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Research Article

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Mathematical Analysis of a Fungal Growth Model: Analyzing the Dynamics of Branching, Tip Death, and Substrate

Ayaat Saleem Habeeb[1*], Ali Hussein Shuaa[2], Ghufran Moneam Ajmee[3]

Education College for pure Sciences, Wasit University, Iraq

* Correspondence: ahabeb@uowasit.edu.iq

Abstract: This research explores the mechanisms of fungal growth and branching mathematical modeling, focusing on the complex mycelia network. The model aims to understand how the fungal network's structure is influenced by several key biological factors, most importantly :

1- The effect of the substrate (nutrient source) as the energy source for growth.

2- Lateral branching of the hyphae.

3- Tip death.

4- Tip death due to overcrowding.

To analyze theses dynamics, a system of three dimensional partial differential equation (PDEs) is employed. This mathematical model is solved using a range of advanced techniques, including stability theory, traveling wave analysis, and numerical solutions. Specialized software, such as MATLAB (using the pdepe solver) and Maple, is also utilized to aid in implementing numerical solutions and verifying the system's stability.

The primary objective of this research is to understand how these biological factors interact and how such models can contribute to saving time, effort, and costs in applied biological research.

Keywords: Mathematical model , Tip death , Tip death due to overcrowding , Tip death , Substrate, Traveling wave, Stability analysis.

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Introduction

The transition from qualitative descriptions of biological phenomena to precise quantitative representation is the primary objective of mathematical modeling. In the context of fungal biology, growth dynamics are often simplified to the exponential growth law ($\frac{dM}{dt} = \alpha M$), a model that assumes ideal, homogeneous conditions and fails to reflect the spatio-temporal complexity of actual fungal colonies.

To address this limitation, and building upon the theoretical framework developed by Leah Edelstein-Keshet for modeling biological patterns, we propose in this research a system of Partial Differential Equation (PDEs), termed the "FXTS" model. This model is designed to investigate the non-linear interactions among four fundamental morphological processes:

1- Lateral Branching (F): The process responsible for increasing network density.

2- Tip Death due to Overcrowding (X): A density dependent regulatory mechanism that limits growth.

3- Tip Death (T): A factor representing the natural attrition rate of hyphal tips.

4- Substrate (S): A dynamic variable representing the availability and diffusion of energy for the aforementioned processes.

Through the mathematical analysis of this system, we aim to identify the conditions that lead to stable structural patterns, thereby providing precise insights into the mechanisms governing morphogenesis in fungal colonies.

Biological type	Symbol	Version	Parameters description
Lateral branching	F	$\delta = \alpha_2 \rho$	α_2 : The number of branches produced per unit length hypha per unit time.
Tip death due to overcrowding	X	$\delta = -\beta_3 \rho^2$	β_3: The rate at which overcrowding density limitation eliminates branching.
Tip death	T	$\delta = -\alpha_3 n$	α_3: The rate loss rate of tips (constant for tip death).

Table 1: Biological type of fungi, symbol of this type, version and description of these parameters.

Mathematical Model

To mathematical model the dynamics of hyphal growth, we define the system using three key state variables:

$\boldsymbol{\rho}(\mathbf{x}, \mathbf{t})$: The density of hyphae, expressed as length per unit area.

n(x,t): The density of active hyphal tips.

s(x,t): The concentration of the available substrate .

Based on these variables, and drawing from established models that describe their

interactions, the spatio – temporal evolution of hyphal growth can be described by the following system of equations:

$$\begin{aligned}\frac{\partial \rho}{\partial t} &= nvs \\ \frac{\partial n}{\partial t} &= -\frac{\partial (nvs)}{\partial x} + \sigma(\rho, n, s) \\ \frac{\partial s}{\partial t} &= -kn\end{aligned} \qquad (1)$$

Where: $\sigma(\rho, n, s)$=$\alpha_2\rho$ - $\beta_3\rho^2 - \alpha_3 n$. So, the system (1) becomes:

$$\begin{aligned}\frac{\partial \rho}{\partial t} &= nvs \\ \frac{\partial n}{\partial t} &= -\frac{\partial (nvs)}{\partial x} + \alpha_2\rho - \beta_3\rho^2 - \alpha_3 n \\ \frac{\partial s}{\partial t} &= -kn\end{aligned} \qquad (2)$$

Non-dimensionalisation and Stability

To simplify the analysis of the system, we perform a nondimensionalisation following the methodologies described by Keshet (1982) and Ali.H. (2011). This process reduces the number of free parameters, allowing the system (2) to be rewritten in the following dimensionless form:

$$\begin{aligned}\frac{\partial \rho}{\partial t} &= ns \\ \frac{\partial n}{\partial t} &= -\frac{\partial ns}{\partial x} + \alpha\rho(s - \rho) - \beta n \\ \frac{\partial s}{\partial t} &= -kn\end{aligned} \qquad (3)$$

Where: $\alpha = \frac{\alpha 2v}{\gamma^2}$, and $\beta = \frac{\alpha 3}{\gamma}$

In this model, the parameter α represents the branching rate, β represents the rate at which overcrowding limits the branching process, and k is a non-negative constant. Consequently, the term $\alpha\rho(s - \rho)$ describes the generation rate of new branches.

To find the steady states (equilibrium points) of system (3), we set the time derivatives to zero, which yields the following algebraic system:

ns = 0 , $\alpha\rho(s - \rho) - \beta n = 0$, -kn = 0

we get two steady state points $(\rho_0, 0, \rho_0)$, $(0,0, S_0)$ for (non – negative) constant ρ_0 and S_0 .

By using Jacobin and eigenvalues of these equations , we can obtain three values of (λ)

$$J(\rho, n, s) = \begin{bmatrix} 0 & s & n \\ \alpha(s - 2\rho) & -\beta & \alpha\rho \\ 0 & -k & 0 \end{bmatrix}$$

$$J(\rho_0, 0, \rho_0) = \begin{bmatrix} 0 & \rho_0 & 0 \\ -\alpha\rho_0 & -\beta & \alpha\rho_0 \\ 0 & -k & 0 \end{bmatrix}$$, $|A - \lambda I| = 0$, then we get :

$$\lambda_1 = 0 \quad , \quad \lambda_{2,3} = \frac{-\beta \pm \sqrt{-4\alpha k\rho_0 - 4\alpha{\rho_0}^2 + \beta^2}}{2}$$

The ODE system associated with the steady state has one – dimensional center manifold and a two – dimensional stable manifold, provided that β > 0.

When $\beta^2 \geq 4\alpha(k\rho_0 + \rho_0^2)$, the stable component is given by a stable node.
if $\beta^2 < 4\alpha(k\rho_0 + \rho_0^2)$, it is a stable focus.
The Jacobain at $(0,0,s_0)$ is:

$$J(0,0,s_0) = \begin{bmatrix} 0 & s_0 & 0 \\ \alpha s_0 & -\beta & 0 \\ 0 & -k & 0 \end{bmatrix}, \quad |A - \lambda I| = 0 \text{ , then we get :}$$

$$\lambda_1 = 0 \quad , \quad \lambda_{2,3} = \frac{-\beta \pm \sqrt{4\alpha s_0^2 + \beta^2}}{2}$$

Since $\lambda_2 > 0$ and $\lambda_3 < 0$ for all positive parameter values, the steady state $(0,0,s_0)$ is a saddle point and is therefore unstable

Traveling wave solution

In this section, we seek traveling wave solutions for system (3) . We assume three solutions represent a pattern moving with a constant speed 'c ' in the positive x - direction. To do this , we transform the coordinates using the variable ' z=x-ct ' . This transformation allows us to express the variables p(x,t) , n(x,t) ,and s(x,t), as functions of the single variable ' z ' , namely P(z) , N(z) , and S(z). As a result of this transformation, the original system of partial differential equation (PDEs) is reduced to a system of three ordinary differential equation (ODEs), which is more amenable to analysis.

$$\frac{\partial \rho}{\partial t} = -c\frac{dP}{dz} \quad , \quad \frac{\partial n}{\partial t} = -c\frac{dN}{dz} \quad , \quad \frac{\partial n}{\partial x} = \frac{dN}{dz} \quad , \quad \frac{\partial s}{\partial t} = -c\frac{dS}{dz}$$

Therefore the above equation becomes:

$$\begin{aligned} \frac{dP}{dz} &= \frac{-1}{c}NS \\ \frac{dN}{dz} &= \frac{1}{s-c}\left[\frac{-k}{c}N^2 + \alpha P(S-P) - \beta N\right. \qquad S \neq c \text{ and } c \neq 0 \qquad (4) \\ \frac{dS}{dZ} &= \frac{k}{c}N \end{aligned}$$

As above we can find steady states for the system(4). Therefor we have two lines of steady state $(P_0,0,P_0)$ and $(0,0,S_0)$. Now, the Jacobian associated with system (4) at (P,N,S) is:

$$J(P,N,S) = \begin{bmatrix} 0 & \frac{-S}{c} & \frac{-N}{c} \\ \frac{\alpha(S-2P)}{s-c} & \frac{-2k}{c}N - \beta & \alpha P(c-P) + \frac{k}{c}N^2 + \beta N \\ & \frac{s-c}{k} & \frac{(s-c)^2}{} \\ 0 & \frac{k}{c} & 0 \end{bmatrix}$$

Therefor the Jacobain at $(P_0,0,P_0)$ is

$$J(P_0,0,P_0) = \begin{bmatrix} 0 & \frac{-P_0}{c} & 0 \\ \frac{-\alpha P_0}{P_0 - c} & \frac{-\beta}{P_0 - c} & \frac{\alpha P_0(c-P_0)}{(P_0-c)^2} \\ 0 & \frac{k}{c} & 0 \end{bmatrix}$$

Which has eigenvalues $\lambda_1=0$, $\lambda_{2,3} = \frac{\pm\beta c + \sqrt{4\alpha c^2 k P_0 - 4\alpha c^2 P_0^2 - 4\alpha c k P_0^2 + 4\alpha c P_0^3 + \beta^2 c^2}}{2c(c-P_0)}$

The ODE system associated with the steady state $(P_0,0,P_0)$ has a one - dimensional center manifold corresponding to the eigenvalue $\lambda_1=0$. The system's behavior in the eigenvalues λ_2 and λ_3.

Assuming $c > P_0$, the real part of the eigenvalue λ_2 is positive. Consequently this

steady state is unstable in the traveling wave system. The nature of this instability depends on the sign of the discriminant ' Δ ' :

- When Δ ≥ 0 , the unstable component is given by an unstable node.
- When Δ < 0 , it is an unstable focus

The instability of this point is a necessary mathematical condition for the existence of traveling wave solution connecting the steady states of the system.

The Jacobain at (0,0, S_0) is

$$J(0,0,S_0) = \begin{bmatrix} 0 & \frac{-S_0}{c} & 0 \\ \frac{\alpha S_0}{s_0 - c} & \frac{\beta}{s_0 - \frac{c}{k}} & 0 \\ 0 & \frac{}{c} & 0 \end{bmatrix}$$

Which has eigenvalues $\lambda_1=0$, $\lambda_{2,3}=\frac{\pm\beta c+\sqrt{4\alpha c^2 S_0^2-4\alpha c S_0^3+\beta^2 c^2}}{2c(c-s_0)}$

The point (0,0,S_0) is a saddle point when c > S_0 , and it is a stable focus when 0 < c < S_0 . From this analysis we have :

- Fixed c , no biologically realistic traveling waves exist with S_0 > c .
- For any given S_0 , any biologically realistic traveling waves that exist must have c > S_0 .

Numerical Solution

Because the system (3) cannot be solved directly, so we resort to numerical solution, and we will using pdepe code in MATLAP.

That is clear the initial condition start from 1 to 0 for ρ and n, See Fig (1)

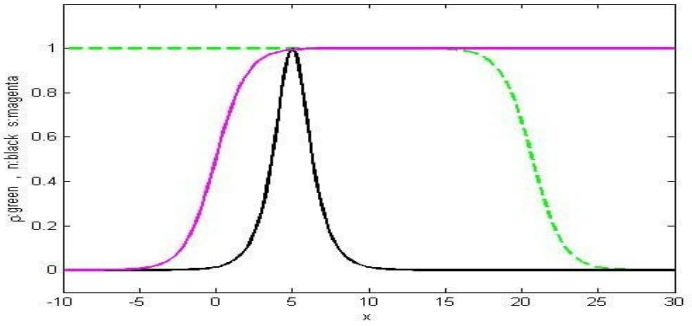


Figure 1: The initial conditions used for the numerical simulation of system (3). The green curve represents the branching density (p), the black curve represents the tip density (n), and the magenta curve represents the substrate concentration(s).

The numerical simulation results show that the autocatalytic coupling between the variables ρ, n, and s leads to the formation of coherent traveling wave fronts for suitable parameter selections. The behavior of the solution is directly determined by the parameters α, υ, d, and k.

Figure (2) illustrates a representative solution type derived for the parameter set : α = 2, β=5, υ = 1, and k = 0.4. The figure displays the stable profiles of the substrate, tip, and branching densities, which propagate as a single unit from left to right.

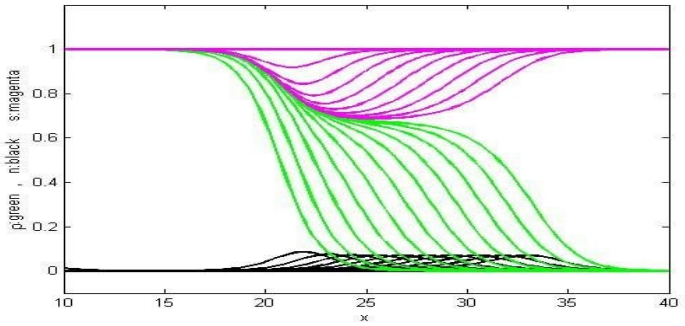


Figure 2: The solution PDEs system (3) for FXTS with the parameters (α=2 , β=5 , v=1 , k=0.4). and the time spacing (30,…,100).

The effects of parameters on the solution behavior

1- The effects of α on the solution behavior

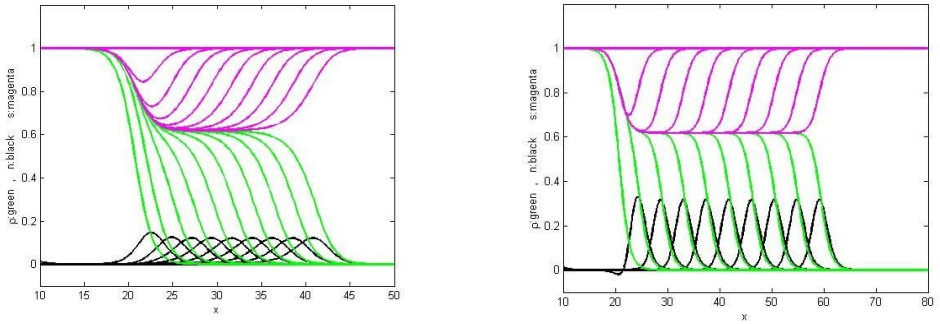
The effect of the branching rate parameter (α) on the traveling wave characteristics was examined.

Numerical simulations showed that while keeping other parameter fixed (β = 2 , v= 1 , k= 0.5),increasing the value of (α) accelerates the wave's propagation and increases its amplitude:

- For α=1.5 , the computed wave speed is c=0.4987.
  .
- For α=4 , the wave speed markedly increases to c= 0.9770.

In addition to the increased wave speed, a comparison of Figures (3 a) and (3 b), reveals that a larger α also leads to a distinct increase in the peak amplitude of the tip density profile n(z) (the black curve). Thus, the α parameter not only determines the propagation speed of the colony but also controls the density of active tips driving the wave front.

As solution in Figure (4) illustrates the wave speed increases with α.



(a) (b)

Figure 3: Solution of PDEs system (3) for type FXTS with parameter α, with β=2 , v=1 , and k=0.5 held constant. (a) solution for α=1.5. (b) solution for α=4. The time spacing (30,…,100).

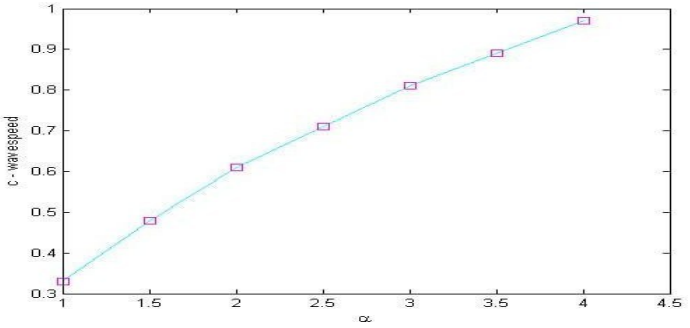


Figure 4: The relationship that exists between α values and wave speed (c) .

2- The effects of β on the solution behavior

In this section, we investigate the effect of the branching inhibition parameter (β) on the characteristics of the traveling

wave solutions .

Numerical simulations were conducted with other parameter fixed (α = 1 , v= 1 , k= 0.5), while the value of (β) was varied to observe its impact. The results demonstrate that the (β) parameter has a fundamental negative influence on both the wave's speed and its profile characteristics. The following results were obtained:

- For β=2 , the computed wave speed is c=0.3242 .
  .
- For β=3.5 , the wave speed markedly decreases to c= 0.0458 .

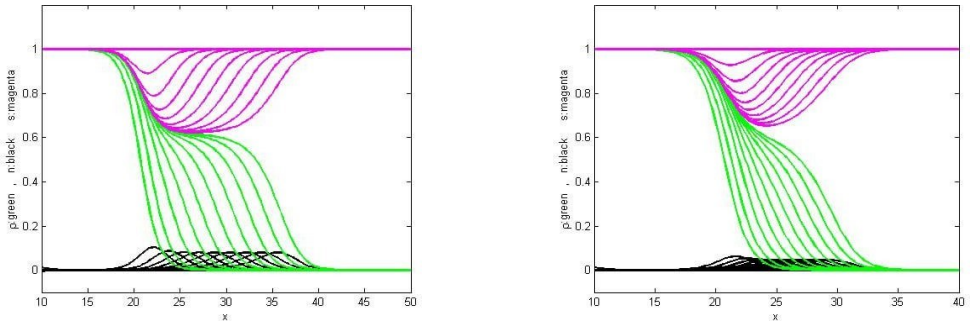
A comparison of Figures (5 a) and (5 b), reveals two key observations:

1- Digressing propagation speed : An increase in β leads to a marked digressing of the wave's propagation, as evidenced by the computed c values.

2- Suppressed Tip Amplitude: Importantly increasing β also results in a near – complete suppression of the peak amplitude of the tip density profile n(z) (the black curve).

Therefore, we conclude that the β parameter plays a critical role in limiting colony growth by slowing its propagation rate and restricting the production of new growth tips.

As solution in Figure (6) illustrates the wave speed decreases with β.



(a) **(b)**

Figure 5: : Solution of PDEs system (3) for type FXTS with parameter β, with α=1 , v=1 , and k=0.5 held constant. (a) solution for β=2. (b) solution for β=3.5. The time spacing (30,…,100).

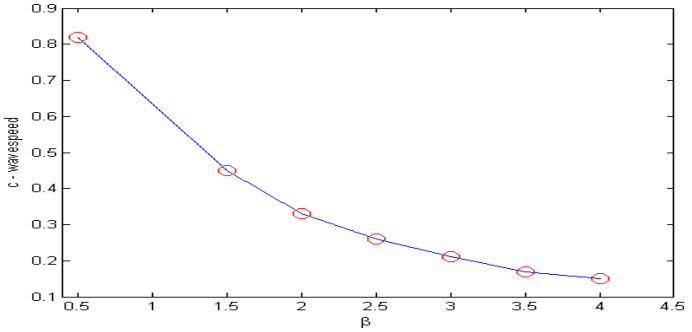
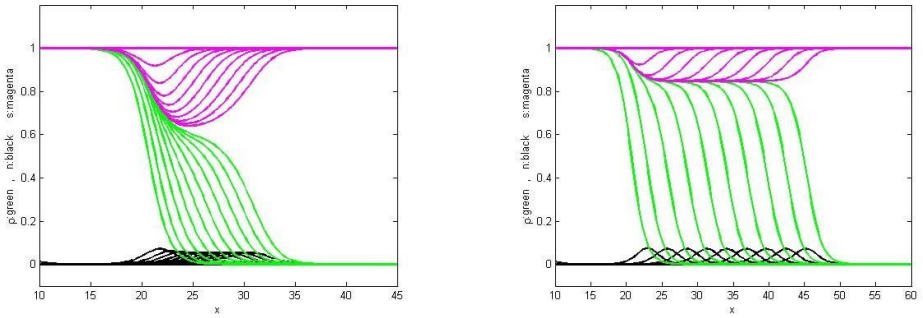


Figure 6: The relationship that exists between β values and wave speed (c) .

3- The effects of v on the solution behavior

The similar methods as above. Figure (7) illustrates the relation between the parameter (v) and wave speed c. In this case fixed the values of parameters α, β, and k are taken the values 1, 3, 0.5 and change values of (v). For v = 1, the wave speed was c =0.1128, whereas for v = 3, the speed increased to c = 0.7787. Therefore, for higher v values the propagation speed is larger. Here, the relation between the parameter v and wave speed c is increasing.

As solution in Figure (8) illustrates the wave speed increases with v.



(a) **(b)**

Figure 7: Solution of PDEs system (3) for type FXTS with parameter v, with α=1, β=3 ,and k=0.5 held constant. (a) solution for v=1. (b) solution for v=3. The time spacing (30,…,100).

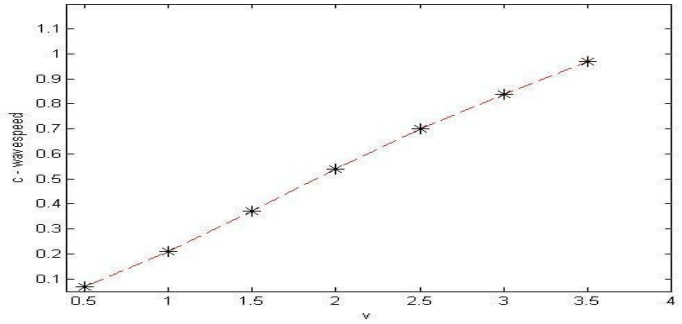


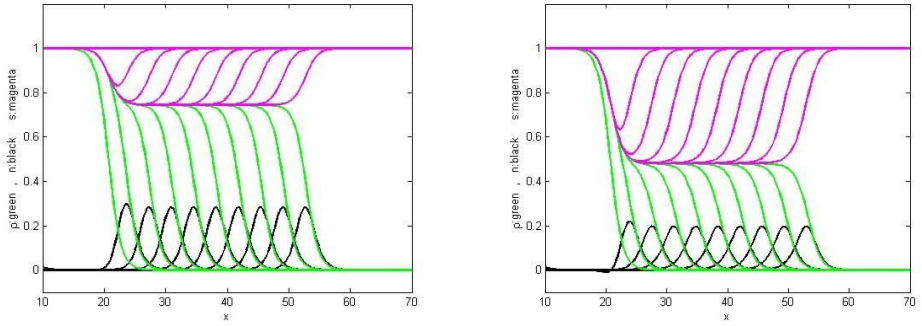
Figure 8: The relationship that exists between v values and wave speed (c) .

4- The effects of k on the solution behavior

The wave speed significantly decreases when the values of the parameter (k) increase. The profile of tips (n) and branching (ρ) also decrease when values k increased, see Fig. (9 a) and (9 b). We fixed the values of parameters α, β, and v are taken the values 3, 2, and 1 and change values of k. For k = 0.3, the wave speed was c = 0.9799, for k = 0.8, the wave speed decreased to c = 0.6323.

From Fig. (9 a) and (9 b), we note the profile of variable ρ (green) and variable n (black) decrease when the value of the parameter k decreases.

As solution in Figure (10) illustrates the wave speed increases with k.



(a) **(b)**

Figure 9 : Solution of PDEs system (3) for type FXTS with parameter k, with α=3, β=2 ,and v=1 held constant. (a) solution for k=0.3. (b) solution for k=0.8. The time spacing (30,…,100).

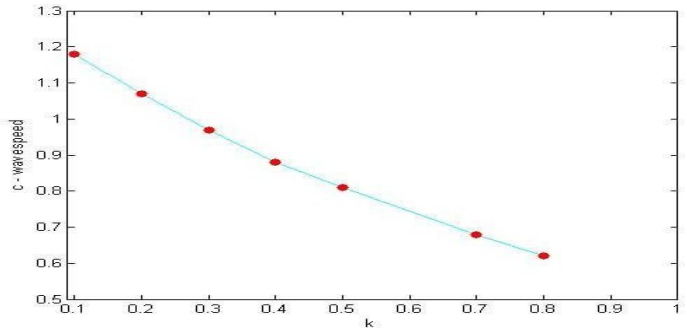


Figure 10: The relationship that exists between k values and wave speed (c) .

Conclusion

We have clarified in this research the effects of the parameters α, β, v, and k on the development of fungal networks. The relationships between these parameters and the wave speed c are clear and direct:

• Looking at Figure (4), it is shown that the wave speed c increases when α is an increasing function.

• Looking at Figure (6), it is clear that the wave speed c decreases when β is an increasing function.

• Looking at Figure (8), we find that the wave speed c increases when v is an increasing function.

• Finally, looking at Figure (10), it is clear that the wave speed c decreases when k is an increasing function.

These findings are consistent with the biological principle that fungal growth is a balanced process between driving factors (branching and propagation) and inhibiting factors (competition and tip density). This model provides a mathematical framework for understanding these complex interactions, fulfilling the main objective of this research.

Based on our model's parameter definitions, ($\alpha = \frac{\alpha 2v}{\gamma^2}, and\ \beta = \frac{\alpha_3}{\gamma}$), the effective growth rate α rises with an increase in α_2 (branching) and v (propagation), while it falls as the value of γ^2increases. Separately, the inhibition parameter β is determined directly only by $\alpha_3$and γ.

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