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Mathematical Model of FHXW Branching Typewith Hyphal Death

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ABSTRACT

A mathematical description of growth and branching in fungi can be derived in terms of continuous variables such as densities of filaments and tips. The general concept of continuum modeling yields the following equations of fungal growth in which a balance is kept for the accumulation of hyphal filaments and their tips.Hyphae are immobile. They are created only through the motion of tips-essentially the trail left behind tips as they moves. The rate of local length accumulation depends on the number of tips and branches present as well as on their rate of motion.

This suggests the following equation

$$\frac{\partial p}{\partial t} = nv - d \quad \cdots\cdots\cdots (1.1)$$

Here, the variables are as follows: $p = p(\mathrm{x,t})$: hyphal density in unit of filament length per unit area;

$n = (\mathrm{x,t})$: tip density (number per unit area);v : tips extension rate; $d = d(\mathrm{p})$: hyphal death rate. Tips do undergo motion so that the flux of tips enters into the equation for tip densities. Assuming that tip growth is a directed motion, in one dimension this equation would take the form :

$$\frac{\partial n}{\partial t} = -\frac{\partial (\mathrm{nv})}{\partial x} + \delta(\mathrm{p,n}) \quad \cdots\cdots \quad (1.2)$$

Where $\delta = \delta(\mathrm{p,n})$ - net creation of tips.

Keywords

Hyphal death; Dichotomous branching; Lateral branching; Tip-hypha anastomosis; Tip-tip anastomosis; Tip death, Tip death due to overcrowding.

Introduction

In this paper, we will study a new type of branching of fungal growth. From the basic tip - growth mechanism: a number of tips n growing at the rate v (in length per unit time) gives rise to a hyphal accumulation rate of nv (in hyphal length per unit time). [3][4] discussed and analyses the above model when $d(\mathrm{p,n}) = 0$ for a variety of biologically relevant functions $\delta(\mathrm{p,n})$. More generally, we can describe hyphal growth by the system below:

$$\left.\begin{aligned} \frac{\partial p}{\partial t} &= J_n - d(\mathrm{p}) \\ \frac{\partial n}{\partial t} &= -\frac{\partial (J_n)}{\partial x} + \delta(\mathrm{p,n}) \end{aligned}\right\} \quad \cdots\cdots \quad (1.3)$$

This second balance equation for tip densities accommodates the fact that tip move (with flux $Jn = nv$) and are moreover created by branching or eliminated by anastomosis [6][5]. The ratio of hyphal length per tips is called the hyphal growth unit, with flux $Jn = nv$.

We investigated from effect hyphal death on development of fugal network, when $d(\mathrm{p}) = \gamma_1 p^k$.

Now we will focus for new work as this model (FHXW Branching Type with Hyphal Death) :

$$\left.\begin{aligned}\frac{\partial\rho}{\partial t} &= nv - \gamma_1\rho \\ \frac{\partial n}{\partial t} &= -\frac{\partial nv}{\partial x} + \alpha_1 n - \alpha_3 n + \alpha_2\rho - \beta_1 n^2 - \beta_2 n\rho - \beta_3\rho^2\end{aligned}\right\} \quad .... \quad (1.4)$$

For solving any system in mathematical with many parameters we need to reduce this parameters, this operation called non-dimensionalisation. The branching and biological type for $\delta(\mathrm{p},\mathrm{n})$ shows as a table below:[2][7]

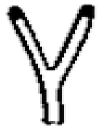
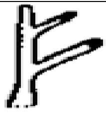
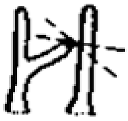
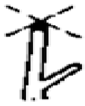
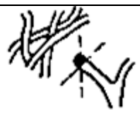
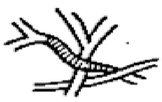
Branching	Biological type	Symbol	Version	Parameters description
	Dichotomous branching	Y	$\delta = \alpha_1 n$	α_1 is the number of tips produced per tip per unit time
	Lateral branching	F	$\delta = \alpha_2 p$	α_2 is the number of branches produced per unit length hypha per unit time
	Tip-hypha anastomosis	H	$\delta = -\beta_2 np$	β_2 is the rate of tip reconnections per unit length hypha per unit time
	Tip-tip anastomosis	W	$\delta = -\beta_1 n^2$	β_1 is the rate of tip reconnections per unit time
	Tip death	T	$\delta = -\alpha_3 n$	α_3 is the loss rate of tips (constant for tip death)
	Tip death due to overcrowding	X	$\delta = -\beta_3 p^2$	β_3 is the rate at which overcrowding density limitation) eliminates branching
	Hyphal death	D	$d = \gamma_1 p$	γ_1 is the loss rate of hyphal (constant for hyphal death)

Table : illustrate biological type of branching and version for every case.

4- Non-dimensionalisation

Some equations contain many parameters and can be difficult to find accurate values for these parameters that resort to non-dimensionalisation as in the following example:

In the system below (1.4)

$$\begin{aligned}\frac{\partial\rho}{\partial t} &= nv - \gamma_1\rho \\ \frac{\partial n}{\partial t} &= -\frac{\partial nv}{\partial x} + \alpha_1 n - \alpha_3 n + \alpha_2\rho - \beta_1 n^2 - \beta_2 n\rho - \beta_3\rho^2\end{aligned}$$

To facilitate the analysis of this system and to assist in its numerical integration, we non - dimensionalise the equations. [1][8]To do so, we choose a reference time T , a reference length scale $\bar{x}$ and reference scales for hyphal density, $\bar{p}$, and tip density, $\bar{n}$. Setting

$$p^* = \frac{p}{\bar{p}} \quad , \quad n^* = \frac{n}{\bar{n}} \quad , \quad t^* = \frac{t}{T} \text{ , and } x^* = \frac{x}{\bar{x}} \qquad (1.5)$$

And substituting into (4.6) yields

$$\left.\begin{aligned} \frac{\partial p^*}{\partial t^*} &= (\frac{Tv\bar{n}}{\bar{p}})n^* - (\frac{\gamma_1 T p^{-1}}{\bar{p}})p^* \\ \frac{\partial n^*}{\partial t^*} &= -(\frac{Tv\bar{n}}{\bar{x}\,\bar{n}})\frac{\partial n^*}{\partial x^*} + (\frac{\alpha_1 T\ \bar{n}}{\bar{n}})n^* - (\frac{\alpha_3 T\ \bar{n}}{\bar{n}})n^* + \frac{\alpha_2 T\ \bar{p}}{\bar{n}}p^* \\ &\quad -(\frac{\beta_1 T\ \bar{n}^2}{\bar{n}})n^{*2} - (\frac{\beta_2 T\ \bar{p}\bar{n}}{\bar{n}})n^* p^* - (\frac{\beta_3 T\ \bar{p}^2}{\bar{n}})p^{*2} \end{aligned}\right\} \ \ldots \quad (1.6)$$

Now, setting $\bar{x} = Tv$ and $\frac{\bar{p}}{\bar{n}} = \bar{x}$, (1.6) becomes

$$\left.\begin{aligned} \frac{\partial p^*}{\partial t^*} &= (\frac{Tv}{Tv})n^* - dp^* \\ \frac{\partial n^*}{\partial t^*} &= -(\frac{\bar{x}}{\bar{x}})\frac{\partial n^*}{\partial x^*} + (\alpha_1 T\ )n^* - (\alpha_3 T\ )n^* + (\alpha_2 v T^{\ 2})p^* \\ &\quad -(\beta_1 T\ \bar{n})n^{*2} - (\beta_2 T^{\ 2}\ \mathrm{v}\bar{\mathrm{n}})n^* p^* - (\beta_3 T^{\ 2} v\ \bar{p})p^{*2} \end{aligned}\right\} \ \ldots \ (1.7) \ ,$$

where $T = \frac{1}{\gamma_1}$, $d = \frac{\gamma_1 T}{p\,\bar{p}}$ and on cancelling get,

$$\left.\begin{aligned} \frac{\partial p^*}{\partial t^*} &= n^* - dp^* \\ \frac{\partial n^*}{\partial t^*} &= -\frac{\partial n^*}{\partial x^*} + (\frac{\alpha_1}{\gamma_1})n^* - (\frac{\alpha_3}{\gamma_1})n^* + (\frac{\alpha_2 v}{\gamma_1^{\ 2}})p^* \\ &\quad -(\frac{\beta_1\,\bar{n}}{\gamma_1})n^{*2} - (\frac{\beta_2\,\mathrm{v}\bar{\mathrm{n}}}{\gamma_1^{\ 2}})n^* p^* - (\frac{\beta_3 v\ \bar{p}}{\gamma_1^{\ 2}})p^{*2} \end{aligned}\right\} \ \ldots\ldots \ (1.8)$$

The remaining choice of $\bar{p}$ or $\bar{n}$ depends on the exact branching kinetics chosen.

In this chapter we will study two cases:

1- FHXW type with hyphal death , that mean our model becomes FHXWD

2- FHXW type without hyphal death.

4.1New Branching Type with Hyphal Death

In this section, we will study a new type of branching of fungal growth, that's mean

$$\delta(\mathrm{p,n}) = \mathrm{F+H+W+X} \qquad \ldots\ldots(1.9)$$

Where, F: Lateral Branching,

H: Tip – Hypha Anastomosis,

W: Tip-tip anastomosis,

X: Tip death due to overcrowding.

The model system for $FHXWD$ is:

$$\left.\begin{aligned}\frac{\partial p^*}{\partial t^*} &= n^* - p^* \\ \frac{\partial n^*}{\partial t^*} &= -\frac{\partial n^*}{\partial x^*} + \left(\frac{\alpha_2 v}{\gamma_1^2}\right)p^* - \left(\frac{\beta_2 v\bar{n}}{\gamma_1^2}\right)n^* p^* - \left(\frac{\beta_1 \bar{\mathrm{n}}}{\gamma_1}\right)\mathrm{n}^{*2} - \left(\frac{\beta_3 v\bar{p}}{\gamma_1^2}\right)\mathrm{p}^{*2}\end{aligned}\right\} \cdots\cdots \ (1.10)$$

After dropping stars, choosing $\bar{n} = \dfrac{\alpha_2}{\beta_2}$, and $\bar{p} = \dfrac{\alpha_2\beta_1\gamma_1}{\beta_2\beta_3 v}$ the system (1.10) becomes

$$\left.\begin{aligned}\frac{\partial p}{\partial t} &= n - p \\ \frac{\partial n}{\partial t} &= -\frac{\partial n}{\partial x} + \alpha p(1-\mathrm{n}) - \beta(\mathrm{n}^2 + \mathrm{p}^2)\end{aligned}\right\} \ldots. \ (1.11)$$

Where

$$\alpha = \frac{\alpha_2 v}{\gamma_1^2} \ \text{ and } \ \beta = \frac{\alpha_2\beta_1}{\beta_2\gamma_1}$$

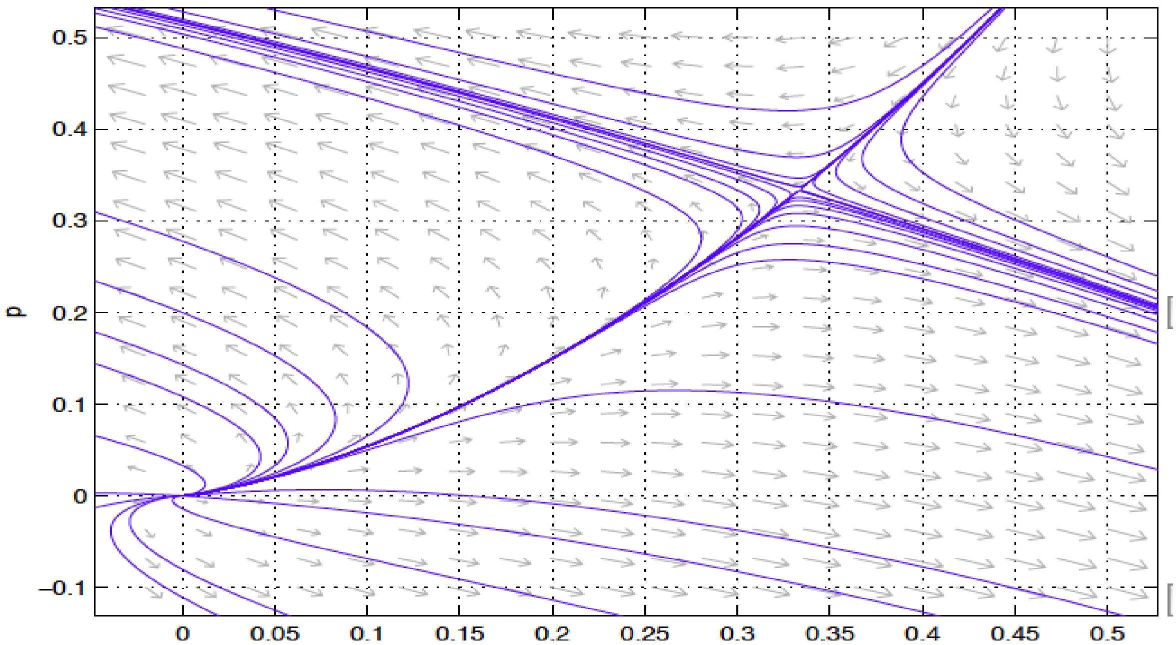
Some techniques to solve above system as:

4-2 The stability of solution

In this section, we will illustrate stability of system (1.11), as:

$$\left.\begin{aligned}&n - p = 0 \\ &\alpha p(1-\mathrm{n}) - \beta(\mathrm{n}^2 + \mathrm{p}^2) = 0\end{aligned}\right\} \ldots \ (1.12)$$

The solution of these equations, we will find values of (p, n), the steady state are :(0,0) unstable node, and $\left(\dfrac{\alpha}{\alpha+2\beta}, \dfrac{\alpha}{\alpha+2\beta}\right)$: saddle point, see Fig (1.1)



Figure(1.1): The (np)-plane: note that a trajectory connects the unstable node (0, 0) to the saddle point $\left(\dfrac{\alpha}{\alpha+2\beta}, \dfrac{\alpha}{\alpha+2\beta}\right)$ where $(\alpha = 1, \beta = 1)$.

4-3Traveling wave solution

Hence we seek travelling wave solutions to (1.11). A mathematical way of saying this that we seek solutions of the form

$$\left.\begin{aligned} p(\mathrm{x},\mathrm{t}) &= \mathrm{P}(\mathrm{z}) \\ n(\mathrm{x},\mathrm{t}) &= N(\mathrm{z}) \end{aligned}\right\} \quad \cdots \quad (1.13)$$

where $z = x - ct$.

Here $P(\mathrm{z})$, $N(\mathrm{z})$ represent density profiles, and c can be interpreted as the rate of propagation of the colony edge. For these to be biologically meaningful, we require P and N to be bounded, non negative functions of z.

Then $p(\mathrm{x},\mathrm{t})$ and $n(\mathrm{x},\mathrm{t})$ are a travelling wave, and it moves at a constant

speed c in the positive x - direction if c positive. Clearly if ($x - ct$) is constant, so are $p(\mathrm{x},\mathrm{t})$ and $n(\mathrm{x},\mathrm{t})$ .It also means the coordinate system moves with speed c.

The wave speed c generally has to be determined. The dependent variable z is sometimes called the wave variable. When we look for travelling wave solutions of an equation or system of equations in x and t in the form (1.13), we have

$$\left.\begin{aligned} \frac{\partial p}{\partial t} &= \frac{dP}{dz}\cdot\frac{\partial z}{\partial t} = \frac{dP}{dz}(-\mathrm{c}) = -\mathrm{c}\frac{dP}{dz} \\ \frac{\partial n}{\partial t} &= \frac{dN}{dz}\cdot\frac{\partial z}{\partial t} = \frac{dN}{dz}(-\mathrm{c}) = -c\frac{dN}{dz} \\ \frac{\partial n}{\partial x} &= \frac{dN}{dz}\cdot\frac{\partial z}{\partial x} = \frac{dN}{dz}(1) = \frac{dN}{dz} \end{aligned}\right\} \quad \cdots \quad (1.14)$$

Thus we can reduce the system (1.11) to a set of two ordinary differential equation:

$$\left.\begin{aligned} \frac{dP}{dz} &= \frac{-1}{c}[N - P] \\ \frac{dN}{dz} &= \frac{1}{1-c}[\alpha P(1-\mathrm{N}) - \beta(\mathrm{N}^2+\mathrm{P}^2)], c \neq 1, -\infty < z < \infty \end{aligned}\right\} \quad \cdots \quad (1.15)$$

4-4 Stability of traveling wave solution

The steady state of system (1.15) are $(\mathrm{P},\mathrm{N}) - (0,0)$, and $(\frac{\alpha}{\alpha+2\beta},\frac{\alpha}{\alpha+2\beta})$ here (0, 0) is stable node and $(\frac{\alpha}{\alpha+2\beta},\frac{\alpha}{\alpha+2\beta})$ is saddle point for all c positive.

See figure (1.2). This information will help us to determine the initial condition of MATLAB pplane7 code,

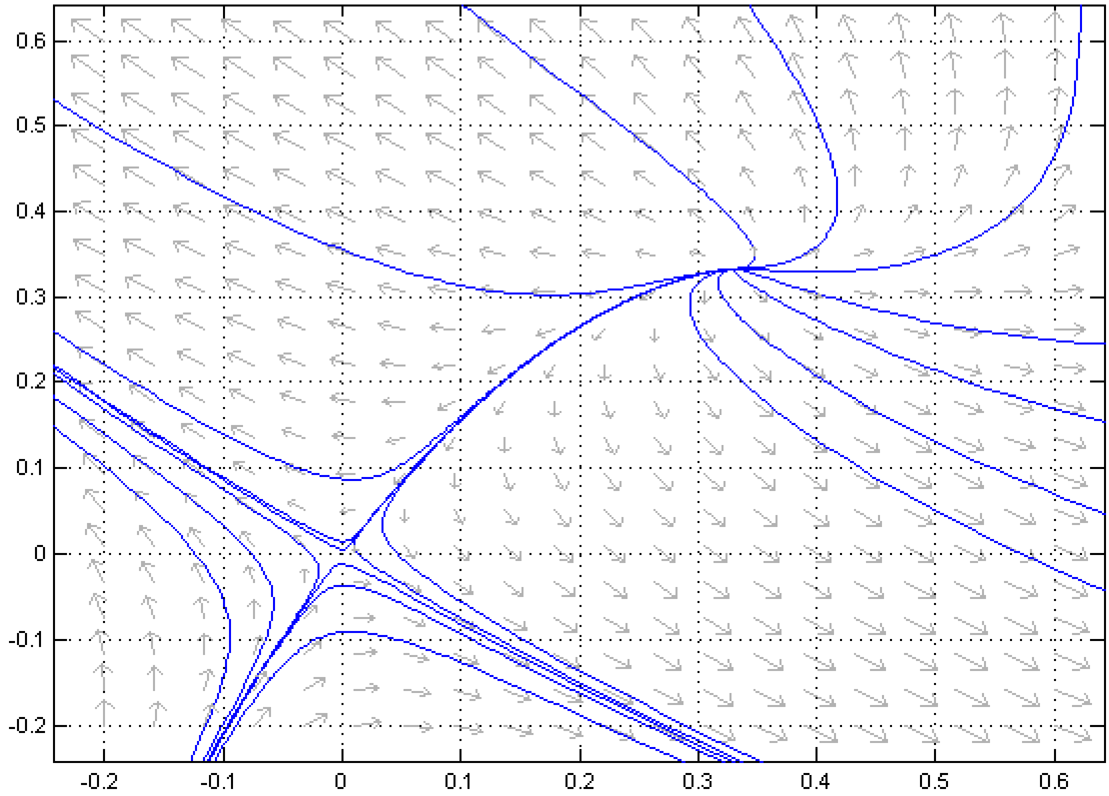


Figure (1.2): The (P, N)-plane: note that a trajectories connects the unstable node $(\frac{\alpha}{\alpha+2\beta},\frac{\alpha}{\alpha+2\beta})$ to the saddle point (0, 0) for all c positive , $\alpha=1$ and $\beta=1$

4-5 Numerical solution

To solve this system (1.11), we will using pdepe *code* in MATLAB. To show behavior branch and tips, see Fig (1.3) that represented the initial condition of branch (p) and tips (n),

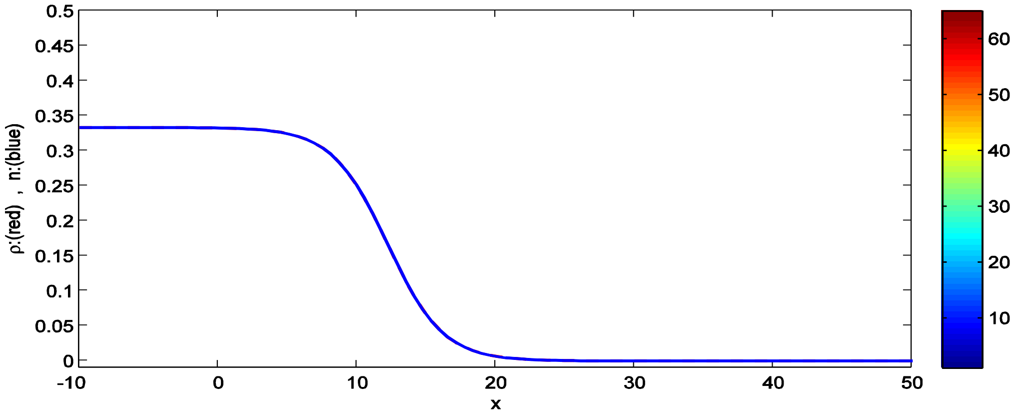


Fig (1.3): The initial condition of (1.13), solution to the system (1.13) with the parameters $\alpha=1$ and $\beta=1$

Fig (1.4) illustrates the traveling waves at the suitable time (t)

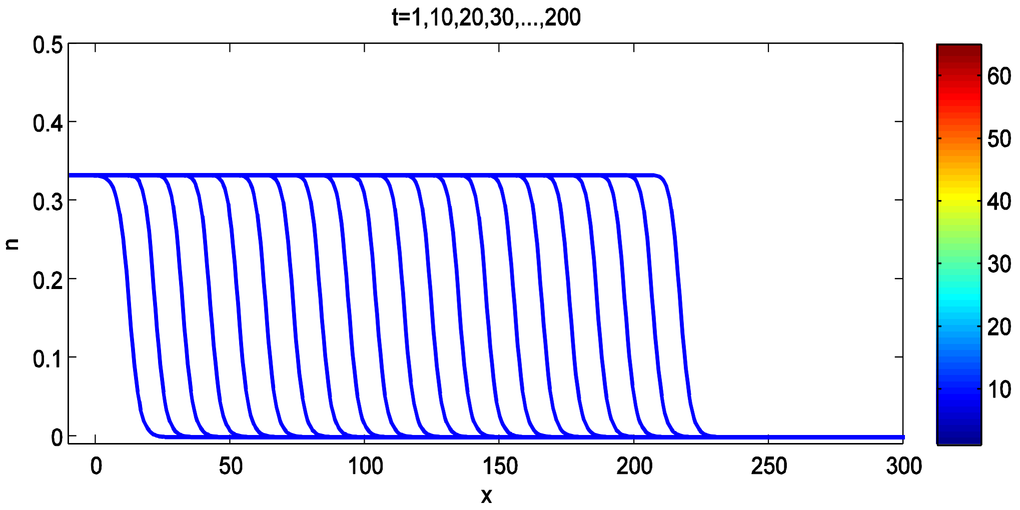


Fig (1.4): Solution to the system (1.13) with the parameters $\alpha = 1$ and $\beta = 1$,for time t=1, 10, 20, …, 200 , where blue line represented tips (n).

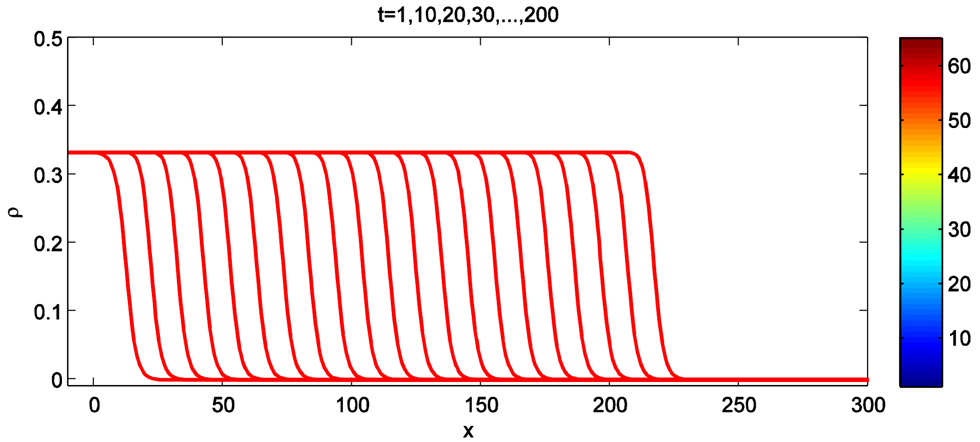


Fig (1.5) : Solution to the system (1.13) with the parameters $\alpha = 1$ and $\beta = 1$, for time t=1, 10, 20, …, 200 , where red line represented branches (p).

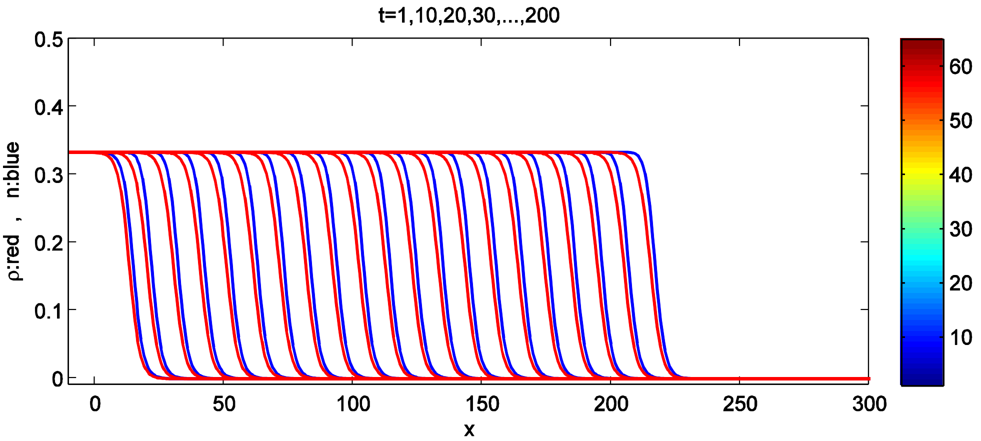


Fig (1.6): Solution to the system (1.13) with the parameters $\alpha = 1$, $\beta = 1$,$c > 0$ and time $t = 1, \cdots, 200$, where blue line represented tips (n), red line represented branches (p).

Fig (1.4) , (1.5) and (1.6) illustrate the solutions of p and n numerically with take values of $\alpha = \beta = 1$, that is very clear the travelling wave solution start from left to right and still the same wave .

From this operations we get the relationship between traveling wave solution (c) and parameters α , and β where α increasing the traveling wave solution (c) is increasing, and β increasing the traveling wave solution (c) is decreasing, see Fig.(1.8) and Fig.(1.10) .

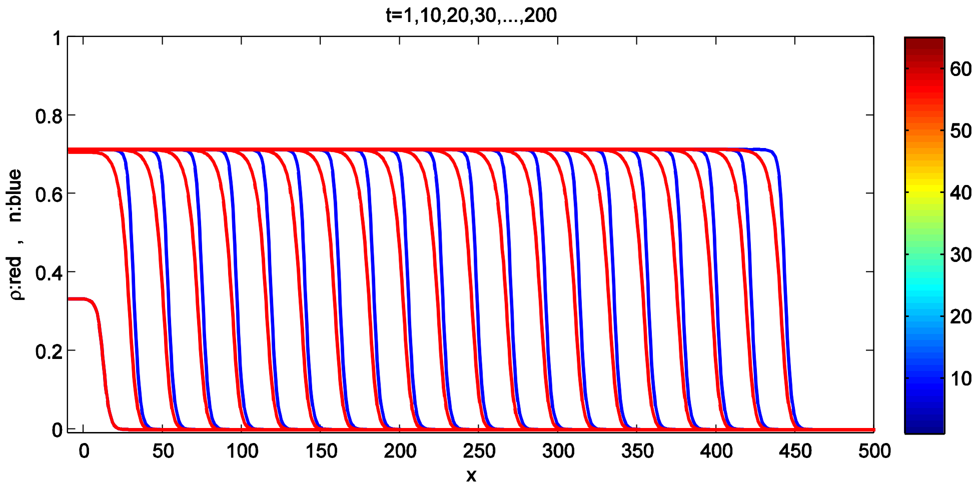


Fig (1.7): Solution to the system (1.13) with the parameters $\alpha = 5, \beta = 1$,$c > 0$ and time $t = 1, \cdots, 200$, where blue line represented tips (n), red line represented branches (p).

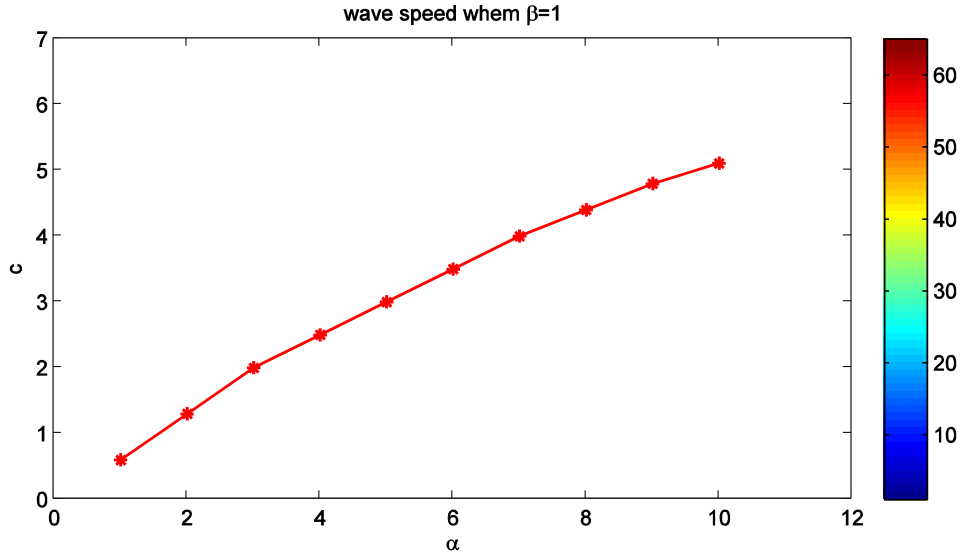


Fig (1.8): The relation between waves speed c and α values and suppose β is taking value = 1.

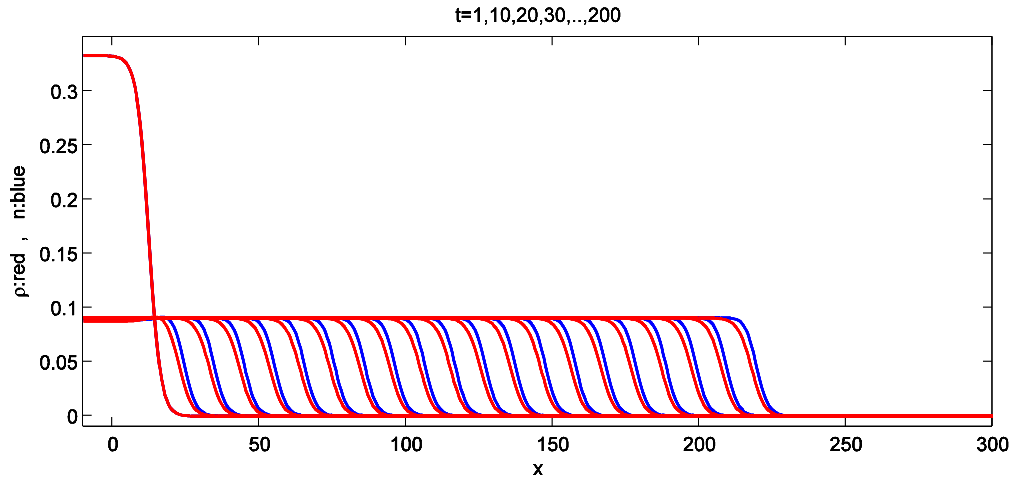


Fig (1.9): Solution to the system (1.13) with the parameters $\alpha = 1$, $\beta = 5$, $c > 0$ and time $t = 1, \cdots, 200$, where blue line represented tips (n), red line represented branches (p).

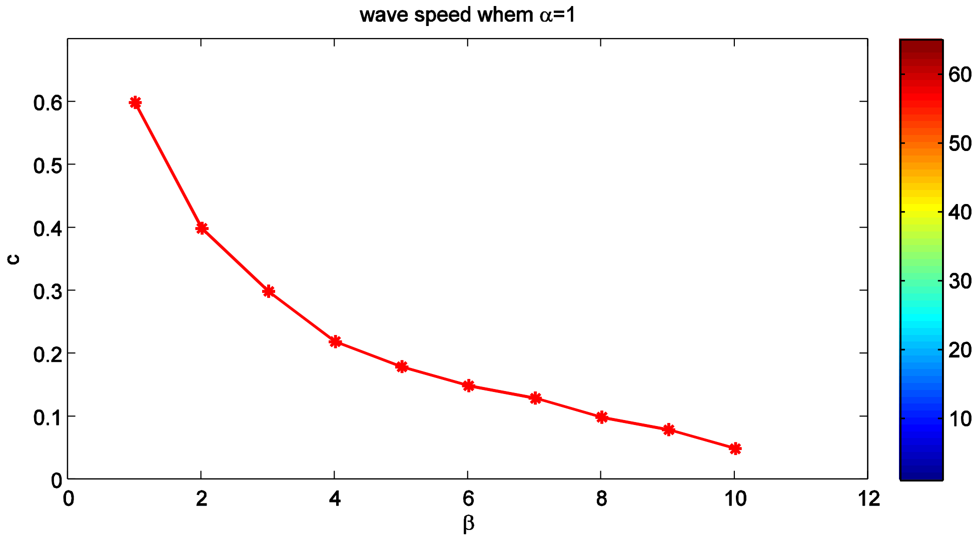


Fig (1.10): The relation between waves speed c and β values and suppose α is taking value = 1.

5- Discussion the results

From above results, see Fig.(1.8) and Fig.(1.10) we conclude that the travilling wave c increase whenever the values of α increase at same time β is still constant.

So, we know the value of $\alpha = \dfrac{\alpha_2 v}{\gamma_1^2}$ and we notes that α directly proportional with α_2 and v, and inversely proportional with γ_1.

Biologically, that is mean the growth increases whenever α increases, and finally that means the growth increases according to α_2 increasing (branches produced per unit length hypha per unit time) and v increasing.

From Fig (1.10) we shows that the travelling wave decrease whenever the value of β increase at same time α is still constant.

So the value of $\beta = \dfrac{\alpha_2 \beta_1}{\beta_2 \gamma_1}$ and we notes that β directly proportional with α_2 and β_1, and inversely proportional with γ_1 and β_2.

Biologically, that is mean the growth decreases whenever β increases. Finally that means the growth decreases according to α_2 increasing (branches produced per unit length hypha per unit time) , β_1 increasing (β_1 is the rate of tip reconnections per unit time) , γ_1 decreasing(γ_1 is the loss rate of hyphal (constant for hyphal death))and β_2 decreasing (β_2 is the rate of tip reconnections per unit length hypha per unit time).

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