in accordance with Murura’s formula.

\[
a(u, n) = \sigma \cdot \frac{1}{\left( 1 + \frac{u}{a_i} \right) \left( 1 + \frac{n}{a_s} \right)} \tag{7}
\]

Where \( \sigma \) is a scaling parameter and \( a_i \) and \( a_s \) are model parameters \((a_s > 0)\).

Each model parameter of equations (1)-(7) was affected by various indoor environmental factors, e.g., temperature, relative humidity, and water activity in building materials. These effects were built into equations (1)-(7) as necessary. In the present study, for purposes of simplification, only nutrient concentration was focused on, and its non-homogeneous distribution on the surface of building materials was a dominant environmental parameter of fungal growth.

The transport equation of nutrients is expressed by equation (8).

\[
\frac{\partial n}{\partial t} = D_s \nabla^2 n - f(u, n) \tag{8}
\]

The first term on the right side of the equation (8) indicates the diffusion of nutrients on the two-dimensional surface, and \( D_s \) is the diffusion coefficient of nutrients. The second term expresses the nutrient consumption by the active fungus.

**Estimation of Model Parameters**

When fungi in indoor environments exist in the form of spores, the concentration of the fungus is given as a concentration, e.g., spores/m² for unit volume or spores/m² for unit surface area. Measurement of the concentration of fungal spores is usually difficult. In general, the fungal concentration is expressed as colony-forming units, CFU/m³ or CFU/m², in which the number of colonies formed on the culture medium are counted instead of measuring the number of spores directly. There is no appropriate unit for expressing fungal density in each colony when the morphological analysis of fungal colony formation is executed. In this analysis, a virtual fungal density on the surface of building materials, i.e., -/m², was assumed. Similarly, the concentration of nutrients on the surface was also expressed as a dimensionless virtual value, -/m². In
this analysis, the nutrient concentration on the surface of PDA medium was assumed to be 1.0 (excessive nourishment).

Other model parameters of the proposed mathematical models were decided by trial-and-error, and the following sensitivity analysis was carried out.

Outline of the Sensitivity Analysis

The impact of each model parameter and the initial condition in the reaction-diffusion models on morphological colony formation were examined qualitatively by executing a sensitivity analysis that systematically changes the model constants.

A two-dimensional plane of 200 mm (x) × 200 mm (y) was targeted as the object surface in this sensitivity analysis. This surface area corresponded to the area of the PDA medium set up in the Petri dish described later. In this analysis, an equally spaced mesh with 1 mm intervals was adopted for the x and y directions. A uniform distribution of nutrient concentration was assumed as the initial condition.

As an initial condition of the active fungus, u = 1.0 was given at the center of the analytical plane (point x=100 mm and y=100 mm). The initial concentration of the inactive fungus is assumed to be zero (v=0.0). A free slip condition (zero gradients) was assumed as the boundary conditions on the edge of the plane under analysis. Each transport equation was discretized by the finite volume method, and unsteady analyses were carried out using the explicit method for solving time-variable partial differential equations. This sensitivity analysis involved a total of 168 hours (7 days) in real time simulation. The stochastic fluctuation as shown in equation (4) was not coupled in this sensitivity analysis.

The analyses carried out are shown in Table 1. Case a1 is the basal case for the conditions under analysis. Each model parameter used in Case a1 was set appropriately, referring to the previously reported research (Kawasaki et al., 1997, and Mimura et al., 2000). In Case a2 (a2-1, a2-2 and a2-3), the initial concentration of the nutrient n0 was gradually changed from 0.1 to 1.0. Especially in Case a2-3, equation (7), which is the transport equation of nutrient concentration, was not solved, and the nutrient concentration force constant value (n=1.0) did not change with the time elapsed. Cases a3-1 and a3-2 were cases that changed the diffusion coefficient of nutrients, Dn. The condition of Case a3-1 indicated a soft agar medium, and the condition of Case a3-2 assumed a hard agar medium. In Case a4, the order of the diffusion coefficient Dn of the active fungus in equation (1) was changed to a relatively small value. Case a5 focused on the model constant of nutrient consumption expressed in equation (6). Finally, in Cases a6-1 and a6-2, the model constant of the conversion term was changed.

Outline of Fundamental Experiments on the Colony Formation on Agar Plates

In order to validate the prediction accuracy of the proposed non-linear reaction-diffusion model, a fundamental experiment on the colony formation on PDA (Potato Dextrose Agar) culture medium was carried out. In this experiment, Cladosporium cladosporioides (NBRC 6348) was used as the target fungi. C. cladosporioides is a hygrophilous fungus and is found in general indoor environments.

In this research, the spore-suspension medium, i.e., the slurry of fungal spores containing the nutrient for each hygrophilous fungus, was prepared on the basis of a report by Abe (1993), and the measurement of the colony formation rate on culture media was carried out at a constant temperature (28 °C).

Preparation of conidia

Cladosporium cladosporioides was incubated on a PDA agar medium plate, followed by cultivation at 20 °C for two weeks. After cultivation, the conidia that formed on the agar plate were suspended in a spore-suspension medium (mixed PDA solution). The conidia were suspended at a concentration of 4.4 × 10^7 spores/mL in the spore-suspension medium.

Experimental setup and experimental cases

The PDA medium was prepared as a thin layer in a Petri dish (diameter 190 mm). The spore-suspension medium (30 mL) was poured onto the PDA medium in the Petri dish, and the dish was sealed. The sealed dish was placed in an incubator at a constant tem-

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**TABLE 1. Cases Analyzed and Model Parameters of the Sensitivity Analysis.**

<table>
<thead>
<tr>
<th>Cases Analyzed</th>
<th>Model Parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Case a1</td>
<td>$\sigma=1.0 \times 10^{-2}$, $d_i=1.0 \times 10^{-5}$, $\sigma=5.0$, $k=f=f=1.0$, $\sigma=5.0$, $a_i=1/2400$, $a_i=1/120$, $n=1.0$, $D_{v_{c}}=1.0 \times 10^{-4}$, $u_{v_{c}}=1.0$, $v_{c}=0.0$</td>
</tr>
<tr>
<td>Case a2-1</td>
<td>$n=0.5$</td>
</tr>
<tr>
<td>Case a2-2</td>
<td>$n=0.1$</td>
</tr>
<tr>
<td>Case a2-3</td>
<td>$n=1.0$ (constant, Eq.(8) is not solved.)</td>
</tr>
<tr>
<td>Case a3-1</td>
<td>$D_{v_{c}}=1.0 \times 10^{-3}$, $\sigma=1.0 \times 10^{-3}$, $D_{v_{c}}=1.0 \times 10^{-5}$, $\sigma=3.0$, $\sigma=0$ (Eq.(7) is not solved.), $\sigma=5.0 \times 10^{10}$</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Model Parameters</th>
<th>Case b1</th>
<th>Case b2</th>
<th>Case b3</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Plan</strong></td>
<td><img src="image1" alt="Plan" /></td>
<td><img src="image2" alt="Plan" /></td>
<td><img src="image3" alt="Plan" /></td>
</tr>
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<td><strong>Section</strong></td>
<td><img src="image4" alt="Section" /></td>
<td><img src="image5" alt="Section" /></td>
<td><img src="image6" alt="Section" /></td>
</tr>
</tbody>
</table>

Fundamental experiments coupled with numerical analysis of the experimental scenarios to obtain fungal growth and distribution on agar plates (PDA) were carried out. Case b1 is the basal case, in which only the PDA medium was poured into the Petri dish. In Cases b2 and b3, the tiles were set up in the Petri dish, and PDA was introduced into the parts that corresponded to the joints placed between tiles. Two-dimensional reaction-diffusion on the surface plane was assumed in the numerical prediction.

The temperature of 28 °C. The relative humidity in the Petri dish was assumed to be maintained at a high level by the free water contained in the PDA medium, and no specific control was analyzed. Following a series of measurements, it was confirmed that the surface of the PDA was not excessively dry. Colony formation was monitored every 24 hours during the incubation period for one week. During each measurement period, the colonies on the Petri dish were photographed with a digital still camera.

Table 2 shows the experimental cases. Case b1 was the basal case in which only the PDA medium was set in the Petri dish. In Cases b2 and b3, tiles were set up in the Petri dish, and PDA was introduced in the parts that corresponded to the joints between the tiles. The tiles were sterilized by autoclaving and dried fully.

Outline of the Numerical Analysis Intended for the Experiments

Numerical analyses intended for the fundamental experiment were carried out. The model parameters adopted for these analyses were fixed under consideration of the results of the sensitivity analysis, as noted above. The target area of calculation and grid design were the same as the setup of the sensitivity analysis. Calculations totaling 312 hours were done in real time according to the experimental data. The analyses of cases of numerical simulation were set by three conditions, for Cases b1~Case b3, under the same conditions as the experimental setup. Case b1 was the basal case that reproduced the simple morphological colony formation on a PDA medium, and Cases b2 and b3 were composed of tiles and the PDA medium. The boundary conditions of the surface treatment of tiles and the PDA medium differed in terms of the initial concentration of nutrients; it was \( n_0 = 0 \) for tiles and \( n_0 = 1.0 \) for the PDA medium. At the interface between tiles and the PDA medium, there were no special boundary conditions, but the diffusion coefficient of the nutrients was assumed to be zero on the surface of the tiles. Table 2 shows the list of model parameters used for this numerical analysis. Stochastic fluctuation as shown in equation (4) was coupled in this analysis.

RESULTS AND DISCUSSION

Sensitivity Analysis

The numerical results of the morphological analysis after 168 hours are shown in Figure 1. The density distribution of the active and inactive fungus is shown as a contour figure (filled), and the overlapping density distribution of the active and inactive fungus (\( u + v \)) is also shown (line). In Case a1, the active fungus formed a ring-like pattern (doughnut shape) and the inactive fungus accumulated from the center part with the passage of time. The total density of the active and inactive fungus (\( u + v \)) formed a disk-like pattern.

The colony formation rate decreased in accordance with the reduction in the initial concentration of nutrients, and the diameter of the colony formed also
The case numbers in these figures (Case a1 - Case a6) correspond to those in Table 1. \( u \) and \( v \) are the densities of the active and inactive fungus, respectively. The total density of the fungus is given by \((u+v)\). The density distribution of the active and inactive fungus is shown in contour figures (filled), and the overlapping density distribution of active and inactive fungi \((u+v)\) is shown in the contour figure (line). The results at 168 hours are shown and only Case a2-3 has the same result as those at 72 hours.

became relatively small. In Case a2-1, in which the initial nutrient concentration was set at 0.1, which was one-tenth of the basal case, the active fungus virtually disappeared by 168 hours. When the diffusion coefficient of the nutrients enlarged compared with the conditions of the basal case (assumption of a soft agar medium), the ring pattern (doughnut shape) was not observed, and a high-density colony formed in the center. A doughnut-shaped colony was clearly generated as the diffusion coefficient of the nutrients
became smaller.
In Case a4, which assigned relatively small value to \( \sigma_i \), the motility of diffusion was controlled, and the fungus colony became relatively small compared with the size of the basal case. In Case a5, which assigned a small value to \( \sigma_j \) in the reaction-generation term from nutrients to the active fungus, the formation rate of a ring-shaped colony by the active fungus was reduced, and the diameter of the colony also decreased. For Case a6-1, which disregarded the conversion term from the active to inactive fungus, the colony formed by the active fungus showed a monotonic increase; the generation of the active fungus stopped in accordance with the consumption of nutrients in the center part and finally maintained a constant concentration. In Case a6-2, which set \( \sigma_j \) at ten times larger than that in the basal case, the generation of the inactive fungus increased, and the ring pattern formed with the active fungus became clear.

Figure 2 shows a conceptual diagram of the morphological characteristics of fungal colony formation based on the results of the sensitivity analysis. The phenomenon of fungal growth was strongly dependent on the nutrient characteristics. For the hard agar medium (small diffusion coefficient of nutrients), the fungal colony formation rate was relatively high. On the other hand, for the soft agar medium (large diffusion coefficient of nutrients), because the nutrients were transported efficiently to the fungus irrespective of fungal growth, the colony size decreased and the colony formation rate also decreased.

It was confirmed that the diffusion coefficient of nutrients, \( D_n \), had a strong influence on the morphological formation of fungal colonies; a morph-like petal appeared when the diffusion coefficient of nutrients increased. Similarly, the density of the initial nutrients also had a dominant effect on colony formation, and when the density of the nutrients was high, the size of the colony increased. In mathematical modeling in which the status of the fungus was separated into active and inactive, when the diffusion coefficient of the active fungus was large, the colony size was also large, and a ring-line pattern was clearly generated. When the diffusion coefficient of the active fungus was relatively small, a small and dense colony tended to be formed.

The term of nutrient consumption by the active fungus \( f(u, n) \) and the term that indicated the transformation from the active to inactive fungus \( a(u, n) \) influenced the ring-like pattern formed around the perimeter of the colony.

**Fundamental Experiments**
The time series of the digital images of the colony formation for each case is shown in Figure 3. Under these experimental conditions, because sufficient nutrients were supplied from the PDA medium to the fungus, a visible colony formed within 24 hours from the start of the experiment. In Case b1, the colony diameter reached about 30 mm after 50 hours, and a disk-like pattern was clearly observed. The tissue composition of the perimeter part appeared different
FIG 3. Results of Colony Formation on PDA medium (Experiments).

The case numbers in these figures (Case b1 - Case b3) correspond to those in Table 2. *Cladosporium cladosporioides* (NBRC 6348) was used. Spore-suspension medium (30 mL) was poured onto PDA medium in the center of the Petri dish, and then the sealed Petri dish was placed in an incubator at a constant temperature of 28 °C. Colony formation was monitored every 24 hours during the incubation period for one week.

Case b1 is the basal case in which only PDA medium was set in the Petri dish. In Cases b2 and b3, the tiles were set in the Petri dish, and PDA was introduced into the parts that corresponded to the joints placed between the tiles.

from that of the center part of the colony, and a ring-like pattern was confirmed. Afterwards, asymmetric and non-homogeneous growth of the colony was observed. In Case b2, in which tiles were laid out at intervals of 10 mm, the fungal colony gradually proliferated uniformly and symmetrically during a period of about one week after the test started. Afterwards, it was observed that fungal growth differed greatly according to location. No fungal proliferation on the surface or in the back of the tiles was observed. In Case b3, in which tiles were laid out at intervals of 30 mm, the fungus avoided the tiles and proliferated uniformly on the PDA medium. The experimental conditions of Cases b2 and b3 were consistent except for the layout of the tiles. Why the experimental results differed greatly between Cases b2 and b3 is not yet known. It was assumed that the initial concentration distribution of nutrient and water contents were dominant factors in fungal colony formation.

Numerical Analysis

Figure 4 shows the results of the numerical analyses intended for experimental conditions. For Case b1, the result of numerical prediction was reasonably consistent with the experimental result for a few days from the test start. Moreover, the morphological characteristics of the fungal colony were schematically predicted in modeling the active and inactive fungus separately. Seven days after the start of the test, the result of numerical analysis tended to exaggerate the colony formation rate compared with the experimental results, and the phenomena of asymmetry and non-uniform diffusion which could be observed in experiments, could not be reproduced by numerical prediction. In Cases b2 and b3, the results of numerical prediction approximately reproduced the experimental results.

CONCLUSIONS

In the present study, a mathematical model based
on the reaction and diffusion of fungus on a two-dimensional plane had been proposed for the prediction of fungal growth in indoor environments. Using this model, sensitivity and morphological analysis were carried out. The morphological characteristics of fungal colony formation were reproduced based on a reaction-diffusion expression in modeling the active and inactive fungus separately.

Concerning morphological colony formation on PDA medium, the results of numerical simulation were reasonably consistent with the experimental results within a few days from the start of the test. However, one week after the test started many problems in prediction remained. As the next step of this research, model parameters must be identified based on detailed experimental data, and it was also necessary to couple numerical analysis with other physical parameters, e.g. temperature and relative humidity (water activity), in the proposed mathematical model.

FIG 4. Results of Numerical Predictions.
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